

Original Articles

Multifaceted patterns of diversity and co-occurrence along an extensive survey of shrubland communities across China



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ABSTRACT

Interpreting biodiversity patterns and the underlying processes is crucial for evaluating the mechanisms of community assembly, but the view of multifaceted diversity patterns spanning broad spatial extents is less strengthened. We implemented an inventory of 1260 vegetation plots from shrublands across China with standardized methods and analyzed patterns of taxonomic and phylogenetic diversity with differential weighting of common and rare species, as well as phylogenetic co-occurrence structures. Taxonomic and phylogenetic diversity were linearly correlated when common and rare species were weighted equally, but had a logarithmic correlation when species were weighted with their relative abundances. While most shrubland communities were phylogenetically unstructured, the correlation between taxonomic and phylogenetic diversity covaried with phylogenetic relatedness when incorporating relative abundance, but only weakly so in phylogenetically overdispersed communities. When we correlated patterns of taxonomic and phylogenetic diversity with different weightings for common versus rare species, we found an important role for geographic (e.g., longitude, altitude), climatic (temperature, precipitation) and soil factors. The importance of underlying variables varied between

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facets of diversity. We found a strong role for altitude in taxonomic, but less so for phylogenetic diversity. Furthermore, the importance of several environmental drivers varied depending on whether diversity metrics were strongly influenced by rare species or put more weight on common and/or dominant species. Overall, our assessment highlights the importance of synthetic analyses of patterns and processes of different facets of biodiversity to capture the full complexity of diversity in conservation studies.

1. Introduction

The diversity and structure of plant communities are generally influenced by a combination of historical, biogeographic and ecological processes operating at different scales (Gotzenberger et al., 2012; Kraft et al., 2015; Leibold and Chase, 2017; Munkemüller et al., 2014). At the largest scale, evolutionary and biogeographic history shapes the regional species pool (Carstensen et al., 2013), local environmental filters select species into the local species (Weiher et al., 2011), and then biotic interactions determine which and how many species can eventually coexist in a local community (Chesson, 2000). In addition, spatial and stochastic processes, including unpredictable disturbances, dispersal limitation and demographic stochasticity can often influence community assembly (Chase and Myers, 2011; Hubbell, 2001; Tilman, 2004). As a result, the structure of local communities is usually thought to reflect the cumulative effects of these processes (HilleRisLambers et al., 2012).

Comparing the roles of biogeographic and environmental variables in explaining patterns of taxonomic diversity across large gradients can disentangle the relative importance of biogeographic and macroevolutionary processes versus local ecological processes driving the co-occurrence and diversity of species (Belmaker and Jetz, 2015; Keil and Chase, 2019; Ricklefs and He, 2016). Historically, an efficient way to describe community compositions is diversity in terms of the number and abundance of species (Pavoine and Bonsall, 2011). Often overlooked in studies examining large-scale patterns of taxonomic diversity is how species relative abundances vary across space, because the vast majority of analyses at this scale focus only on patterns of species richness. We can measure aspects of diversity that differentially include information about common and rare species using the framework of Hill (1973) numbers and their conversion into an effective number of species (i.e., the number of species that would be present for a given diversity entropy if all species were equally abundant) (Chao et al., 2014a; Hill, 1973; Jost, 2006). Hill numbers allow ecologists to calculate patterns of diversity where a weighting coefficient (q) progressively transitions from species richness, which weights all species equally ($q = 0$), to an effective number of species given Shannon's entropy (common species weighted more than rarer species; $q = 1$) or Simpson's diversity index (dominant species weighted most strongly and rarer species strongly down-weighted; $q = 2$) (Hsieh et al., 2016; Jost, 2006). By comparing measures of diversity that differentially include variation in the relative abundances of species and how they vary through space or time, we can gain greater insights into the potential mechanisms underlying changes in diversity (Blowes et al., 2022; Tuomisto et al., 2014). For example, if species richness shows a strong relationship along an ecological gradient (e.g. temperature or precipitation), whereas diversity measures that weight common species show weaker or non-existent relationships, we can conclude that it was the rarer species in the community that were most strongly affected by the gradient. Alternatively, if measures of species richness and those that include relative abundances strongly covary, we could instead conclude that the ecological gradient affected both common and rare species in a relatively proportional way.

Comparing how other facets of diversity, such as phylogenetic diversity, and how that compare to patterns of taxonomic diversity across broad environmental gradients can help to disentangle large gradients in taxonomic diversity (Devictor et al., 2010; Pavoine and Bonsall, 2011; Swenson, 2011). Phylogenetic diversity can be variously measured (Tucker et al., 2017), but we here focus on phylogenetic diversity

