

Original article:

**INFLUENCE OF ENVIRONMENTAL VARIABILITY ON
PHYLOGENETIC DIVERSITY AND TRAIT DIVERSITY WITHIN
CALLIGONUM COMMUNITIES**

Jian-Cheng Wang, Hong-Lan Yang, Xi-Yong Wang, Wei Shi, Bo-Rong Pan *

Key Laboratory of Biogeography and Bioresource in Arid Land, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Urumqi, 830011, P.R. China

* Corresponding author: Bo-rong Pan; E-mail: www-1256@ms.xjb.ac.cn

ABSTRACT

Since phylogenetic data provide the evolutionary history of the species and traits are the result of adaptation to the environmental conditions, joint analysis of these two aspects and ecological data may illuminate that how ecological processes affect the evolution of species and assembly of communities. In this study, we compared the community structure of sibling communities in order to illuminate the influence of environmental variability. We chose different *Calligonum* communities as research subjects which grow in active sand dunes and stabilized sand fields. Our results show that species which co-occurred in *C. rubicundum* community have greater phylogenetic evenness compared to species in other communities where co-occurring plants had similar traits. Soil variability might legitimately explain this result. Based on the similarity between the pattern of trait diversity and the pattern of phylogenetic diversity, we inferred that the evolution of traits is conservative and species of all but *C. rubicundum* communities are under more intense selection pressure.

Keywords: *Calligonum*, community composition, ecological process, phylogenetic community structure, phylogenetic signal

INTRODUCTION

An important goal of community ecology is to illuminate the processes governing the assembly and coexistence of species (Hardy, 2008). Because phenotypes are not randomly distributed with respect to phylogeny, we should expect a direct link to exist between the evolutionary relatedness of organisms in a community, the characters they possess, and the ecological processes that determine their distribution and abundance (Kraft et al., 2007). A phylogenetic perspective that recognizes the dual role of evolutionary history in generating species diversity and in shaping phenotypes may provide insight into the relative im-

portance of different processes affecting species coexistence and community assembly (Whitfeld et al., 2012). Nowadays, evolutionary ecologists are increasingly combining phylogenetic data with distributional and ecological data to assess how and why communities of species differ from random expectations for evolutionary and ecological relatedness (Emerson and Gillespie, 2008).

Community composition at any point in time is the result of past immigration, speciation and extinction, together with associated interactions that vary according to the sequence of assembly and/or disturbance (Emerson and Gillespie, 2008). Patterns of community structure can be interpreted us-

ing a simple schematic (Figure 1). Numerous processes contribute to the assembly of communities (Kraft et al., 2007). Environmental filters can select for the species that possess phenotypes necessary for survival and successful reproduction resulting in a community of species that share a similar phenotype (Webb et al., 2002). By contrast, competition among different species leads to that related traits show evenness (Eiserhardt et al., 2013). The likelihood that a pathogen can infect two plant species decreases continuously with the phylogenetic distance between the plants which tend to yield patterns of over-dispersion (Gilbert and Webb, 2007). Facilitation derived from related species sharing pollinators is predicted to yield communities with phenotypically similar species (Sargent and Ackerly, 2008). Nurse species facilitate distantly related species and increase phylogenetic diversity (Valiente-Banuet and Verdu, 2007).

Abiotic factors, which include high air temperature, low relative humidity, low water, low nutrient availability, act as environmental filters selecting for species with tolerant traits in arid areas (Rajaniemi et al., 2012). These have resulted in lower species diversity in community composition. However, along with the variation in the type and gradient of limiting factor, community structure does not remain the same. On the contrary, similar communities, whose constituent species have a close genetic relationship, may experience smaller differentiated ecological processes. Here, we chose different *Calligonum* communities as research subjects which grow in active sand dunes and stabilized sand fields. We address two critical questions: 1) whether differences exist in the community structure in terms of phylogeny and phenotype among sibling communities? 2) what kind of link exists among traits, phylogenetic relationships and environmental conditions of these communities?

