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Research Article

A phylogenetic perspective on the evolutionary processes of floristic assemblages within a biodiversity hotspot in eastern Asia

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Abstract How to maximize the conservation of biodiversity is critical for conservation planning, particularly given rapid habitat loss and global climatic change. The importance of preserving phylogenetic diversity has gained recognition due to its ability to identify some influences of evolutionary history on contemporary patterns of species assemblages that traditional taxonomic richness measures cannot identify. In this study, we evaluate the relationship between taxonomic richness and phylogenetic diversity of angiosperms at genus and species levels and explore the spatial pattern of the residuals of this relationship. We then incorporate data on historical biogeography to understand the process that shaped contemporary floristic assemblages in a global biodiversity hotspot, Yunnan Province, located in southwestern China. We identified a strong correlation between phylogenetic diversity residuals and the biogeographic affinity of the lineages in the extant Yunnan angiosperm flora. Phylogenetic diversity is well correlated with taxonomic richness at both genus and species levels between floras in Yunnan, where two diversity centers of phylogenetic diversity were identified (the northwestern center and the southern center). The northwestern center, with lower phylogenetic diversity than expected based on taxonomic richness, is rich in temperate-affinity lineages and signifies an area of rapid speciation. The southern center, with higher phylogenetic diversity than predicted by taxonomic richness, contains a higher proportion of lineages with tropical affinity and seems to have experienced high immigration rates. Our results highlight that maximizing phylogenetic diversity with historical interpretation can provide valuable insights into the floristic assemblage of a region and better-informed decisions can be made to ensure different stages of a region's evolutionary history are preserved.

Key words: biodiversity conservation, evolutionary history, floristic assemblages, historical biogeography, phylogenetic diversity, taxonomic richness.

1 Introduction

Biodiversity conservation has long been a focus of research because species extinction risks resulting from global climate change, habitat fragmentation, exotic species invasion, and increased human population density have grown in recent decades (Strauss et al., 2006; Thuiller et al., 2011; Ceballos et al., 2015). To date, the conservation of biodiversity has largely focused on maximizing gain of specific features diversity, whether it is species, functional traits, or phylogenetic diversity (PD) (Orme et al., 2005; Devictor et al., 2010; González-Maya et al., 2016). However, in recent years, the evolutionary processes that generate and maintain biodiversity have also been recognized as important factors that need to be accounted for in conservation planning (Mace & Purvis, 2008; Winter et al., 2013; Lu et al., 2018). Unfortunately, the science of maximizing the conservation of biodiversity has operated separately from the science of understanding how biodiversity has diversified and dispersed across the globe through time, until relatively recently (Costion et al., 2015; Thornhill et al., 2016; Sosa et al., 2018). To better-informed decisions can be made to preserve biodiversity, it is important to bring these two disciplines closer together.

Phylogenetic diversity is a measure of biodiversity that incorporates information on evolutionary relationships between taxa, which has become increasing relevant to applied conservation (Faith, 1992; González-Orozco et al., 2016; Spalink et al., 2018). As ecologists have been aware since Darwin, closely related species tend to share similar physiological and ecological traits because of their shared evolutionary histories (Webb, 2000; Webb et al., 2002). As a result, two closely related species could perform similar ecosystem functions and provide similar ecosystem services. Therefore, it has been assumed that the value of biodiversity measures that incorporate phylogenetic information will better predict feature diversity of organisms (Rodrigues & Gaston, 2002; Davies & Buckley, 2011; Morlon et al., 2011). Thus, maximizing PD can maximize feature diversity and hence biodiversity option value (Faith, 1992).