measures that calculate richness by the branch lengths of species in a given community (e.g., Faith, 1992), as well as measures that can be weighted by species commonness and rarity in a similar way as taxonomic diversity (Chao et al., 2010; Chao et al., 2014b). While patterns of phylogenetic co-occurrence of species in a community cannot definitively elucidate filtering or competitive mechanisms (Gerhold et al., 2018; Mayfield and Levine, 2010), it can help us to understand deviations between patterns of taxonomic and phylogenetic diversity. For example, if species in a community are more similar to one another phylogenetically than expected by chance (i.e., clustered), then the increase in phylogenetic diversity with increasing taxonomic diversity will be low (i.e., the correlation coefficient being shallow), whereas if species in a community are more different from one another than expected by chance (i.e., over-dispersed) the increase in phylogenetic diversity will be high relative to the increase in taxonomic diversity (i.e., the correlation coefficient being steep). In either case, the asymmetrical decoupling of taxonomic and phylogenetic diversity facets might lead to different associations of diversity patterns along broad environmental gradients, from which we could infer that macroevolutionary and/or biogeographic processes that influence the phylogenetic structure of local communities play some role underlying patterns along those gradients (Pavoine and Bonsall, 2011; Sandel, 2018). Alternatively, if the relationship between taxonomic diversity and phylogenetic diversity is more symmetrical (i.e., linear correlated), we would expect similar patterns of both biodiversity facets in response to environmental or biogeographic gradients. Importantly, when these diversity metrics incorporate the relative abundances of species, associations between taxonomic and phylogenetic diversity can be strongly influenced by the relative abundances of species in a given community depending on whether more closely or more distantly related species tend to be more similar in their relative abundances (Chao et al., 2014b).

Former studies have demonstrated that the taxonomic diversity of woody plants is strongly correlated with temperature (Qian et al., 2003; Wang et al., 2011). However, the patterns, relationships and environmental determinants of multiple facets diversity of plant communities are still unclear. Here, we take advantage of a standardized survey of 1260 vegetation plots from different types of shrublands across China (The Editorial Committee of Vegetation Map of China, 2007), allowing us to develop an analysis unprecedented in spatial extent comparing multiple facets of diversity along biogeographic and environmental gradients from across China. Based on the extensive survey of shrubland communities, we aim to examine the patterns, and relationships of taxonomic and phylogenetic diversity and co-occurrence (phylogenetic structure) of shrubland communities and the underlying environmental determinants.

2. Materials and methods

2.1. Study site, community inventory, and environmental variables

We implemented an extensive inventory of vegetation communities from Chinese shrublands from 2015 to 2020. Specifically, we selected 1260 plots from across China; shrublands were defined from the Vegetation map of China (The Editorial Committee of Vegetation Map of China, 2007, Fig 1a). Plots were established with a 10 m buffer on each side to ensure it was placed away from any obvious human activities. Within each plot, we sampled shrubs (perennial woody species that are usually less than 5 m tall) in three 5 × 5 m subplots (Fig 1b). In each

subplot, species were identified in the field or collected for subsequent identification in the laboratory, then we recorded their density.

To measure soil properties that could influence community diversity, we collected a 10-cm deep mixed soil sample from five sites in each of the three larger shrub subplots and tested the density of soil organic carbon (SOC), total nitrogen (TN), total phosphorus (TP) and pH (Fig 1b). To measure the environmental properties of each site, we used 19 bioclimatic variables extracted from the WorldClim data set (Fick and Hijmans, 2017). The 19 bioclimatic variables include 11 temperature variables and 8 precipitation variables, representing both annual features (e.g., mean annual temperature, annual precipitation) and monthly/seasonal features (e.g., temperature of the coldest and warmest month, and precipitation of the wet and dry quarters) of precipitation and temperature (see Table S1 in Supporting information for detailed information on environment variables).

For each plot, we computed three types of taxonomic diversity that differentially included relative abundances of species. These are known as ‘Hill numbers qD ’, the most common of which can be derived from a weighting factor, q (Chao et al., 2014a; Hill, 1973; Jost, 2006). When $q = 0$, this corresponds to species richness (all species weighted equally can be interpreted as the effective number of rare species); when $q = 1$, this corresponds to the Shannon entropy (the relative evenness of species incorporated) and can be interpreted as the effective number of common species; when $q = 2$, this corresponds to the Simpson index (the most common species weighted the most) and can be interpreted as the effective number of dominant species (Hsieh et al., 2016). The Shannon and Simpson diversity entropies were converted into an effective number of species (the number of species that would be present if all species were equally abundant) to facilitate statistical comparisons between the measures (Chao et al., 2014a; Jost, 2006). We calculated the taxonomic diversity of different Hill numbers using the R package ‘iNEXT.3D’ (Chao et al., 2021). For comparative purposes, we classified the 1260 communities into five different vegetation types of shrubland (bamboo, deciduous broadleaf, evergreen broadleaf, evergreen needleleaf, and succulent) using the standard vegetation classification in China (Guo et al., 2020).

2.2. Phylogenetic construction, phylogenetic diversity, and structure

Based on the list of species that occurred in the inventory, we constructed a specie-level phylogeny with the branch length using the R

package ‘V.PhyloMaker’, which utilizes a mega-tree as a backbone (Jin and Qian, 2019; R Core Team, 2022). The mega-tree is the largest dated phylogeny available, and includes a combination of a phylogeny (GenBank taxa with a backbone provided by Open Tree of Life version 9.1) for seed plants (Smith and Brown, 2018) and a phylogeny for pteridophytes (Zanne et al., 2014), including more than 74,533 species and all families of extant vascular plants.

Based on the phylogeny we constructed, we can calculate three types of phylogenetic diversity of each plot as outlined by Chao et al. (2010, 2014b, 2021), with similar weighting based on q discussed above for taxonomic diversity ($q = 0$ is phylogenetic richness based on branch lengths, while order $q = 1$ and $q = 2$ wt common and the dominant species by the transformation of phylogenetic entropy and Rao’s quadratic entropy, respectively). We calculated phylogenetic diversity with different Hill numbers using the R package ‘iNEXT.3D’ (Chao et al., 2021).

