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Seed plant phylogenetic diversity and species richness in conservation planning within a global biodiversity hotspot in eastern Asia

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Abstract: One of the main goals of conservation biology is to understand the factors shaping variation in biodiversity across the planet. This understanding is critical for conservation planners to be able to develop effective conservation strategies. Although many studies have focused on species richness and the protection of rare and endemic species, less attention has been paid to the protection of the phylogenetic dimension of biodiversity. We explored how phylogenetic diversity, species richness, and phylogenetic community structure vary in seed plant communities along an elevational gradient in a relatively understudied bigb mountain region, the Dulong Valley, in southeastern Tibet, China. As expected, phylogenetic diversity was well correlated with species richness among the elevational bands and among communities. At the community level, evergreen broad-leaved forests had the highest levels of species richness and phylogenetic diversity. <u>Using null model</u> analyses, we found evidence of nonrandom phylogenetic structure across the region. Evergreen broad-leaved forests were phylogenetically overdispersed, whereas other vegetation types tended to be phylogenetically clustered. We suggest that communities with high species richness or overdispersed phylogenetic structure should be a focus for biodiversity conservation within the Dulong Valley because these areas may belp maximize the potential of this flora to respond to future global change. In biodiversity hotspots worldwide, we suggest that the phylogenetic structure of a community may serve as a useful measure of phylogenetic diversity in the context of conservation planning.

Keywords: biodiversity conservation, evolutionary history, phylogenetic structure La Diversidad Filogenética y la Riqueza de Especies de Plantas de Semillas en la Planeación de la Conservación dentro de un Hotspot de Biodiversidad Global en el Este de Asia

Resumen: Uno de los principales objetivos de la biología de la conservación es el entender los factores que causan la variación en la biodiversidad a lo largo del planeta. Este entendimiento es crítico para que quienes planean la conservación sean capaces de desarrollar estrategias efectivas de conservación. Mientras muchos estudios se ban enfocado en la riqueza de especies y la protección de especies raras y endémicas, se ba prestado una menor atención a la protección de la dimensión filogenética de la biodiversidad. Exploramos cómo la diversidad filogenética, la riqueza de especies y la estructura de la comunidad filogenética varían en las comunidades de plantas de semillas a lo largo de un gradiente de elevación en una región montana relativamente sub-estudiada: el Valle Duglong, en el sureste del Tíbet, China. Como se esperaba, la diversidad filogenética estuvo bien correlacionada con la riqueza de especies entre las bandas de elevación y entre las comunidades. A nivel de comunidades, los bosques perennes de bojas anchas tuvieron el nivel más alto de riqueza de especies y de diversidad filogenética. Utilizamos análisis de modelos nulos y encontramos evidencia de una estructura filogenética no-aleatoria en toda la región. Los bosques perennes de hoja ancha se encontraban sobre-dispersados filogenéticamente, mientras que otros tipos de vegetación tendían a estar agrupados filogeníticamente. Sugerimos que las comunidades con una riqueza de especies alta o una estructura filogenítica sobre-dispersada deberían ser un foco para la conservación de la biodiversidad en el Valle

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Dulong, ya que estas áreas podrían ayudar a maximizar el potencial de que esta flora responda a un futuro cambio global. En los hotspots de biodiversidad a nivel mundial, sugerimos que la estructura filogenética de una comunidad puede servir como una medida útil de la diversidad filogenético en el contexto de la planeación de la conservación.

Palabras Clave: conservación de la biodiversidad, estructura filogenética, historia evolutiva

Introduction

Biodiversity conservation has long been a focus of research because species extinction risks resulting from global climate change, habitat fragmentation, and increased human population density have grown in recent decades (e.g., Sechrest et al. 2002; Thuiller et al. 2011; Cardinale et al. 2012). Although many studies have focused on the conservation of species richness, others have argued that conservation should include additional dimensions of diversity, including functional and phylogenetic components (Vane-Wright et al. 1991; Faith 1992; Swenson 2011). Historically, biodiversity conservation has focused on using rarity, endemism, and distinctiveness to set priorities (Myers et al. 2000; Kier et al. 2009). However, in recent years, the evolutionary processes that maintain and generate biodiversity have also been recognized as important factors that need to be accounted for in conservation planning (e.g., Moritz 2002; Mace & Purvis 2008; Winter et al. 2013). In these studies, phylogenetic information is often used to prioritize conservation of species assemblages that have a distinct evolutionary history relative to others in the region (Devictor et al. 2010). The rationale of this approach is that the extinction of the most phylogenetically distinct species would result in the loss of a greater proportion of biological diversity (Faith 2008, 2013; Thuiller et al. 2011), which may decrease the ability of the biota in a region to persist in the face of environmental change (Prinzing et al. 2001; McNyset 2009).

A number of studies explicitly compared biodiversity conservation prioritizations based on both taxonomic (e.g., species richness) and evolutionary (e.g., phylogenetic diversity) criteria to assess the efficacy of each approach (Forest et al. 2007; Vandergast et al. 2008; Kraft et al. 2010). Some studies show that species richness can be inconsistent with phylogenetic diversity if the underlying phylogenetic composition is unequally distributed across spatial scales (Tucker & Cadotte 2013). For example, Forest et al. (2007) and Tucker et al. (2012) found that although the flora in the western part in the Cape Floristic Region of South Africa has twice the species richness of the eastern region, the western flora is less phylogenetically diverse. Conversely, several studies show that high taxonomic and phylogenetic diversity tends to occur in the same places. For example, Rodrigues and Gaston (2002) found that phylogenetic and generic richness of birds in northwest South Africa showed high spatial congruence. This variable relationship between richness and phylogenetic diversity at the landscape scale poses a challenge for conservation planning because it can raise the dilemma of which diversity component (taxonomic or phylogenetic) should be favored in large-scale conservation actions.