Although most studies have reported a direct correlation between taxonomic richness (TR) and PD (e.g., Sechrest et al., 2002; Davies et al., 2008; Li et al., 2015; Huang et al., 2016; Qian et al., 2017), the residuals of the relationship between TR and PD have been shown to identify some influence of evolutionary history on contemporary patterns of TR that are not apparent using taxonomic diversity alone (e.g., Forest et al., 2007; Davies et al., 2008). For example, if a species-rich area exhibiting low underlying PD relative to species richness where speciation has been rapid, but if a species-rich assemblage contains high relative PD due to the presence of many phylogenetic lineages where immigration of multiple lineages has maintained this diversity over time (Davies et al., 2007; Davies & Buckley, 2011; Fritz & Rahbek, 2012). In addition to measuring the PD residuals, historical biogeography can provide information about the biogeographic affinities of the component taxa (Wiens & Donoghue, 2004; Weeks et al., 2016). By considering the relationship between TR and PD together with the spatial pattern of the residuals of this relationship, and incorporating data on historical biogeography, one can understand the processes that shaped contemporary biotic assemblages. For example, by integrating data on historical biogeography into a model to explain the spatial distribution of PD and the PD residuals in the community assembly of northeastern Queensland in Australia, Costion et al. (2015) found that the areas with unusually high and low PD are correlated with the biogeographic affinities of extant plant lineages. However, few studies have attempted this for the entire flora at either a global or regional scale.

The Yunnan Province is known for its species-richness and high level of endemism in certain fauna and flora that forms a major part of the Indo-Burma biodiversity hotspot (Myers et al., 2000). It is generally accepted that the flora of northern Yunnan has evolved with the uplift of the Himalayas by gradual proliferation of mainly cosmopolitan and north temperate floristic elements, whereas the flora of southern Yunnan has evolved with extrusion of the Indochina block to Southeast Asia by the influence of mainly tropical Asian elements since the late Tertiary (Li & Walker, 1986; Li & Li, 1997; Zhu, 2012). Moreover, the evolutionary patterns of flora in this region were influenced by the Quaternary glacial–interglacial climatic changes (Li, 1985; Feng et al., 2016). Further to this exceptional evolutionary legacy, accumulating molecular evidence now suggests that diversification and dispersal have left strong signatures on the extant distribution of plants in Yunnan (e.g., Hou et al., 2016; Li & Wen, 2016; Luo et al., 2016). Historically, northwestern Yunnan and southern Yunnan were identified as two of 20 biodiversity centers in China based on the richness of endemic taxa (Li, 1994; López-Pujol et al., 2011; Huang et al., 2012). However, this region has not been analyzed from a phylogenetic perspective, so we lack an understanding of the critical evolutionary dimension of floristic diversity in this area.

The goal of this study is to evaluate the relationship between TR and PD of angiosperms at genus and species levels and to explore the spatial pattern of the residuals of this relationship and then incorporate data on historical biogeography to understand the process that shaped contemporary floristic assemblages. Specifically, we address the following questions: (i) Where are the PD centers that agree with previously identified biodiversity centers? (ii) Do the residuals from the relationship between TR and PD show spatial structure? (iii) Do the macro-evolutionary processes, such as diversification and dispersal, leave a detectable signal in contemporary patterns of species richness?

2 Material and Methods

2.1 Study area

Yunnan Province is located in southwestern China at 21°8′32″–29°15′8″N and 97°31′39″–106°11′47″E (Fig. 1). Yunnan is a highland province with a terraced terrain stretching from the northwest (6740 m a.s.l.) to the southeast (76 m a.s.l.) (Wu, 1987). This region is one of the most botanically diverse terrestrial regions on Earth and contains nearly 18 000 plant taxa (in 3008 genera and 433 families), which account for over 50% of China's overall floristic diversity (Wu, 1977–2006). The region in particular contains the highest concentration of basal angiosperm groups in China and has a high level of endemism including 2718 endemic species (Li, 1985, 1994; Huang et al., 2011). The region also possesses a rich diversity of community types, including tropical rain forest, subtropical evergreen broad-leaved forest, temperate coniferous broad-leaved mixed forest, subalpine coniferous forest, alpine shrub, alpine meadow, and alpine scree (Wu, 1987).

2.2 Distribution data

We used the data from *Flora of Yunnan* published in 21 volumes by Wu and his colleagues (Wu, 1977–2006). The flora presents a comprehensive synonymized inventory of plant species in each county ($n = 125$) in Yunnan. In order to analyze the spatial pattern in the residuals of the relationship between TR and PD, the study area was divided into 125 county-level geographical units (the average for the county area is 3065.67 ± 1855.23 km^2; mean ± standard deviation). We determined the presence or absence of each angiosperm genus and species in each county by extracting generic and species distribution information from *Flora of Yunnan* and generating a presence–absence genus matrix and a presence–absence species matrix. Genera and species that are not native to Yunnan were excluded. Infraspecific taxa were combined with their parent species. We assigned each genus and species to a family, following the Angiosperm Phylogeny Group nomenclature (APG IV, 2016). A total of 101 987 records in 11 558 angiosperm species, belonging to 1956 genera and 213 families, were included in this study.