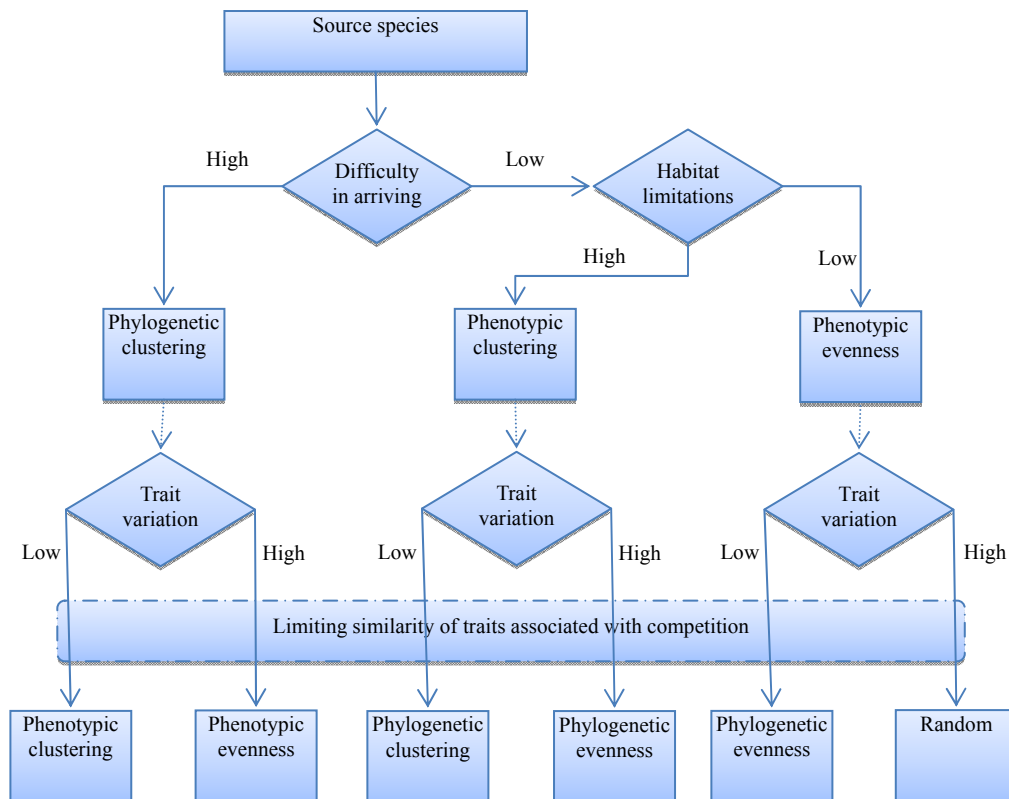


Figure 1: Patterns of community structure predicted to be produced by various community assembly processes

MATERIAL AND METHODS

Data

Calligonum Linnaeus is a genus in the family Polygonaceae with 35 species across the Mediterranean Sea region, Asia and North Africa (Wu et al., 2003). Based primarily on fruit morphology and anatomy, *Calligonum* species were divided into four sections, including Sect. Calliphysa, Sect. Calligonum, Sect. Medusa and Sect. Pterococcus (Mao and Pan, 1986). A representative of each section was selected as the comparison target, including *C. calliphysa*, *C. ebi-nuricum*, *C. klementzii*, and *C. rubicundum*. We consulted the plant specimens collected in several units of Chinese Academy of Sciences including Institute of Botany, Cold and Arid Regions Environmental and Engineering Research Institute, Xinjiang Institute of Ecology and Geography, Kunming Institute of Botany, Jiangsu Institute of Botany, The Northwest Institute of Plateau Biology, and Northwest A&F University, Lanzhou University, Inner Mongolia University, Inner Mongolia Agricultural University, Xinjiang University, Xinjiang Agricultural University. According to the distribution of each species, we identified 22 plots. In July 2007, we randomly placed three quadrats in each plot and computed the number of each species in each quadrat. Plant voucher specimens were deposited in the specimen museum of Xinjiang Institute of Ecology and Geography.

We obtained the state of relatively stable traits (smaller intraspecific variation) from Flora of China and Flora Xinjiangensis. Plant traits are encoded according to [supplementary Table 1](#), which shows the characters and character states scored for plant morphology. In total 16 characters were taken into consideration. 9 characters were scored as binary and the remaining characters were scored as multi-state characters.

We used Phylomatic version 3 web service (<http://phylodiversity.net/phyloomatic/>) to construct a phylogeny for the species list,

using the stored tree R20120829 (Phylogenetic tree R20120829 for plants). Phylogenetic distance between species should ideally be proportional to divergence time (Blomberg and Garland, 2002). We approximated divergence times in phylocom 4.2 using the branch length adjustment (BLADJ) function.