In addition to measures of phylogenetic diversity, phylogenetic community structure can be used to quantify the average degree of phylogenetic relatedness among coexisting species at the local scale (Webb et al. 2002; Kembel & Hubbell 2006). Phylogenetic clustering indicates that species in the local communities are more closely related than expected, whereas phylogenetic overdispersion or evenness indicates that species are more distantly related than expected. This is important because two communities of equal species richness may be composed of species with either highly similar or distinct phylogenetic histories (Webb et al. 2002). Some have argued, for example, that preserving a site containing a few highly diverse distantly lineages may be more beneficial, ultimately, than preserving a site with a large number of closely related taxa (Lyashevska & Farnsworth 2012; Diniz-Filho et al. 2013). More recently, patterns of phylogenetic structure are increasingly being used to gain insight into community assembly (Emerson & Gillespie 2008; Cavender-Bares et al. 2009; Vamosi et al. 2009), although to date these types of null-model analyses have not been widely used in conservation.

The Dulong Valley forms a major part of the Indo-Burma biodiversity hotspot (Myers et al. 2000), which lies in the southeastern Tibetan Plateau. This region contains a broad elevational gradient (1200-5242 m asl) and a rich flora (Liu et al. 2000). Biodiversity in this region faces mounting threats because of the combined effects of habitat loss and fragmentation, overexploitation of natural resources (e.g., logging, collection of non-timber forest products), and climate change (Xu & Wilkes 2004). Previous studies have identified evergreen broad-leaved forests in this region as a conservation priority because of the high species richness of these communities relative to other areas in the region (Li et al. 2011). However, this region has not been analyzed from a phylogenetic perspective, so we lack an understanding of the critical evolutionary dimension of the biodiversity in this region (Li 1994; Li et al. 2007).

We evaluated the relationship between species richness and phylogenetic diversity and explored community phylogenetic structure across a floristic biodiversity

hotspot in Dulong Valley. We hope our results can guide conservation efforts in this area and contribute to understanding of variation in these important issues globally (Myers & Knoll 2001; Webb et al. 2002; Maherali & Klironomos 2007). Specially, we addressed whether phylogenetic structure can be applied to biodiversity conservation in these communities and how evolutionary information might be incorporated into the future conservation actions in the Dulong Valley.

Materials and Methods

Study Area

The Dulong Valley is at the border between China and Burma (Fig. 1), which extends about 20 km west into Burma (He 1998). Due to the absence of data from the Burmese side, our study area was the portion of the Dulong Valley that occurs in China, which covers 4116 km². The area below 1300 m asl is highly disturbed by deforestation and farming, is generally low in species richness, and was not accessible for a survey in many localities. Therefore we restricted our analyses to elevations above 1300 m asl.

The Dulong Valley is home to 2816 native seed plant species (778 genera and 171 families), 132 of which are endemic species (Li et al. 2007, 2011). The high levels of species richness and endemism in the flora can be attributed to the geologic, topographic, and climatic diversity in the area (Chaplin 2005). Acute topographical relief has created many peaks exceeding 4000 m asl as well as deep valleys in this area. This topographic complexity presents substantial barriers to dispersal and is thought to have been critical to the formation and development of the flora in this region (Li 1994).

Six different vegetation community types have been recognized at various elevations (Table 1), ranging from low elevation subtropical evergreen forests to high elevation alpine meadows (Supporting Information) (Liu et al. 2000). Because deciduous broad-leaved forest and coniferous broad-leaved mixed forest as well as alpine shrub and alpine meadow community types greatly overlap in elevation, we combined them into 2 groups (temperate forest and alpine zone) that we subdivided into 4 zones (subtropical forest, temperate forest, subalpine forest, and alpine zone) that occur along the elevational gradient in Dulong Valley (Table 1). These 6 community types and 4 zones form the basis of the subsequent analyses.

Data Sources

We compiled a database based on data collected during numerous scientific expeditions to this region since the 1930s, data in published monographs, including the Flora of Dulongjiang Region (Li 1993) and the Flora of Gaoligong Mountains (Li et al. 2000), and data in the

Chinese Virtual Herbarium (http://www.cvh.org.cn). This database includes taxonomic information for each seed plant taxon, including elevational range, whether it is a native or cultivated (non-native) species, and whether the species is endemic to the region. We considered only native species.

In mountain areas, elevation is an important driver of biodiversity patterns because it captures changes in both temperature and rainfall (Körner 2000). To analyze the elevational changes in species richness and phylogenetic diversity, the study area was divided into 29 elevational bands at 100-m vertical intervals. Each taxon was considered as present at every 100-m band between its upper and lower elevational range limits. This method assumes that each species has the potential to be distributed between its upper and lower limits. This approach has been commonly used to investigate patterns of species richness and phylogenetic structure along the elevational gradients (e.g., Rahbek 1997; Wang et al. 2007; Li et al. 2014).