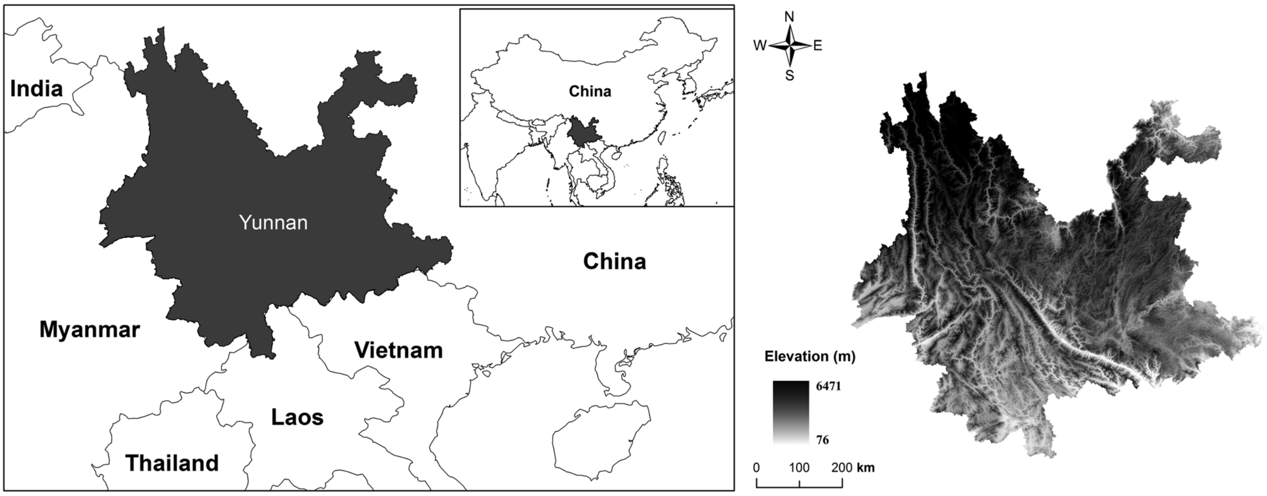

Fig. 1. Location of Yunnan Province in China. The map was generated using ArcGIS 10.2.

2.3 Phylogeny construction

We constructed a genus-level phylogenetic tree and a species-level phylogenetic tree by grafting the genera and species present in the study area, respectively, onto a backbone phylogenetic hypothesis using the function S.PhyloMaker (Qian & Jin, 2016) in R 2.15.3 software (R Development Core Team, 2018) with the "phytools" package (Revell, 2012). The backbone of the supertree was Zanne et al.'s (2014) phylogeny, which is the largest and most up-to-date time-calibrated species-level phylogeny of plants and uses seven gene regions in addition to fossil data. Given the scarcity of comprehensive time-calibrated phylogenies within families and genera, we followed previous studies to treat unresolved genera as polytomies within families (Fig. S1) and unresolved species as polytomies within genera (e.g., Hardy et al., 2012; Kerkhoff et al., 2014; Qian et al., 2016).

2.4 Statistical analyses

To quantify taxonomic composition and phylogenetic composition of Yunnan angiosperm assemblages among county-level floras, we calculated TR and Faith's PD for each county at genus and species levels because they are both commonly used in conservation studies and reflect different aspects of biodiversity (Cavender-Bares et al., 2009; Cadotte et al., 2010; Huang et al., 2016). Taxonomic richness is the number of angiosperm genera (generic richness) or the number of angiosperm species (species richness) represented in a spatial unit. Faith's PD is the sum of all phylogenetic branch lengths connecting taxa in a defined region (Faith, 1992).