We also calculated the phylogenetic relatedness (mean nearest taxon distance) of species that co-occurred in each plot. To evaluate the degree of non-random phylogenetic community structure, we constructed null models by randomizing species co-occurrences 1000 times per randomization while maintaining species occurrence frequency and sample species richness (Kembel, 2009). Next, we calculated the nearest taxa index (NTI) to quantify the number of standard deviations that the observed mean nearest taxon distance is from the mean of the null distribution. For a single community, $NTI > 2$ indicates phylogenetic clustering, while $NTI < -2$ indicates phylogenetic overdispersion (Stegen et al., 2012). For a vegetation type, the mean NTI is significantly different from zero indicating clustering ($NTI > 0$) or overdispersion ($NTI < 0$) on average (Kembel, 2009). The phylogenetic community structure was analyzed using the R package ‘picante’ (Kembel et al., 2010).

2.3. Statistical analysis

We used a non-parametric Kruskal-Wallis test to compare the differences in diversities (taxonomic and phylogenetic diversity) and co-occurrence (phylogenetic relatedness) among vegetation types. To test the effects of phylogenetic relatedness on the relationship between taxonomic and phylogenetic diversity, we grouped communities with similar phylogenetic relatedness (i.e., communities with difference in NTI were less than a threshold), and calculated the correlations between

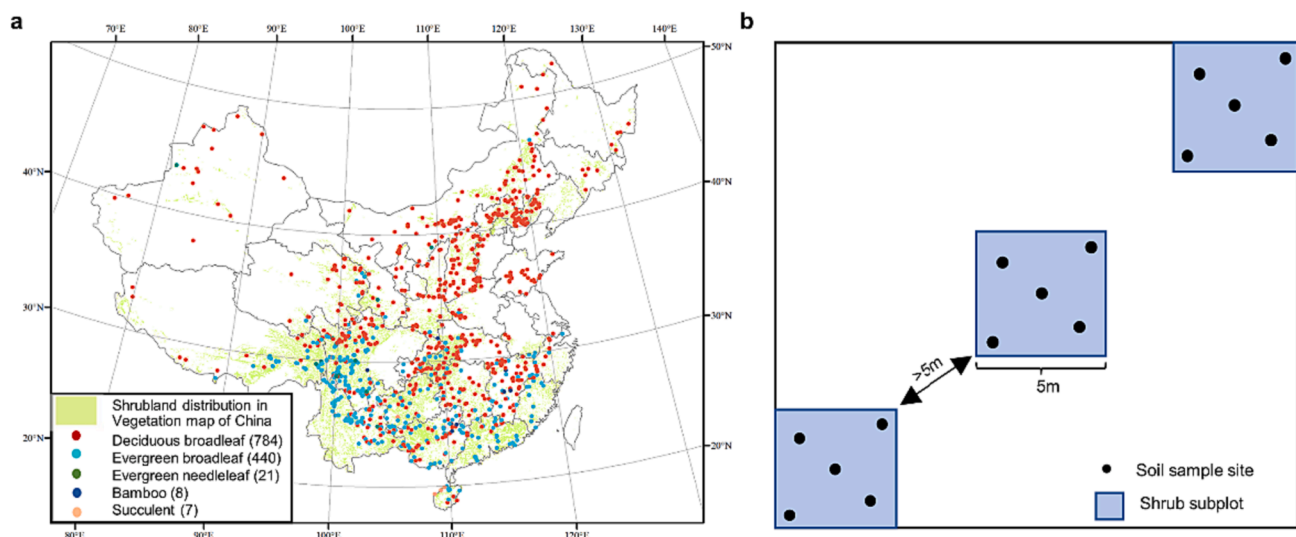


Fig. 1. (a) The spatial distribution of the 1260 study sites along a broad geographic extent of shrubland communities throughout China. The green shading indicates the distribution of shrubland in the Vegetation map of China, and the numbers behind each vegetation type in the legend indicate the number of sample sites of each vegetation type in our inventory. (b) The spatial arrangement of plot and subplots in each study site. Each plot was comprised of three shrub subplots (5 × 5 m). In addition, we took 3 mixed soil samples from each plot as illustrated.

taxonomic and phylogenetic diversity of each group with different Hill numbers using the non-parametric Spearman's rho coefficient. To test the sensitivity of the grouping, we varied the threshold from 0.05 to 0.2. We tested the relationship between taxonomic and phylogenetic diversity and the joint effects of vegetation type with generalized linear models.