Taxonomic Metrics

We estimated the areal size for each community type and each zone based on a digital elevation model. To eliminate the area effect on species richness in community types of different sizes, taxon density (*D*) for each community type and zone was calculated based on the following equation (Vetaas & Grytnes 2002):

$$D = \frac{S}{\ln A},\tag{1}$$

where A is area of each community type and each zone and S is number of taxa in each community type and each zone

Phylogeny Construction

We constructed a phylogenetic tree by grafting the species present in the study area onto a backbone phylogenetic hypothesis using the online program Phylomatic (Webb & Donoghue 2005). The backbone of the supertree was the phylomatic tree version R20120829, which was based on Angiosperm Phylogeny Group's system (APG III 2009). Branch lengths in the supertree were adjusted to match clade age, as estimated and reported by Wikstrom et al. (2001), with the BLADI algorithm implemented in the software Phylocom (Webb et al. 2008). Given the scarcity of comprehensive time-calibrated phylogenies within families and genera, we followed previous studies (e.g., Hardy et al. 2012) in treating species as polytomies within genera (Supporting Information).

Phylogenetic Metrics

We calculated two diversity measures for each elevational band, each community type, and each zone. Faith's

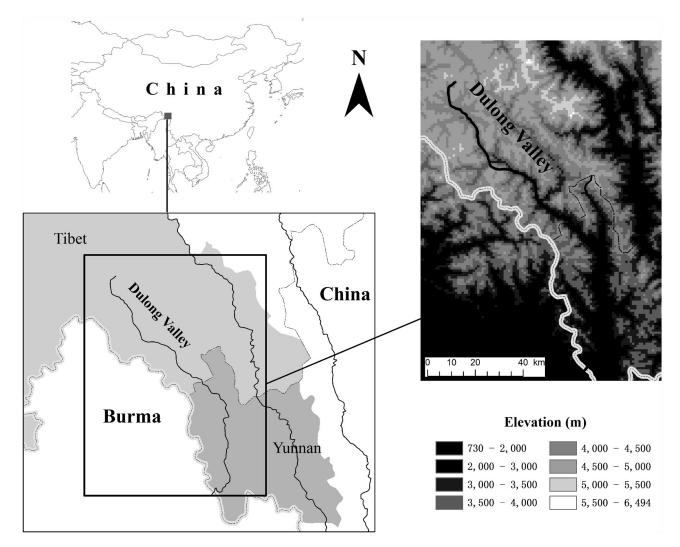


Figure 1. Location and topography of the Dulong Valley.

phylogenetic diversity (PD) is the sum of all phylogenetic branch lengths connecting species in a community (Faith 1992) and is widely used in conservation studies (Cadotte et al. 2009, 2010; Cavender-Bares et al. 2009). Because PD is positively correlated with species richness in most datasets, we also used a null model to standardize PD measurements to the observed species richness. Specifically, we compared the observed PD with the distribution of expected PD values produced by a null model in which taxa labels were shuffled across the tips of the tree 999 times. We then calculated a standard effect size (SES_PD) by dividing the difference between the observed and expected PD by the standard deviation of the null distribution. We then tested for correlations between species richness, PD, and SES_PD with linear models.

To test for nonrandom phylogenetic structure in each community type and each zone, we calculated net relatedness index (NRI) (Webb 2000). The NRI measures the standardized effect size of the mean phylogenetic distance (MPD), which estimates the average phylogenetic relatedness between all possible pairs of

taxa in an assemblage. The NRI is defined as follows (Webb 2000; Webb et al. 2008):

$$NRI = -1 \times \frac{MPD_{observed} - MPD_{randomized}}{sdMPD_{randomized}}, (2)$$

where MPD_{observed} is the observed MPD, MPD_{randomized} is the expected MPD of the randomized assemblages, and sdMPD_{randomized} is the standard deviation of the MPD for the randomized assemblages. Null communities were randomly assembled from the species pool of our study regions with a null model that shuffled tip names across the entire phylogeny for each iteration and kept species richness within samples constant. We used 999 null communities (iterations) for each analysis to assess the statistical significance of the observed patterns. Positive NRI values indicate phylogenetic clustering, whereas negative NRI values indicate phylogenetic overdispersion or evenness. Because the gymnosperms present in many of the communities in our study may inflate patterns of phylogenetic overdispersion due to the deep branches

Community type Dominant Area Richness PDSES*_PD (or zone) Elevation (m) species (km^2) (taxa) Density (million years) Evergreen 1300-2600 Garcinia 451 1759 287.82 121095.09 1.46 broad-leaved forest nujiangensis, Cyclobalanopsis glauca, C. lamellosa, Lithocarpus variolosus, L. dealbatus 2500-3100 449 160.80 71823.66 Deciduous Betula utilis 982 -5.37broad-leaved forest Tsuga dumosa 585 146.12 67678.67 -6.67Coniferous 2600-3300 931 broad-leaved mixed forest 3100-3700 758 618 93.20 -11.14Coniferous forest Pinus bhutanica. 44344.33 Abies delavayi 3500-4200 -11.96Alpine shrub Rhododendron spp. 1190 428 60.44 31456.18 3600-4200 49.17 25846.86 -11.77Alpine meadow Primula spp., 1049 342 Pedicularis spp. 287.82 121095.09 Subtropical forest 1300-2600 451 1759 1.46 2500-3300 75881.05 Temperate forest 1066 164.86 -6.32643 Subalpine forest 3100-3700 758 618 93.20 44344.33 -11.38

1190

428

Table 1. Variables used in examination of phylogenetic diversity (PD) for 6 community types and 4 zones in the Dulong Valley.