A published dataset of biogeographic affinities data was utilized that assigned two categories of biogeographic affinity to all genera and species present in Yunnan (Wu et al., 2006): (i) tropical – plants that have tropical affinities and dispersed north from the tropical region; and (ii) temperate – plants that have temperate affinities. Richness of tropical-affinity taxa and temperate-affinity taxa were counted for each county at genus level and species level, respectively. The percentage of each floristic element was then calculated by dividing these numbers by the total number of taxa in each county at both genus and species levels. Given the changes in TR are primarily determined by the taxa with tropical affinity (Wang et al., 2011), we used the percentage of the taxa with tropical affinity per county as an estimate of biogeographic affinities.

To evaluate the effects of space on the TR, PD, and percentage of tropical-affinity taxa, spatial autocorrelation was first examined with Moran's *I* correlogram using spatial eigenvector mapping, generated through principal coordinates of neighbor matrices (Diniz-Filho & Bini, 2005). Moran's *I*-value as calculated using eight neighboring cells, with *P*-values estimated using 999 randomizations. This test showed that TR, PD, and the percentage of tropical-affinity taxa were all strongly spatially autocorrelated at genus and species levels (Fig. S2). In order to control the effects of spatial autocorrelation, we then calculated simultaneous spatial autoregression, which uses neighbor matrices to estimate spatially independent data points that can be utilized for analysis (Yang et al., 2014). To examine the ability of TR to predict PD at both genus and species levels, we modeled the relationship between them by linear regression. Also, we modeled the relationship between PD and TR but including one further predictor variable, an estimate of biogeographic affinities of floristic assemblages. We compared for their explanation power to describe PD based on the Akaike information criterion. The model with the lowest Akaike information criterion score was considered to be most informative (Burnham & Anderson, 1998).

All of the phylogenetic metrics and generalized least-squares model with first-order spatial neighbor spatial autoregression was implemented in "picante" and "spdep" packages (Bivand, 2010; Kembel et al., 2010) of R (R Development Core Team, 2018). To visualize the geographic distribution of the component of PD that could not be explained by TR, we then plotted the residual values from the regression analyses using DIVA-GIS version 7.5 and investigated the distribution of residuals in geographic space.

3 Results

3.1 Diversity centers of PD and TR

We found that, in Yunnan, PD was strongly and positively correlated with TR (Pearson correlation coefficient $r = 0.993$,

$P < 0.001$ at genus level; $r = 0.989$, $P < 0.001$ at species level). The close correlation between PD and TR in Yunnan's angiosperm flora was also illustrated by the general spatial congruence in phylogenetic composition and taxonomic composition of floristic assemblages (Figs. 2A, 2B, 2D, 2E). Diversity centers of PD and TR are nearly identical at both genus and species levels, which were found to be concentrated in two primary areas in Yunnan (Figs. 2A, 2B, 2D, 2E). A southern center occurs in lowland regions and a northwestern center concentrates in high mountains ranges.

3.2 Mapping the residuals of PD

In our first round of analyses, generic richness was identified as a significant explanatory variable in determining genus-level PD. A high proportion of the variation in genus-level PD could be explained by generic richness ($R^2 = 98.6\%$, $P < 0.001$), only 1.4% of observed variation in PD could not be attributed to the effect of generic richness. When this 1.4% variation (PD residuals) was mapped, two spatial patterns were revealed from the residuals of the regression model for two diversity centers in Yunnan (Fig. 2C). The southern center notably had high PD that was higher than expected based on generic richness (positive residuals). The northwestern center had high PD overall but lower than expected (negative residuals). These findings were also observed in analyses of PD based on the species-level phylogeny, in which a high proportion of the variation in species-level PD could be explained by species richness ($R^2 = 97.8\%$, $P < 0.001$). When species-level PD residuals were plotted, similar patterns were seen for two diversity centers in Yunnan (Fig. 2F). The positive PD residuals appeared in the southern center, and the negative PD residuals occurred in the northwestern center.

3.3 Modeling PD with historical biogeography data

The second round of regression analyses included one new predictor variable, which is the percentage of taxa with tropical affinity in each county. The model showed TR combined with biogeographic affinities of floristic assemblages can explain PD better (Tables 1, 2). Moreover, the standardized coefficient for the percentage of the tropical-affinity taxa per county was positive at both genus and species levels (Figs. 3A, 3B), which indicates that an increased proportion of taxa with tropical affinity within local floristic assemblages is associated with higher PD values.