To test the environmental effects on patterns of diversities

(taxonomic and phylogenetic diversity) and co-occurrence (phylogenetic relatedness) among the shrubland communities, we implemented a random forest algorithm to determine the importance of the influence of 28 variables related to climate (11 temperature variables and 8 precipitation variables), soil (4 variables), and geography (5 variables). The random forest algorithm is a data-driven ensemble learning model that computes an average over many regression trees, each of which predicts

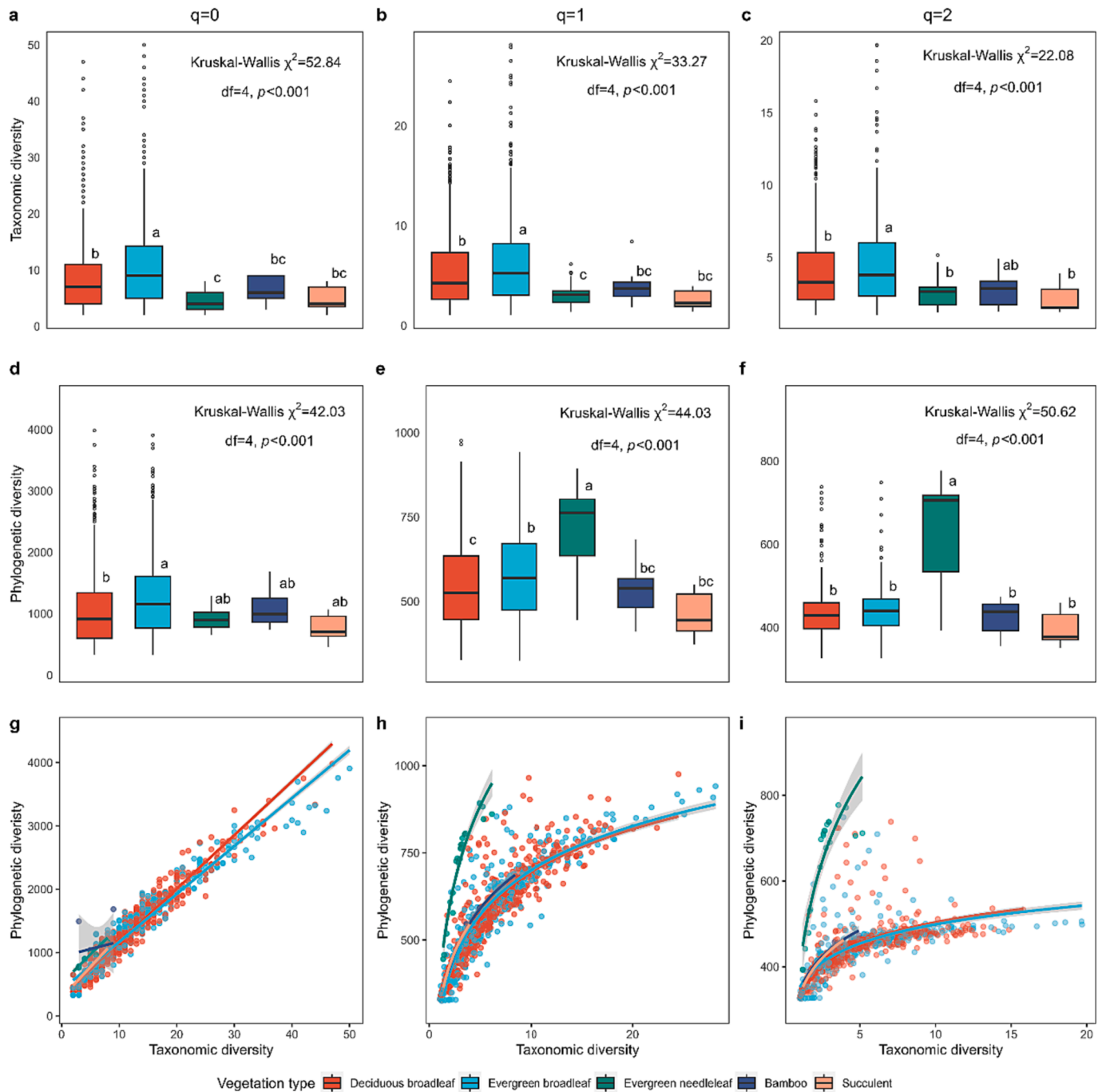


Fig. 2. Comparison of taxonomic diversity, phylogenetic diversity, and relationships between them of five vegetation types of different Hill number q . (a-c) Taxonomic diversity of shrubland communities of five vegetation types for measurements that differentially weight common versus rare species ($q = 0, 1, 2$). (d-f) phylogenetic diversity of shrubland communities of five vegetation types for measurements that differentially weight common versus rare species ($q = 0, 1, 2$). (g-h) the relationships between taxonomic and phylogenetic diversity of five vegetation types of different q . When $q = 0$, linear relationships fit best, while logarithmic relationships fit best when $q = 1$ and 2. In box-whisker plots (a-f), the central mark indicates the median, and the bottom and top edges of the box indicate the 25th and 75th percentiles, respectively. The maximum whisker lengths are 1.5 times the interquartile range and circles represent outliers. Different letters mean significant differences between different vegetation types ($p < 0.001$, non-parametric Kruskal-Wallis test, post-hoc Pairwise Wilcoxon Rank Sum test). The significance of models fitted in (g-i) is provided in Table S2 and Table S3 in Supporting information.

the outcome using a random subset of all the model variables (Breiman, 2001). The algorithm manages highly correlated variables by spreading the importance of the variable across all variables, and has been successfully applied to global analyses (Liang et al., 2016; Steidinger et al., 2019; Yang et al., 2021; Zhong et al., 2021). Prior to running the random forest model, we performed a variable selection procedure based on a preliminary ranking of the predict variables using the random forests permutation-based score of importance followed by a stepwise forward strategy for variable introduction using the R package 'VSURF' (Genuer et al., 2015). We then ran the model to determine the effects of environmental variables on taxonomic diversity, phylogenetic diversity with different Hill numbers, and phylogenetic relatedness of shrub communities. Variable importance was calculated according to the percentage increase in mean squared error (MSE), which quantifies the increase in model error because of shuffling the order of values in the vector of predictors randomly. Moreover, to estimate the significance of the environmental variables, we performed the random forest algorithm by the R package 'rfPermute' (Archer, 2022), which permutes the response variable and generates a null distribution of importance and p-value of observed of each predictor variable. We ran each model using 1000 regression trees, and the response variable was permuted 1000 times. Then we selected significant predictors with a threshold $p < 0.05$.