Alpine zone

connecting them to the angiosperms, we repeated the phylogenetic structure analysis for each community type and each zone with the gymnosperms removed (Supporting Information). All the phylogenetic analyses were performed in R 2.15.3 software (R Development Core Team 2013) with the picante package (Kembel et al. 2010).

3500-4200

Results

Patterns of Taxonomic Diversity and Phylogenetic Diversity

Along the elevational gradient, taxonomic diversity showed a pronounced mid-elevational peak at 1900–2100 m asl (Fig. 2a). Taxonomic diversity ranged from 35 to 938 taxa per elevational band (mean = 536.86 taxa). Phylogenetic diversity followed a pattern similar to species richness; maximum diversity at the mid-elevational bands was between 1900 and 2100 m asl (Fig. 2b).

Across community types and zones, the highest levels of taxon density and taxonomic and phylogenetic diversity were found in the evergreen broad-leaved forest (subtropical forest zone) (Table 1 & Fig. 3). The lowest taxon density and taxonomic and phylogenetic diversity occurred in the alpine meadow at the community level and in the alpine zone at the zone level.

Correlation between Species Richness and Phylogenetic Diversity

Among the elevational bands, phylogenetic diversity was strongly and positively correlated with species richness $(R^2 = 0.99, P < 0.001)$ (Fig. 4a). The SES_PD (which

accounts for the inherent correlation between richness and PD) also was moderately and positively correlated with species richness ($R^2 = 0.84$, P < 0.001) (Fig. 4b). Similar patterns were seen for results of analyses at the community level (richness vs. PD, $R^2 = 0.99$, P < 0.001; richness vs. SES_PD, $R^2 = 0.98$, P < 0.001) (Figs. 4c & 4d) and at the zone level (richness vs. PD, $R^2 = 0.99$, P < 0.001; richness vs. SES_PD, $R^2 = 0.99$, P = 0.003) (Figs. 4e & 4f).

60.44

31456.18

-12.38

Phylogenetic Structure

Phylogenetic structure varied along the elevational gradient (Table 2 & Supporting Information). Several community types (e.g., deciduous broad-leaved forest, coniferous forest, alpine meadow) and zones (e.g., temperate forest, alpine zone) showed phylogenetic clustering, indicating that co-occurring species in these communities or zones are more related than expected based on a null model randomization of species across all locations. In contrast, evergreen broad-leaved forest (subtropical forest zone) showed phylogenetic overdispersion, indicating this forest type tended to be composed of distant relatives.

Discussion

Role of Phylogenetic Structure in Conservation Planning

Overall, we found a strong correlation between areas of high species richness and areas of high phylogenetic diversity. At first pass, this indicated a limited role for

^{*} Standard effect size.

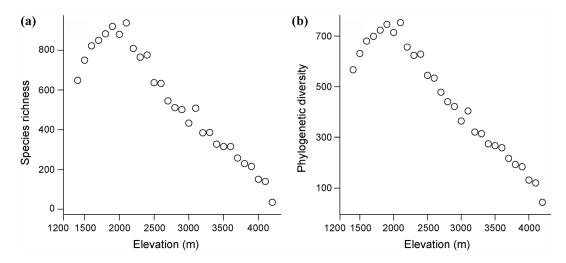


Figure 2. Patterns of (a) species richness and (b) phylogenetic diversity (100 million years) of native seed plants along the elevational gradient in Dulong Valley.

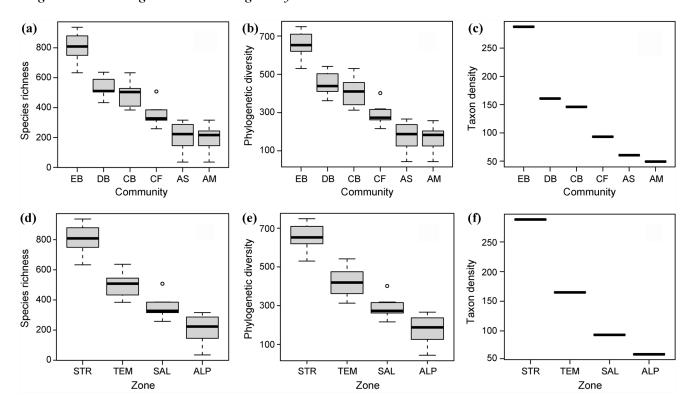


Figure 3. (a, d) Species richness, (b, e) phylogenetic diversity (100 million years), and (c, f) taxonomic density for 6 community types and 4 zones across the elevational bands in Dulong Valley (EB, evergreen broad-leaved forest; DB, deciduous broad-leaved forest; CB, coniferous broad-leaved mixed forest; CF, coniferous forest; AS, alpine shrub; AM, alpine meadow; STR, subtropical forest; TEM, temperate forest; SAL, subalpine forest; ALP, alpine zone).

phylogenetic diversity in conservation planning in this region. However, after using a null model to correct for this relationship, we still detected a strong positive correlation between SR and the standard effect size of PD (Fig. 4). The similarity in distribution between species richness and the standardized effect size of PD may be driven by difference in phylogenetic composition along

the elevational gradient in the Dulong Valley flora. Most areas had higher or lower phylogenetic diversity than expected based on random sampling of the regional flora. Based on community phylogenetic structure, phylogenetic structure in Dulong Valley flora was strong along the elevational gradient. Five of the 6 community types (and 3 of the 4 zones) showed phylogenetic clustering, whereas