4 Discussion

In this study, we have evaluated the relationship between TR and PD at genus and species levels in Yunnan angiosperm assemblages and explored the spatial pattern of the residuals of this relationship in this area to understand the process that shaped contemporary floristic assemblages from an evolutionary perspective. Two diversity centers of PD and TR identified are consistent with two diversity centers of endemism previously identified for the Yunnan region (Li, 1994; López-Pujol et al., 2011; Huang et al., 2012). The correlation between PD centers and TR centers is statistically significant and suggested that both of these areas might have similar patterns of floristic assemblages. The linear regression residuals, however, showed that two diversity centers have unusually high or low residuals from the relationship between PD and TR as measured by Faith's PD, implying a significant difference in the evolutionary history of these two diversity centers on contemporary floristic assemblages.

4.1 Evolutionary history of extant flora in diversity centers

Residuals of Faith's PD against TR at both genus and species levels highlighted the northwestern diversity center in the Yunnan region as containing lower PD for the number of genus or species present (Figs. 2C, 2F), which signifies the presence of radiation. The results suggest that these areas might be species-rich due to rapid speciation. The center lies in the eastern fringe of the Himalayas, which has experienced an uninterrupted uplift since the late Neogene as a result of the collision between the Indian plate and the Eurasian plate (Harrison et al., 1992; Li & Fang, 1999; An et al., 2001), resulting in a vast array of new habitats across wide elevational ranges (up to 5000 m in this area) and a much greater physiographic heterogeneity than elsewhere in China (Zhang et al., 2000). The large topographic relief in huge mountains (e.g., Hengduan Mountains) and deep canyons (e.g., Salween, Mekong, and Yangtze rivers) not only led to tremendous habitat differentiation that benefits the coexistence of species, but also generates dispersal barriers that might have promoted species diversification and radiation through allopatric speciation and interspecific diploid hybridization (Liu et al., 2014; Yu et al., 2014; Xing & Ree, 2017). Recent phylogenetic studies revealed that many plant lineages (e.g., *Gentiana* L., *Saxifraga* L., and *Rhodiola* L.) rapidly diversified and radiated in this region during the uplift of the Himalaya–Tibetan Plateau (Zhang et al., 2014; Favre et al., 2016; Ebersbach et al., 2017). Recent rapid diversification might have also resulted in high concentrations of neoendemic taxa in this area (e.g., *Smithorchis* Tang & F. T. Wang, *Formania* W. W. Sm. & J. Small, and *Nannoglottis* Maxim.) which further contributes to the unusually high species richness with lower PD than predicted (Liu et al., 2002; Tang et al., 2014; Favre et al., 2015). The overall high TR with lower PD than expected in northwestern Yunnan confirms the importance of diversification processes on contemporary floristic assemblages and its historical signal in the floristic diversity patterns. A similar floristic assemblage pattern was observed in South America, where the recent phases of the northern Andes uplift (from the Pliocene onwards) are correlated with many speciation events (Fjeldså, 1994; Richardson et al., 2001).

At the other end of the spectrum, the southern diversity center in the Yunnan region contained unusually high PD for the number of genera or species present (Figs. 2C, 2F). Therefore, the rich taxa in this area could be a result of high immigration rates of multiple lineages. Our results also indicate that the southern diversity center has a higher concentration of lineages with tropical affinity (Figs. 3A, 3B). The center is located at the northern edge of tropical Southeast Asia, which was connected with the tropics even during the Quaternary glacial cycles (Zhu et al., 2006). Given most extant angiosperm lineages originated and initially diversified in the tropics, the tropical conservatism hypothesis assumes that the lineages with tropical affinities evolved in an ancient tropical-like climate (Crane & Lidgard, 1989;