To test the sensitivity of the random forest models, we performed K-fold cross-validations with the R package 'rfUtilities' (Evans and Murphy, 2018). In the cross-validation, we withheld 10 % of the model training data and ran 99 iterations. In addition, we estimated partial dependence and the direction of the effects of each predictor on the response variables.

3. Results

3.1. Patterns of shrubland diversity

From the 1260 plots we surveyed, we found 102,891 records (individuals) of 1782 shrub species from 445 families. We classified each plot into five different vegetation types based on the dominant species (Fig. 1): deciduous broadleaf (784 plots), evergreen broadleaf (440 plots), evergreen needleleaf (21 plots), bamboo (8 plots), and succulent (7 plots). When we compared total species richness ($q = 0$) among the different categories of shrubland vegetation types, we found that the evergreen broadleaf community type had more species in a given survey plot than the other types (Fig. 2a, Kruskal-Wallis $\chi^2 = 52.84$, $df = 4$, $p < 0.001$). This pattern was similar when incorporating relative abundance for the effective numbers of species for Shannon entropy ($q = 1$, Fig. 2b, Kruskal-Wallis $\chi^2 = 33.27$, $df = 4$, $p < 0.001$) and Simpson diversity ($q = 2$, Fig. 2c, Kruskal-Wallis $\chi^2 = 22.08$, $df = 4$, $p < 0.001$). For the phylogenetic diversity, we found that variation among the five vegetation types was largely similar to that of taxonomic diversity for richness ($q = 0$, Fig. 2d, Kruskal-Wallis $\chi^2 = 42.03$, $df = 4$, $p < 0.001$), but the evergreen needleleaf community had higher phylogenetic diversity when measures placed greater emphasis on common species using Shannon's entropy ($q = 1$, Fig. 2e, Kruskal-Wallis $\chi^2 = 44.03$, $df = 4$, $p < 0.001$) and on the most abundant species using Simpson's diversity ($q = 2$, Fig. 2f, Kruskal-Wallis $\chi^2 = 50.62$, $df = 4$, $p < 0.001$).

Overall, we found that patterns of taxonomic diversity and phylogenetic diversity were highly correlated (Fig. 2 g-i, Table S2 in Supporting information). However, there were differences in the relationships among vegetation types. For example, for richness ($q = 0$), correlations between species diversity and phylogenetic diversity were all similarly positive (slopes significantly different from zero), except for the bamboo community which had no clear relationship (slope not different from zero), (Fig. 2 g, Table S2 in Supporting information). When we compared the coefficient of the slopes, we found that evergreen broadleaf has a lower slope than the others (Fig. 2 g, Table S2, S3 in Supporting information). When we weighted taxonomic diversity and

phylogenetic diversity for relative abundances ($q = 1$ and $q = 2$), we found that the relationship between taxonomic and phylogenetic diversity became logarithmic (Fig. 2 h, i). There was also an important variation in the slopes of the relationship among vegetation types (Fig. 2 h, i, Table S2, S3 in Supporting information). Specifically, for both $q = 1$ and $q = 2$, the relationship between taxonomic and phylogenetic diversity was steepest in the evergreen needleleaf communities, while the relationships of the other four vegetation types were similar to each other.

3.2. Phylogenetic relatedness and its effects on community diversity

We found that the NTI of most shrubland communities was distributed between -2 and 2 , suggesting that there was no significant structure (clustering or overdispersion) among co-occurring species in a given plot (Fig. 3a). However, a small subset of the individual plots (16 out of 1260 communities) was significantly phylogenetic over-dispersed ($NTI < -2$), while another subset (60 out of 1260 communities) was significantly clustered ($NTI > 2$). Moreover, significant variation in the phylogenetic relatedness occurred among the five vegetation types (Fig. 3a). For example, even though they were not significantly over-dispersed ($NTI < -2$), bamboo communities had lower phylogenetic relatedness than deciduous and evergreen broadleaf communities. Furthermore, the majority of the plots in the evergreen needleleaf communities had an $NTI < -2$, suggesting phylogenetic overdispersion in this vegetation type (Fig. 3a).

While no clear relationship between phylogenetic relatedness and diversity metrics was detected, however, we found that the correlations between taxonomic and phylogenetic diversity of shrubland communities varied with phylogenetic relatedness of species within a community (Fig. 3b, Fig. S1, S2 in Supporting information). Specifically, the correlation between taxonomic and phylogenetic diversity was close to 1 when $q = 0$, regardless of the phylogenetic relatedness. However, when incorporating relative abundance ($q = 1$, $q = 2$), correlations between taxonomic and phylogenetic diversity increased with phylogenetic relatedness. For example, the correlations between taxonomic and phylogenetic diversity in communities with lower phylogenetic relatedness were weaker than when $q = 0$, especially when $q = 2$. Deviations in correlations among different q decreased in communities with higher phylogenetic relatedness, where correlation between taxonomic and phylogenetic diversity generally with greater values of all q .