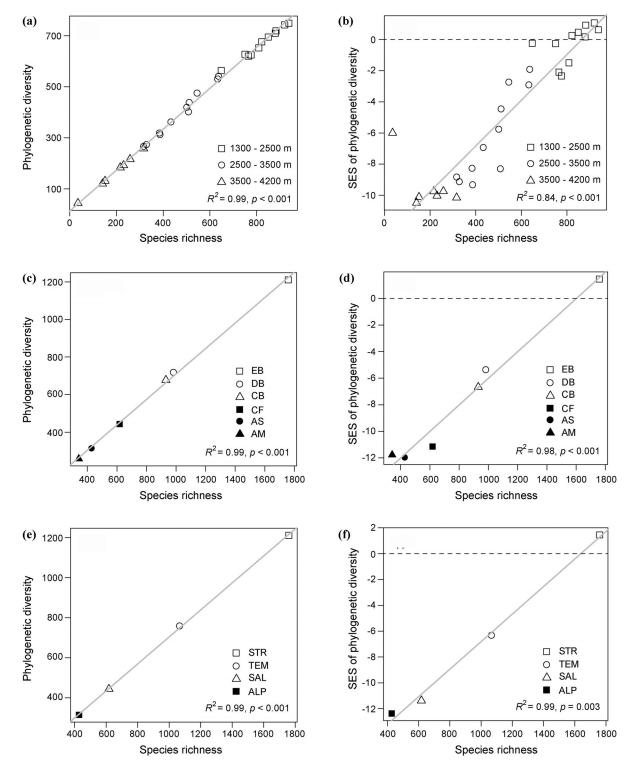


Figure 4. Relationships between (a) species richness and phylogenetic diversity ($R^2 = 0.99$, P < 0.001) among elevations, (b) species richness and the standardized effect size (SES) of phylogenetic diversity ($R^2 = 0.84$, P < 0.001) among elevations, (c) species richness and phylogenetic diversity ($R^2 = 0.99$, P < 0.001) among 6 communities, (d) species richness and the SES of phylogenetic diversity ($R^2 = 0.98$, P < 0.001) among 6 communities, (e) species richness and phylogenetic diversity ($R^2 = 0.99$, P < 0.001) among 4 zones, and (f) species richness and the SES of phylogenetic diversity ($R^2 = 0.99$, P = 0.003) among 4 zones (EB, evergreen broad-leaved forest; DB, deciduous broad-leaved forest; CB, coniferous broad-leaved mixed forest; CF, coniferous forest; AS, alpine shrub; AM, alpine meadow; STR, subtropical forest; TEM, temperate forest; SAL, subalpine forest; ALP, alpine zone).

Table 2. Phylogenetic structure for 6 community types and 4 zones in the Dulong Valley calculated using net relatedness index (NRI).

Community type (or zone)	NRI	P	Phylogenetic structure
Evergreen	-1.82	0.964	overdispersed
broad-leaved			
forest			
Deciduous	2.17	0.018	underdispersed
broad-leaved			•
forest			
Coniferous	3.41	0.001	underdispersed
broad-leaved			_
mixed forest			
Coniferous forest	4.63	0.001	underdispersed
Alpine shrub	8.36	0.001	underdispersed
Alpine meadow	8.70	0.001	underdispersed
Subtropical forest	-1.90	0.973	overdispersed
Temperate forest	2.12	0.019	underdispersed
Subalpine forest	4.81	0.001	underdispersed
Alpine zone	8.82	0.001	underdispersed

only evergreen broad-leaved forest (subtropical forest zone) showed phylogenetic overdispersion (Table 2 & Supporting Information). The pattern likely resulted from fundamental evolutionary and palaeoclimatic processes in this region. The orogenic processes accompanying the uplift of the Himalava in the Tertiary created regional topographic complexities in Dulong Valley (Harrison et al. 1992; An et al. 2001; Spicer et al. 2003). The diverse ecosystems combined with the climatic change of the Quaternary may have facilitated species assemblages along the elevational gradient (Chaplin 2005). Heterogeneous environments and mild climate at low elevation (e.g., subtropical forest) may contribute to species coexistence, which leads to a more diverse evolutionary composition. In contrast, the harsh environments in alpine zone may limit survival of many species, resulting in less diverse phylogenetic composition.

Facing an uncertain future, it is difficult to predict the characteristics that lineages in the Dulong Valley will need to adapt and persist. Therefore, we assert that maximizing the conservation of phylogenetic diversity in the region will in turn maximize the options within the flora for future diversification. Across the global plant phylogeny, species diversification is highly variable across different lineages in temporal scales (Davies et al. 2004; Zanne et al. 2014). We suggest that biodiversity conservation is maximized by the inclusion of communities with overdispersed phylogenetic structure because such natural communities include phylogenetically distantly related lineages. In this case, evergreen broad-leaved forest should be considered a conservation priority to protect local biodiversity because it is the most phylogenetically diverse community type. This community type showed greater phylogenetic diversity than predicted based on random sampling from the Dulong Valley flora. Evergreen broad-leaved forest contains members of all the major seed plant clades (e.g., representatives from Pinaceae in the gymnosperms, Orchidaceae in the monocots, Rosaceae and Sapindaceae in the rosids, Ericaceae in the asterids). Conversely, the other community types within the region showed phylogenetic clustering, which is indicative of lower than expected phylogenetic diversity given the species richness. For example, the alpine shrub community is dominated by members of closely related families in the Ericales, including Ericaceae and Primulaceae. These results demonstrate that the phylogenetic patterns of community can be a helpful tool in identifying regions of high conservation priority in the Dulong Valley.