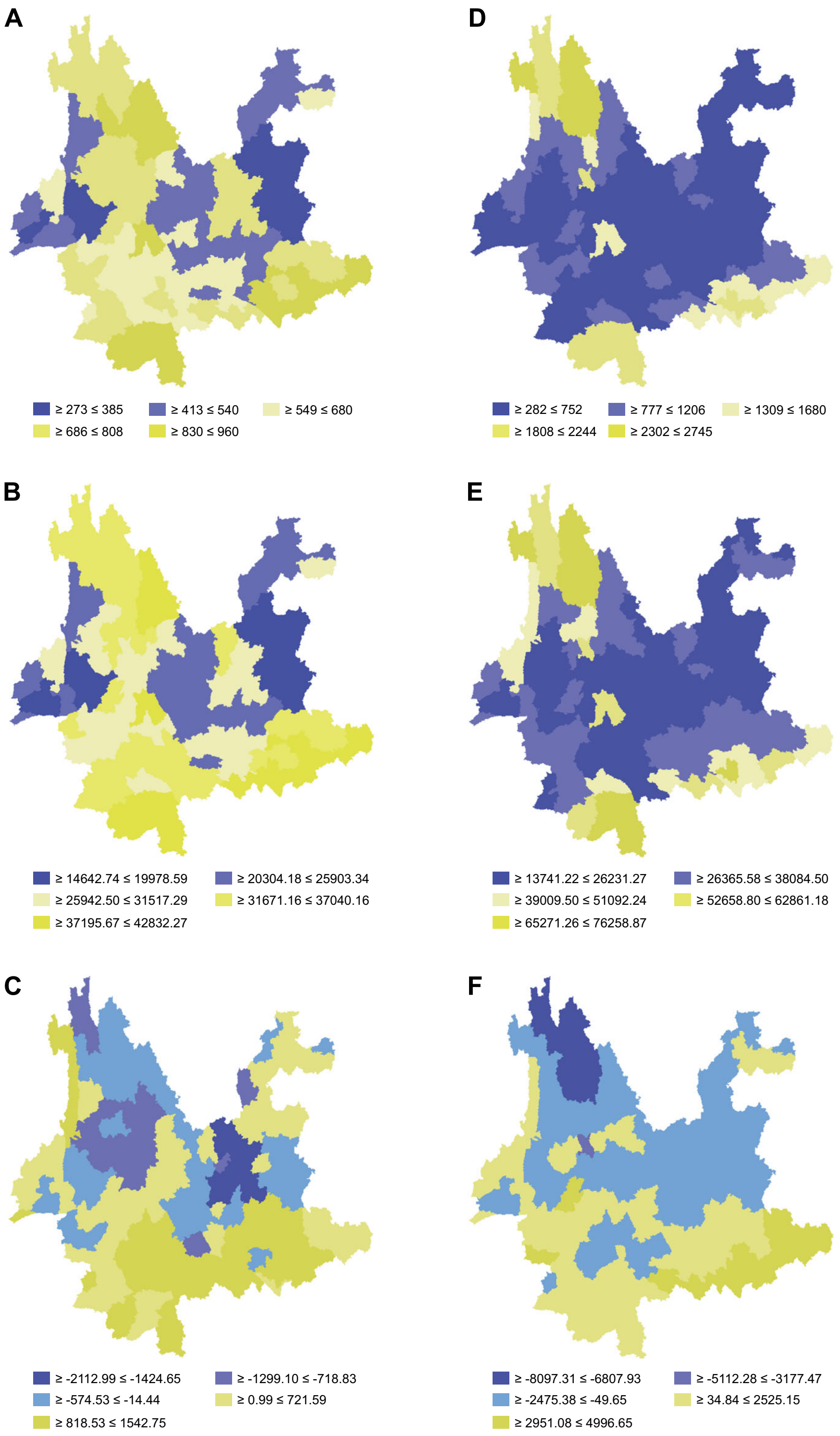

Fig. 2. Patterns of taxonomic richness, phylogenetic diversity, and residuals of phylogenetic diversity against taxonomic richness for the angiosperm flora of Yunnan, China. **A,** Generic richness. **B,** Genus-level phylogenetic diversity. **C,** Residuals from a linear regression model of genus-level phylogenetic diversity against generic richness. **D,** Species richness. **E,** Species-level phylogenetic diversity. **F,** Residuals from a linear regression model of species-level phylogenetic diversity against species richness. The map was generated using ArcGIS 10.2.