Analyses

When conducting analysis of phylogenetic community composition, communities with fewer species can cause large errors. Therefore, community collection in accordance with the constructive species was used as analysis objects. We used the function `pcd` in the R package “picante” to calculate phylogenetic community dissimilarity (PCD) that is partitioned into a nonphylogenetic component that reflects shared species between communities and a phylogenetic component that reflects the evolutionary relationships among nonshared species (Ives and Helmus, 2010), and subsequently used the function `hclust` in the R package “stats” to implement hierarchical cluster analysis.

Phylogenetic community structure was quantified as the net relatedness index (NRI), which is based on the mean phylogenetic distance (MPD) between taxa in an observed sample compared to random draws from the species pool (Webb et al., 2002). NRI expresses the deviation of the mean pairwise distance from random in a given community, and positive NRI indicates phylogenetic clustering, while negative NRI indicates evenness. We used the abundance-based construct algorithm in Phylocom to calculate NRI. Significance of the NRI values is assessed by comparing the observed MPD value with the expected MPD value based on the null distribution of the 999 random assemblages. The species pool was all species found in the 22 plots.

In this study, we calculated measures of trait diversity within communities in a manner analogous to the methods we used to calculate phylogenetic diversity by sub-

stituting a trait distance matrix for the phylogenetic distance matrix. Its statistics Trait SES (MPD) is equivalent to -1 times NRI. Negative values indicate relatively similar traits, while positive value indicates evenness.

RESULTS

We sampled 67 species from 16 families and 51 genera in 22 plots. The largest plant families in *Calligonum* communities are Amaranthaceae (24 species) and Asteraceae (11 species). The number of taxa in *C. rubicundum* community was highest among 4 kinds of communities at different levels of family, genera and species. Phylogenetic relationships of co-occurring species in *Calligonum* community were shown in Figure 2.

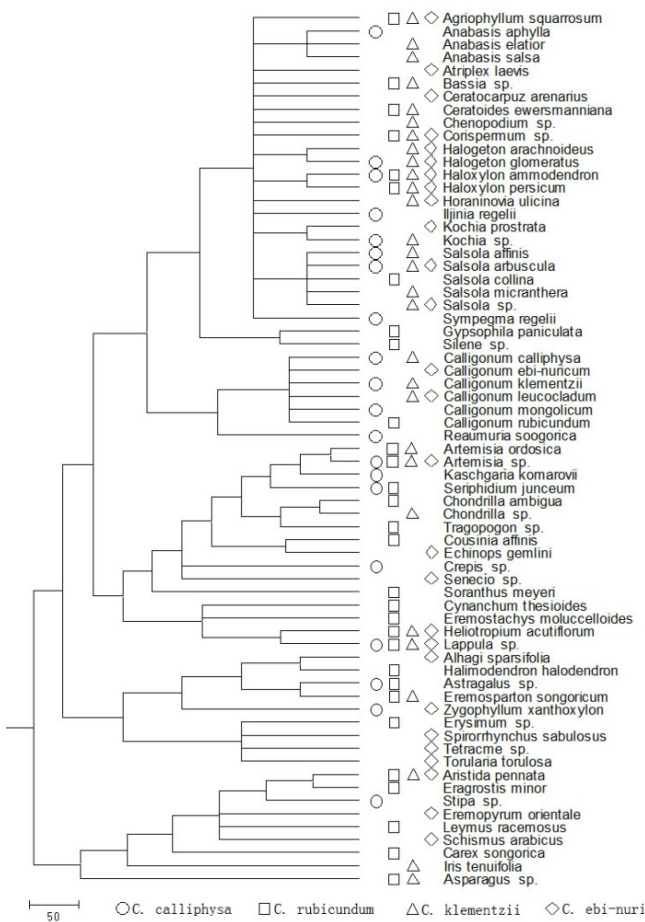


Figure 2: Phylogenetic relationships of seed plants occurring in *Calligonum* community. Graphic located in front of species name shows the community that the species may occur.

The distance among communities is inconsistent in terms of phylogenetic relationship. According to the results returned by pairwise dissimilarity in phylogenetic community composition, hierarchical cluster analysis was carried out and shown by Figure 3. *C. rubicundum* community showed a larger dissimilarity in phylogenetic community composition with other communities. *C. calliphysa* and *C. klementzii* showed the highest similarity, due to a larger number of shared species between communities (10 species).