Our results show that a simple correspondence between species richness and phylogenetic diversity can hide a fundamental difference in evolutionary composition of flora and give rise to a different conservation outcome if only taxonomic criteria are considered. However, the conservation of evolutionarily distinct lineages is now acknowledged as the prioritized strategy for preserving biodiversity in the face of global change (Forest et al. 2007; Thuiller et al. 2011). In biodiversity hotspots worldwide, given that data on phylogenetic diversity can be difficult to obtain and that our understanding of the phylogenetic relationships in diverse lineages outside of the vertebrates is often incomplete, there are real obstacles to incorporating a phylogenetic perspective in conservation planning in many regions. As a practical matter, we recommend that phylogenetic structure of species assemblages may serve as an alternative approaches to measure phylogenetic diversity and guide biodiversity conservation. One should be able to use the phylogenetic structure of floristic composition to identify those key regions that maximize future options for the continuing evolution of life on Earth.

Conservation Threats to the Dulong Valley Region

The rich flora of the Dulong Valley plays a key role in ensuring the provisioning of goods and service to the local people and represents an important part of the floristic evolutionary history of the planet. The current network of protected areas is adequate to protect much of floral diversity in the region (Ma et al. 2006). Despite this protection, local economic pressures due to the natural resource needs of local people pose a continued threat to these areas (Xu & Wilkes 2004). For example, evergreen broad-leaved forest has undergone severe fragmentation because of the increasing construction of infrastructure for commercial tourism, roads, and hydropower development (Li et al. 2011). Charcoal production is an important direct threat to the dominant trees in evergreen broad-leaved forest because this activity is focused mainly on the Fagaceae family (particularly Lithocarpus and Cyclobalanopsis) (Xu & Wilkes 2004). Additional threats in this community come from logging and conversion of forests into cropland. For example, swidden cultivation is practiced in the region (i.e., plots of land are cultivated temporarily and then abandoned and allowed to revert to their natural vegetation while the cultivator moves on to another plot). This cultivation method has been the main agricultural technique for centuries among many of the area's ethnic groups (Shen et al. 2010) and has resulted in the fragmentation of forests at lower elevations. In most regions, expansion of cultivated fields due to the increasing population has meant the permanent replacement of forest, particularly in forest areas close to villages (Xu & Wilkes 2004).

In addition to threats described above, the overexploitation of species of economic interest may seriously threaten the survival of some plant taxa in all of Dulong Valley. Several valuable medicinal plants, such as *Dendrobium candidum*, *Gastrodia elata*, *Paris* spp., *Panax* spp., and *Taxus* spp., are dwindling in wild areas because of overharvesting (Li et al. 2011). Widespread cultivation of some of these species has yet to reduce pressure on wild populations, which in many cases remain severely depleted (e.g., *Coptis teeta*) (Li et al. 2011). In addition to medicinal plants, non-timber forest products, including edible vegetation, have been subjected to overcollection (e.g., *Maianthemum* spp.), as have some orchids (e.g., *Cymbidium* spp.) for their horticultural value (Meng et al. 2006; Li et al. 2011).

Given the current biodiversity crisis, conservation actions must be enhanced if we want to preserve these species and the features of the landscape that have been associated with the evolutionary diversification in this region. We suggest keeping the whole region in Dulong Valley as a conservation target. However, to maximize the evolutionary potential of the flora to respond to environmental changes in the future, more attention should be paid to the evergreen broad-leaved forest communities because they contain high levels of species richness and phylogenetic diversity within the region. Admittedly, our analysis of biodiversity conservation incorporating evolutionary information is only an initial step in identifying areas with highly diverse phylogenetic lineages where further protection may be warranted. The consideration of evolutionary information for conservation schemes design should complement future efforts within other organismal groups (e.g., ferns, insects, birds) because different organisms might show patterns that are distinct from what we report for seed plants species (Wu et al. 2014).

Our findings have important implications for conservation programs across the Indo-Burma and adjacent Himalayan biodiversity hotspots, which have similar natural history and vegetation land cover to the Dulong Valley (Harrison et al. 1992; An et al. 2001; Spicer et al. 2003). Considering floristic composition, we suggest that evergreen broad-leaved forests be given more conserva-

tion attention because they have both high species richness and diverse phylogenetic lineages.

Acknowledgments

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Supporting Information

Vegetation in the Dulong Valley (Appendix S1), the Newick version of the phylogeny of seed plants in the Dulong Valley (Appendix S2), and phylogenetic structure for 6 community types and 4 zones without gymnosperms (Appendix S3) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than omitted material) should be directed to the corresponding author.