3.3. Environmental determinants

We found that all 28 variables were relevant for the interpretation of response variables (Fig. S3, Fig. S4 in Supporting information), and so we used the random forests model to estimate the significance of the 28 environmental variables on the 7 response variables. With the random forests model, we found that for taxonomic diversity (Fig. 3a-c), phylogenetic diversity (Fig. 3d-f) and phylogenetic relatedness (Fig. 3 g), geographical (e.g., altitude and longitude) and climatic factors (e.g., temperature and precipitation) were among the most important predictors, with soil variables also playing a role in determining taxonomic and phylogenetic diversity. However, the relative importance of the different driver variables changed across biodiversity facets (taxonomic versus phylogenetic) and with different weighting for common and rare species through Hill numbers ($q = 0, 1, 2$).

For taxonomic diversity, we found important roles for geography (e.g., latitude, longitude, altitude), local soil conditions (total nitrogen, carbon), and several aspects of precipitation and temperature for all three aspects of taxonomic diversity. However, several more factors, especially those involving climate variables (temperature and precipitation), played a role in affecting taxonomic diversity when $q > 0$. For example, seasonal/monthly features of precipitation (e.g., light blue bars in Fig. 4a-c) have significant effects on patterns of taxonomic diversity of all q , but annual precipitation (AP, dark blue bar in Fig. 4a-c)

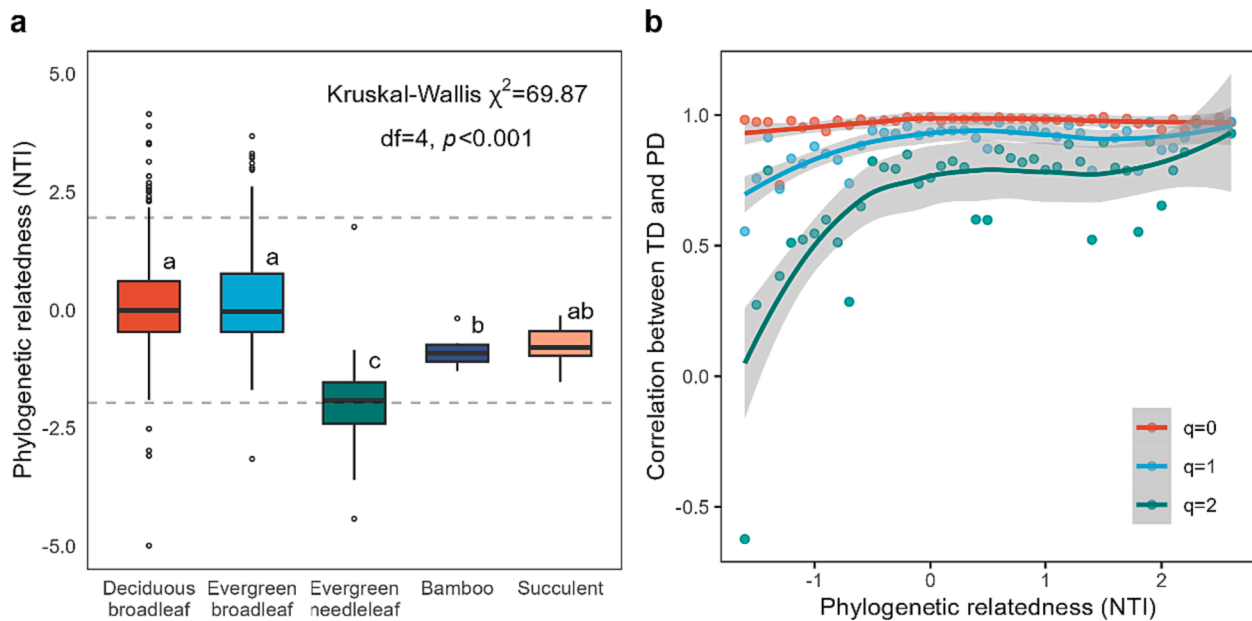


Fig. 3. (a) The phylogenetic relatedness of shrubland communities in the five vegetation types. Dashed lines indicated the thresholds of clustering (>2 for single community and >0 for vegetation type) or overdispersion (<-2 for single community and <0 for vegetation). Different letters indicate significant differences between vegetation types ($p < 0.001$, non-parametric Kruskal-Wallis test, post-hoc Pairwise Wilcoxon Rank Sum test). (b) The effects of phylogenetic relatedness on the correlations between taxonomic diversity (TD) and phylogenetic diversity (PD) of different q . Correlations between taxonomic and phylogenetic diversity were calculated using non-parametric Spearman's rho. The relationship between the correlation coefficient and phylogenetic relatedness (NTI) was fit by local polynomial regression.

played a role only when incorporating relative abundance ($q > 0$). Likewise, seasonal features of temperature (e.g., TDR, Isoth and orange bars in Fig. 4a–c) influenced the patterns of taxonomic diversity for all q , but annual temperature (e.g., AMT) was significant only when $q > 0$. This suggests that climate in particular had a strong influence on the commonness and rarity of species.