Table 1 Summary of model selection for the two models describing the distribution of phylogenetic diversity at genus level

Model	Adjusted R^2	AICc
GR	0.986	−528.359
GR, percentage of tropical-affinity genera	0.992	−595.718

Predictor variables are generic richness (GR) and percentage of tropical-affinity genera (proportion of genera with tropical affinity in each county). AICc, Akaike information criterion.

Table 2 Summary of model selection for the two models describing the distribution of phylogenetic diversity at species level

Model	Adjusted R^2	AICc
SR	0.978	−491.085
SR, percent of tropical-affinity species	0.989	−573.216

Predictor variables are species richness (SR) and percentage of tropical-affinity species (proportion of species with tropical affinity in each county). AICc, Akaike information criterion.

Wiens & Donoghue, 2004; Romdal et al., 2013). Thus, based on this line of reasoning, high current floristic diversity in this region could be related to past migration of plants from southern tropics along the physiographic trending. This process implicates ancient dispersal events rather than *in situ* diversification in playing a major role in shaped contemporary floristic assemblages. Previous studies have shown this pattern. For example, Zhu (1997, 2012, 2013) showed that the floristic composition of southern Yunnan has closely affinities with the flora of Southeast Asia mainly by tropical elements, especially tropical Asia and pantropic elements. The region is also characterized by high levels of paleoendemism (e.g., *Malania* Chun & S. K. Lee, *Bretschneidera* Hemsl., *Lagarosolen* W. T. Wang) because the relative tectonic and environmental stability in this area since the late Tertiary might have facilitated the persistence of relict and ancient plant lineages, which has led to the observed high species richness with higher PD than expected (Li, 1995; Tzedakis et al., 2002; Zhu, 2008). The relatively stable floristic composition in this center was verified by previous broad-scale studies on vegetation reconstruction. For instance, using pollen records, early studies have reconstructed glacial biomes in China, finding that the vegetation in southern Yunnan has not changed much since the Last Glacial Maximum, with evergreen broad-leaved forest being the dominant vegetation type throughout the entire period (Yu et al., 2000).

As in other regions in the world, there is evidence for the impact of the Quaternary glacial–interglacial climate change on the evolutionary history of the extant flora in Yunnan, with effect on, for example, phylogenetic age differences in floristic assemblages (Feng et al., 2017). The relatively stable climates during the Quaternary glacial–interglacial oscillations drive the emergence of species assemblages with large phylogenetic age differences between the basal and crown lineages due to the accumulation of both relict species and newly arisen species through reduced extinction and increased speciation in Yunnan angiosperm flora.

4.2 Conservation implications

Overall, we found a strong correlation between PD and TR at genus and species levels. Moreover, PD has mostly been promoted for its use in guiding conservation strategy by identifying areas of conservation significance. Recent studies (Kissling et al., 2012; Costion et al., 2015; Thornhill et al., 2016) have identified and interpreted links between PD and historical processes shaping extant species assemblages. Our study integrates historical biogeography data into a regional-scale PD analysis for an entire flora and illustrates how important this is for interpreting biodiversity patterns in