Literature Cited

- An ZS, Kutzbach JE, Prell WL, Porter SC. 2001. Evolution of Asian monsoons and phased uplift of the Himalaya-Tibetan plateau since late Miocene times. Nature 411:62-66.
- APG III. 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. Botanical Journal of the Linnean Society **161:**105–121.
- Cadotte MW, Cavender-Baresn J, Tilman D, Oakley TH. 2009. Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. PLOS ONE 4 (e5695) DOI: 10.1371/journal.pone.0005695.
- Cadotte MW, Davies TJ, Regetz J, Kembel SW, Cleland EE, Oakley TH. 2010. Phylogenetic diversity metrics for ecological communities: integrating species richness, abundance and evolutionary history. Ecology Letters 13:96–105.
- Cardinale BJ, et al. 2012. Biodiversity loss and impact on humanity. Nature 486:59-67.
- Cavender-Bares J, Kozak KH, Fine PVA, Kembel SW. 2009. The merging of community ecology and phylogenetic biology. Ecology Letters 12:693–715.
- Chaplin G. 2005. Physical geography of the Gaoligong Shan area of southwest China in relation to biodiversity. Proceedings of the California Academy of Sciences 56:527-556.
- Davies TJ, Barraclough TG, Chase MW, Soltis PS, Soltis DE, Savolainen V. 2004. Darwin's abominable mystery: insights from a supertree of the angiosperms. Proceedings of the National Academy of Sciences of the United States of America 101:1904–1909.

Devictor V, Mouillot D, Meynard C, Jiguet F, Thuiller W, Mouquet N. 2010. Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for integrative conservation strategies in a changing world. Ecology Letters 13:1030–1040.

- Diniz-Filho JAF, Loyola RD, Raia P, Mooers AO, Bini LM. 2013. Darwinian shortfalls in biodiversity conservation. Trends in Ecology & Evolution 28:689-695.
- Emerson BC, Gillespie GR. 2008. Phylogenetic analysis of community assembly and structure over space and time. Trends in Ecology & Evolution 23:619-630.
- Faith DP. 1992. Conservation evaluation and phylogenetic diversity. Biological Conservation 61:1-10.
- Faith DP. 2008. Threatened species and the potential loss of phylogenetic diversity: conservation scenarios based on estimated extinction probabilities and phylogenetic risk analysis. Conservation Biology 22:1461-1470.
- Faith DP. 2013. Biodiversity and evolutionary history: useful extensions of the PD phylogenetic diversity assessment framework. Annals of the New York Academy of Sciences 1289:68–89.
- Forest F, et al. 2007. Preserving the evolutionary potential of floras in biodiversity hotspots. Nature 445:757–760.
- Hardy OJ, Couteron P, Munoz F, Ramesh BR, Pélissier R. 2012. Phylogenetic turnover in tropical tree communities: impact of environmental filtering, biogeography and mesoclimatic niche conservatism. Global Ecology and Biogeography 21:1007–1016.
- Harrison TM, Copeland P, Kidd WSF, Yin A. 1992. Raising Tibet. Science **255**:1663–1670.
- He D. 1998. Comprehensive study on the Dulong river area. Yunnan Geographic Environmental Research 10:8–14.
- Kembel SW, Hubbell SP. 2006. The phylogenetic structure of a Neotropical forest tree community. Ecology 87:S86–S99.
- Kembel SW, Cowan PD, Helmus MR, Cornwell WK, Morlon H, Ackerly DD, Blomberg SP, Webb CO. 2010. Picante: R tools for integrating phylogenies and ecology. Bioinformatics 26:1463–1464.
- Kier G, Kreft H, Lee TM, Jetz W, Ibisch PL, Nowicki C, Mutke J, Barthlott W. 2009. A global assessment of endemism and species richness across island and mainland regions. Proceedings of the National Academy of Sciences of the United States of America 106:9322-9327
- Körner C. 2000. Why are there global gradients in species richness? Mountains might hold the answer. Trends in Ecology & Evolution 15:513-514.
- Kraft NJB, Baldwin BG, Ackerly DD. 2010. Range size, taxon age and hotspots of neoendemism in the California flora. Diversity and Distribution 16:403-413.
- Li H. 1993. Flora of Dulongjiang region. Yunnan Science and Technology Press, Kunming.
- Li H. 1994. Delineation and feature of Dulong Valley flora. Acta Botanica Yunnanica Supplement 6:1-100.
- Li H, Guo H, Dao Z. 2000. Flora of Gaoligong mountains. Science Press,
- Li R, Dao Z, Li H. 2011. Seed plant species diversity and conservation in the northern Gaoligong Mountains in western Yunnan, China. Mountain Research and Development 31:160-165.
- Li R, Dao Z, Ji Y, Li H. 2007. A floristic study on the seed plants of the northern Gaoligong Mountains in western Yunnan, China. Acta Botanica Yunnanica 29:601–615.
- Li X, Zhu X, Niu Y, Sun H. 2014. Phylogenetic clustering and overdispersion for alpine plants along elevational gradients in the Hengduan Mountains Region, southwest China. Journal of Systematics and Evolution **52:**280–288.
- Liu L, Dao Z, Guo H, Li H. 2000. Vegetation of the Gaoligong mountains. Pages 6-48 in Li H, Guo H, and Dao Z, editors. Flora of Gaoligong mountains. Science Press, Beijing.
- Lyashevska O, Farnsworth KD. 2012. How many dimensions of biodiversity do we need? Ecological Indicators 18:485-492.

Ma C, Robert M, Chen W, Zhou Z. 2006. Plant diversity and priority conservation areas of northwestern Yunnan, China. Biodiversity and Conservation 16:757–774.