For phylogenetic diversity, patterns of significant factors in each category (geography, soil and climate) were largely similar to that of taxonomic diversity when $q = 0$ (Fig. 4a, d). Interestingly, however, altitude, which played one of the strongest roles in determining taxonomic diversity played little role in determining phylogenetic diversity when $q = 0$. This suggests that the influence of altitude on diversity is via phylogenetically similar species. In addition, there were overall more predictors associated with phylogenetic diversity than taxonomic diversity, many of which were associated with temperature. As with taxonomic diversity, there were more variables of each type that explained patterns of phylogenetic diversity when $q = 1$. However, when the most dominant species were weighted more heavily ($q = 2$), there were many fewer of each variable type playing an important role (Fig. 4f).

When we used the phylogenetic relatedness of species within a community (nearest taxa index) as an indicator of the difference between species richness and phylogenetic richness, we found a few key variables were associated with variation in this parameter (Fig. 4g). Notably, none of the soil variables appeared to be important in explaining the NTI, although several precipitation variables and one climate variable were important. This result also confirmed the important difference between taxonomic and phylogenetic diversity responses to altitude, as this variable was also important in explaining the differences in NTI.

4. Discussion

Previous studies related to biodiversity generally focused on one dimension of the diversity of rare species (i.e., species richness). However, an accurate definition of biodiversity should jointly address the

diversity dimensions due to their intrinsic correlation. Our study on 1260 shrubland plots from across the extent of China allowed us to develop a series of analyses on patterns of both taxonomic and phylogenetic diversity that weight common and rare species differently. In shrubland communities, significant correlations were detected between taxonomic and phylogenetic diversity due to phylogenetic relatedness, but associated environmental variables were varied. In addition, longitude and soil total nitrogen impact all facets of shrubland diversity, but species with different abundance correlate to different environmental features. Common and dominant species were associated more with annual environmental features (e.g., annual precipitation, annual mean temperature) while rare species were associated more with seasonal environmental features (e.g., Max Temperature of Warmest Month). Overall, our results provide insights into the patterns and potential environmental drivers of diversity of shrubland communities across broad spatial extents.

4.1. Multi-facets diversity associated species abundance

Overall, both species richness and phylogenetic richness ($q = 0$) were highest in the evergreen broadleaf vegetation type compared to the other vegetation types. This community is dominated by the evergreen broadleaf species, but also contains deciduous species. We suspect that a likely reason for the higher number of species in this community type is that it is generally found in lower-latitude areas (Tang, 2015). Indeed, the strong negative association of both taxonomic and phylogenetic richness that we found with latitude supports this idea. The bamboo community type was the only one that showed no strong correlation between taxonomic and phylogenetic richness ($q = 0$). Although most bamboo communities have higher phylogenetic diversity and lower phylogenetic relatedness, some had a large number of species from a single taxonomic group (bamboo), which resulted in greater taxonomic diversity but lower phylogenetic diversity. When common species were weighted more than rarer species ($q = 1$, $q = 2$), the patterns for taxonomic diversity among the different vegetation types remained largely the same. However, the pattern switched for phylogenetic diversity and