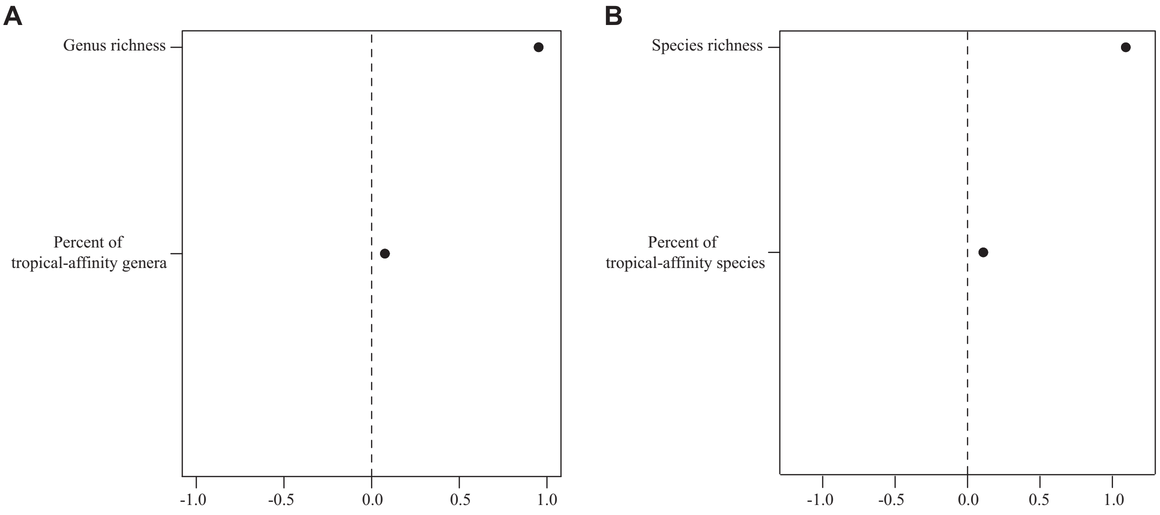

Fig. 3. Standardized regression coefficients of the fit linear regression model to explain phylogenetic diversity based on taxonomic richness and percentage of tropical-affinity taxa for the angiosperm flora of Yunnan, China. **A,** Standardized regression coefficient at genus level. **B,** Standardized regression coefficient at species level.

a species-rich region. In this case, we identified different evolutionary processes (dispersal and *in situ* diversification) on contemporary species assemblages. But which is more important for biodiversity conservation? One may be especially interested in preserving the areas with rapid speciation, that is, those places that contribute most to the growth of the Tree of Life, but one may also focus on areas with assemblages of dispersal lineages that carry unique gene combinations and biological characters (Erwin, 1991; Cowling & Pressey, 2001; Mace et al., 2003). Although there is no clear answer to this question, it brings up important points for the field of conservation. Simply choosing a site or a series of sites that maximize PD in this scenario misses a fundamental story and the underlying processes that created the PD to begin with.

When focusing on the Yunnan region, we should have in mind two important evolutionary considerations. As discussed above, Yunnan maintains a rich sample of ancient and relict lineages, generally consisting of unique, very deep evolutionary lineages, in some cases that represent entire families or even higher taxonomic levels (e.g., Sargentodoxaceae, Rhoipteleales). Additionally, Yunnan harbors perhaps the largest area of rapid speciation in the world's temperate zone, the Hengduan Mountains, which are still active because the Qinghai–Tibetan Plateau is uplifting (Zhang et al., 2000), and which have experienced an extensive explosive radiations in the last million years (Wen et al., 2014; Yu et al., 2019). The extirpation of relict taxa would imply the loss of unique, irreplaceable evolutionary history (Faith, 2008). For instance, their potential economic uses could be lost because these taxa generally do not have close living relatives. In radiating areas, in contrast, flora tends to be phylogenetically clustered, that is, plant taxa usually have many close relatives (Cowling & Pressey, 2001). Thus, the extinction of a given taxon will not involve a significant loss of evolutionary history because of the presence of its congeners (Mace et al., 2003). However, rapid speciation is regarded as very important for assuring the maximum levels of both present and future biodiversity (Erwin, 1991) because biodiversity is rapidly replaced after any extinction event (Crozier, 1997).

Fortunately, the extant flora in the Yunnan region is well protected, thus we have explored these complex questions without the "agony of choice." Many other species-rich regions of the world are not in the same position and could benefit from the methods proposed here to help make informed long-term management decisions under a range of different conservation criteria. This integrated approach could be used to verify or provide further support for the influence of phylogenetic history in extant floristic assemblages inferred using traditional approaches, such as climate modeling and population genetics for individual species (Keppel et al., 2012) and can rapidly advance knowledge on the evolutionary history of large species assemblages in other parts of the globe.

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Supplementary Material

The following supplementary material is available online for this article at http://onlinelibrary.wiley.com/doi/10.1111/jse.12539/suppinfo:

Fig. S1. The phylogeny for all the 1956 genera of angiosperm in Yunnan. Genera in the same group (basal angiosperms, monocots, magnoliids, basal eudicots, superrosids, superasterids) are shown in the same color.

Fig. S2. Moran's *I* correlogram for taxonomic richness, phylogenetic diversity, and percent of tropical-affinity taxa for the Yunnan angiosperm flora in all 125 counties. Spatial autocorrelation was significant ($p < 0.001$) for all six measures.