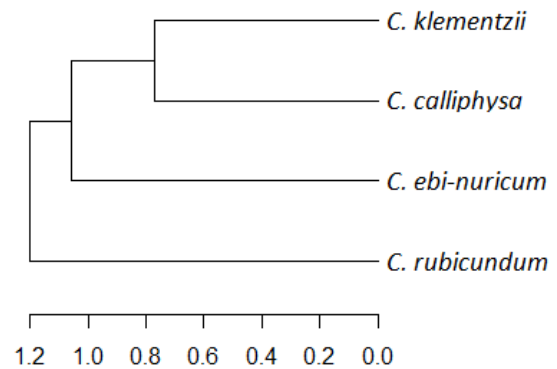


Figure 3: Phylogenetic community dissimilarity (PCD) of communities. Distance reflects the degree of dissimilarity among different communities.

Each community had different performance in phylogenetic community structure (Figure 4). The NRI was significant negative value in *C. rubicundum* community, and became positive values in the other three communities. The results indicated that species that co-occurred in *C. rubicundum* community have greater phylogenetic evenness compared to species in other communities. That is to say, co-occurring plants were more distantly related than expected by chance in *C. rubicundum* community ($NRI < 0$).

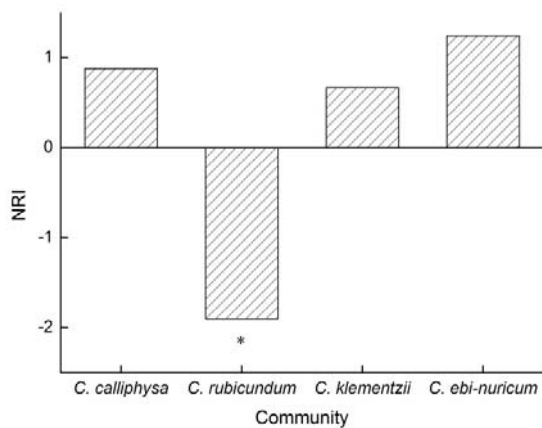


Figure 4: Comparison of phylogenetic community structure among different communities. Positive NRI indicates phylogenetic clustering, while negative NRI indicates evenness.

Trait SES (MPD) represents the standardized effect size of trait diversity by measuring trait dissimilarity among co-occurring species. These metrics of all communities but *C. rubicundum* community were below 0, and trait diversity was lower than expected (Figure 5). The statistical test demonstrated that trait diversities within *C. ebi-nuricum* and *C. Klementzii* communities were significantly different from randomization. The results indicated that co-occurring plants had similar traits, and this pattern of trait clustering was stronger in *C. ebi-nuricum* and *C. Klementzii* communities. The pattern of trait diversity was similar to the pattern we saw for phylogenetic diversity.

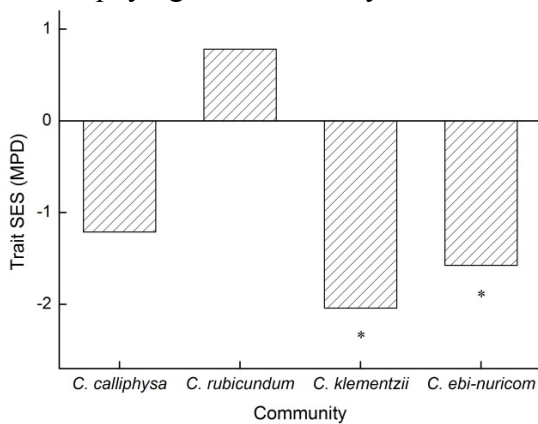


Figure 5: Comparison of trait diversity among different communities. Negative Trait SES (MPD) indicates relatively similar traits, while positive value indicates evenness.

DISCUSSION

Phylogenetic data provide a historical framework to quantify evolutionary and ecological patterns and infer evolutionary and ecological processes (Emerson and Gillespie, 2008). For example, pattern of phylogenetic clustering was generally considered to result from (1) difficulty in dispersing to some habitats or, (2) environmental filtering for a conserved niche. In this study, *C. rubicundum* community was distinguished from other three communities in phylogenetic community composition, and the latter in community structure displayed as phylogenetic clustering. In addition, to test for community assembly processes we need to quantify both the trait evolution and the phylogenetic structure of the community (Pausas and Verdu, 2010). Our results showed that phenotypic pattern of these traits are identical with phylogenetic community structure among different communities. Thus, there were differences in the community structure in terms of phylogeny and phenotype among sibling communities and gives an affirmative answer to question 1.