- Mace GM, Purvis A. 2008. Evolutionary biology and practical conservation: bridging a widening gap. Molecular Ecology 17:9–19.
- Maherali H, Klironomos JN. 2007. Influence of phylogeny on fungal community assembly and ecosystem functioning. Science 316:1746–1748.
- McNyset KM. 2009. Ecological niche conservatism in North American freshwater fishes. Biological Journal of the Linnean Society 96:282-295
- Meng Y, Yang YP, Weckerle CS. 2006. Conservation status of *Maianthe-mum* species in the Hengduan mountains: a case study analyzing the impact of new policies on wild collected plant species. Ethnobotany Research and Applications 4:167–173.
- Moritz C. 2002. Strategies to protect biological diversity and the evolutionary process that sustain it. Systematic Biology 51: 238-254.
- Myers N, Knoll AH. 2001. The biotic crisis and the future of evolution. Proceedings of the National Academy of Sciences of the United States of America 98:5389-5392.
- Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J. 2000. Biodiversity hotspots for conservation priorities. Nature 403:853-858.
- Prinzing A, Durka W, Klotz S, Brandl R. 2001. The niche of higher plants: evidence for phylogenetic conservatism. Proceedings of the Royal Society of London, Series B 268:2383-2389.
- R Development Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- Rahbek C. 1997. The relationship among area, elevation, and regional species richness in Neotropical birds. The American Naturalist 149:875–902.
- Rodrigues ASL, Gaston KJ. 2002. Maximizing phylogenetic diversity in the selection of networks of conservation areas. Biological Conservation 105:103-111.
- Sechrest W, Brooks TM, da Fonseca GAB, Konstant WR, Mittermeier RA, Purvis A, Rylands AB, Gittleman JL. 2002. Hotspots and the conservation of evolutionary history. Proceedings of the National Academy of Sciences of the United States of America 99:2067–2071.
- Shen S, Wilkes A, Qian J, Yin L, Ren J, Zhang F. 2010. Agrobiodiversity and biocultural heritage in the Dulong Valley, China. Mountain Research and Development 30:205–211.
- Spicer RA, Harris NBW, Widdowson M, Herman AB, Guo S, Valdes PJ, Wolfe JA, Kelley SP. 2003. Constant elevation of southern Tibet over the past 15 million years. Nature 421:622-624.
- Swenson NG. 2011. The role of evolutionary processes in producing biodiversity patterns, and the interrelationships between taxonomic, functional and phylogenetic biodiversity. American Journal of Botany 98:472–480.
- Thuiller W, Lavergne S, Roquet C, Boulangeat I, Lafourcade B, Araujo MB. 2011. Consequences of climate change on the tree of life in Europe. Nature 470:531-534.
- Tucker CM, Cadotte MW. 2013. Unifying measures of biodiversity: understanding when richness and phylogenetic diversity should be congruent. Diversity and Distribution 19:845-854.
- Tucker CM, Cadotte MW, Davies TJ, Rebelo AG. 2012. Incorporating geographical and evolutionary rarity into conservation prioritization. Conservation Biology 26:593–601.
- Vamosi SM, Heard SB, Vamosi JC, Webb CW. 2009. Emerging patterns in the comparative analysis of phylogenetic community structure. Molecular Ecology 18:572–592.
- Vandergast AG, Bohonak AJ, Hathaway SA, Boys J, Fisher RN. 2008. Are hotspots of evolutionary potential adequately protected in southern California? Biological Conservation 141:1648– 1664.

- Vane-Wright RI, Humphries CJ, Williams PH. 1991. What to protect?Systematics and the agony of choice. Biological Conservation 55:235-254.
- Vetaas OR, Grytnes JA. 2002. Distribution of vascular plant species richness and endemic richness along the Himalayan elevation gradient in Nepal. Global Ecology and Biogeography 11:291–301.
- Wang Z, Tang Z, Fang J. 2007. Altitudinal patterns of seed plant richness in the Gaoligong Mountains, south-east Tibet, China. Diversity and Distributions 13:845–854.
- Webb CO. 2000. Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. The American Naturalist 156:145-155.
- Webb CO, Donoghue MJ. 2005. Phylomatic: Tree assembly for applied phylogenetics. Molecular Ecology Notes 5:181–183.
- Webb CO, Ackerly DD, Kembel SW. 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. Bioinformatics 24:2098–2100.

- Webb CO. Ackerly DD, Mcpeek MA, Donoghue MJ. 2002. Phylogenies and community ecology. Annual Review of Ecology and Systematics 33:475-505.
- Wikstrom N, Savolainen V, Chase MW. 2001. Evolution of the angiosperms: calibrating the family tree. Proceedings of the Royal Society B-Biological Sciences 268:2211–2220.
- Winter M, Devictor V, Schweiger O. 2013. Phylogenetic diversity and nature conservation: Where are we? Trends in Ecology & Evolution 28:199-204.
- Wu Y, Colwell RK, Han N, Zhang R, Wang W, Quan Q, Zhang C, Song G, Qu Y, Lei F. 2014. Understanding historical and current patterns of species richness of babblers along a 5000-m subtropical elevational gradient. Global Ecology and Biogeography 23:1167-1176.
- Xu J, Wilkes A. 2004. Biodiversity impact analysis in northwest Yunnan, southwest China. Biodiversity and Conservation 13:959–983.
- Zanne AE, et al. 2014. Three keys to the radiation of angiosperms into freezing environments. Nature **506:**89–92.