When species enter a community, species possessing the necessary traits to complete their life cycle within that habitat are retained by ecological processes controlling community assembly. In other words, environmental conditions impose absolute bounds on the phenotype space (Lovette and Hochachka, 2006). Thenceforth, the competition as an important factor drives competitive exclusion or niche differentiation of similar traits related to competition. Other literature reports that total salt content and pH values of soil are significantly different among communities, and all but *C. rubicundum* communities have distinct degrees of salinization and alkalization (Tan et al., 2009). Compared with the *C. rubicundum* community, trait diversity was lower than expected in the other three communities and similar to the pattern we saw for phylogenetic diversity. Therefore, we can infer that species of these communi-

ties are under more intense selection pressure and evolution of traits is conservative. There were more than expected annuals in *C. ebi-nuricum* and *C. klementzii* community, and we guessed that it is an environmental filtering to directional selection under stressful conditions. There was a definite relationship that environmental conditions limit phylogenetic diversity and trait diversity within communities.

In order to potentially restore the ecosystem functioning of desert plant communities, understanding how ecological process affects community composition is an essential prerequisite. In this study, we compared the community structure of similar communities in order to illuminate the influence of environmental variability governing the assembly and coexistence of species. Based on the similarity between the pattern of trait diversity and the pattern of phylogenetic diversity, we inferred that the evolution of traits is conservative and species of all but *C. rubicundum* communities are under more intense selection pressure.

ACKNOWLEDGMENTS

This work was supported by the National Natural Science Foundation of China (Grant No 31100150) and the West Light Talents Cultivation Program of Chinese Academy of Sciences (XBBS 201202).

REFERENCES

- Blomberg SP, Garland T. Tempo and mode in evolution: phylogenetic inertia, adaptation and comparative methods. *J Evol Biol* 2002;15: 899-910.
- Eiserhardt WL, Svenning JC, Borchsenius F, Kristiansen T, Balslev H. Separating environmental and geographical determinants of phylogenetic community structure in Amazonian palms (Arecaceae). *Bot J Linn Soc* 2013;171:244-59.
- Emerson BC, Gillespie RG. Phylogenetic analysis of community assembly and structure over space and time. *Trends Ecol Evol* 2008;23:619-30.
- Gilbert GS, Webb CO. Phylogenetic signal in plant pathogen-host range. *Proc Natl Acad Sci USA* 2007; 104:4979-83.
- Hardy OJ. Testing the spatial phylogenetic structure of local communities: statistical performances of different null models and test statistics on a locally neutral community. *J Ecol* 2008;96:914-26.
- Ives AR, Helmus MR.. Phylogenetic metrics of community similarity. *Am Nat* 2010;176:E128-42.
- Kraft NJB, Cornwell WK, Webb CO, Ackerly DD. Trait evolution, community assembly, and the phylogenetic structure of ecological communities. *Am Nat* 2007;170:271-83.
- Lovette IJ, Hochachka WM. Simultaneous effects of phylogenetic niche conservatism and competition on avian community structure. *Ecology* 2006;87:S14-28.
- Mao Z, Pan B. The classification and distribution of the genus *Calligonum* L. *China Acta Phytotaxon Sin* 1986;24:98-107.
- Pausas JG, Verdu M. The jungle of methods for evaluating phenotypic and phylogenetic structure of communities. *Bioscience* 2010;60:614-25.
- Rajaniemi TK, Goldberg DE, Turkington R, Dyer AR. Local filters limit species diversity, but species pools determine composition. *Perspect Plant Ecol* 2012;14:373-80.
- Sargent RD, Ackerly DD. Plant-pollinator interactions and the assembly of plant communities. *Trends Ecol Evol* 2008;23:123-30.
- Tan Y, Pan B, Duan S, Xu G. α diversity of four *Calligonum* L. communities and soil interpretation in the Junggar Basin. *J Arid Land Resour Environ* 2009;23:136-42.
- Valiente-Banuet A, Verdu M. Facilitation can increase the phylogenetic diversity of plant communities. *Ecol Lett* 2007;10:1029-36.
- Webb CO, Ackerly DD, McPeck MA, Donoghue MJ. Phylogenies and community ecology. *Annu Rev Ecol Syst* 2002;33:475-505.
- Whitfeld TJS, Kress WJ, Erickson DL, Weiblen GD. Change in community phylogenetic structure during tropical forest succession: evidence from New Guinea. *Ecography* 2012;35:821-30.
- Wu Z, Raven P, Hong D. *Flora of China*, Vol. 5. Beijing, China: Science Press, 2003.