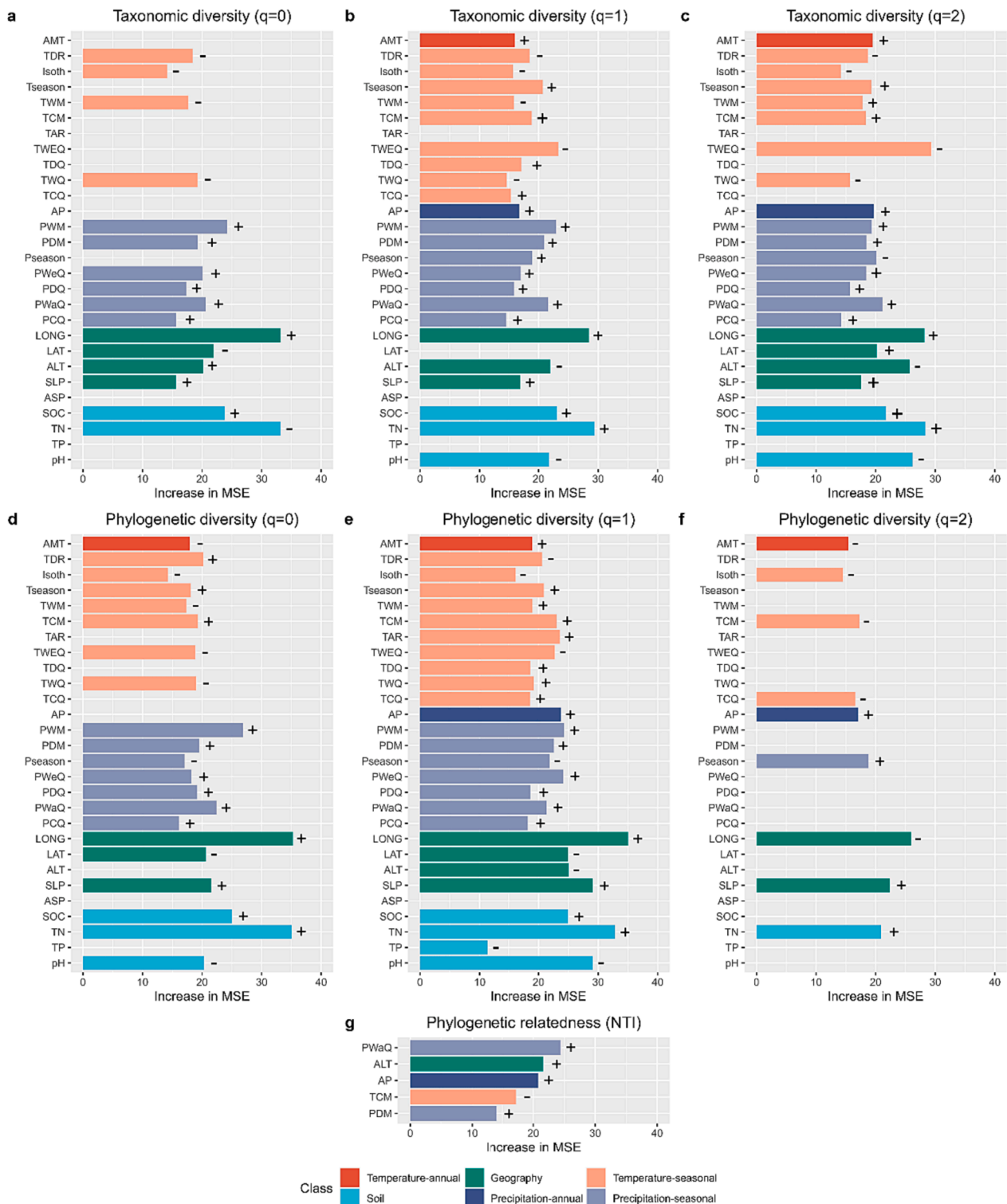


Fig. 4. Significant environmental variables and their importance to community structure (a-c: taxonomic diversity with different Hill numbers; d-f: phylogenetic diversity with different Hill numbers; g: phylogenetic relatedness). For comparison between different Hill numbers and diversity facets, in a-f, variable was ranked in terms of the class of environmental variables: **Temperature-annual**: AMT, Annual Mean Temperature; **Temperature-annual**: TDR, Mean Diurnal Range; Isoth, Isothermality (TDR/TCM) (*100); Tseason, Temperature Seasonality (standard deviation *100); TWM, Max Temperature of Warmest Month; TCM, Min Temperature of Coldest Month; TAR, Temperature Annual Range (TWM-TCM); TWEQ, Mean Temperature of Wettest Quarter; TDQ, Mean Temperature of Driest Quarter; TWQ, Mean Temperature of Warmest Quarter; TCQ, Mean Temperature of Coldest Quarter; **Precipitation-annual**: AP, Annual Precipitation; **Precipitation-seasonal**: PWM, Precipitation of Wettest Month; PDM, Precipitation of Driest Month; Pseason, Precipitation Seasonality (Coefficient of Variation); PWeQ, Precipitation of Wettest Quarter; PDQ, Precipitation of Driest Quarter; PWaQ, Precipitation of Warmest Quarter; PCQ, Precipitation of Coldest Quarter; **Geography**: LAT, Latitude; LONG, longitude; ALT, Altitude; ASP, Aspect; SLP, Slope; **Soil**: SOC, Soil Organic Carbon; TN, Total Nitrogen of Soil; TP, Total Phosphorus of Soil; pH, Soil pH. In g, variables were ranked in terms of the variable importance (increase in MSE). +/- in the bar plot indicates the positive/negative effect of predictors on the response variables. The partial dependence for all predict variables of each model was provided in Fig. S5 in Supporting information.

the evergreen needleleaf community became more diverse, indicating that common and dominant species in those communities had a greater branch length than rare species.

4.2. Phylogenetic pattern explains relationship between multi-facet diversities

When analyzing patterns of co-occurrences of species using the NTI, we found that only the evergreen needleleaf community had significant structuring, tending towards over-dispersion. This community type is generally distributed in cooler sites at higher altitudes and latitudes. One possible reason for its overdispersion could be if interspecific interactions between close relatives are particularly strong in regulating community assembly in the cooler regions where this habitat type occurs. Besides, the majority of communities were phylogenetically unstructured. Such null outcomes of phylogenetic structuring are commonly observed in natural communities (Anderson et al., 2011; Godoy et al., 2014), despite some theoretical expectations to the contrary. There are several potential reasons for this result. First, neutral processes and/or a balance of competition and environmental filtering would lead to no phylogenetic structure in a community (Kembel, 2009). Second, different competitive mechanisms influencing species coexistence can lead to more, or less, phylogenetically similar species than expected by chance (Mayfield and Levine, 2010). The combination of these factors would result in a null effect. Third, species that were abundant in a community might respond to different assembly processes than rare species, and by combining both groups of species, any phylogenetic signal could be obscured (Arnillas et al., 2021).

On average, when $q = 0$, common and rare species were weighted equally, we found that taxonomic and phylogenetic diversity were linearly correlated, although there was some variation among vegetation types. This positive relationship might result from the ancient speciation events (long terminal branches) and relatively evenly distributed branch lengths across clades (Cadotte et al., 2010; Tucker and Cadotte, 2013). However, when incorporating relative abundance ($q = 1, q = 2$), the measurement of phylogenetic diversity is sensitive to the topology of the regional phylogenetic tree, which leads to a disproportionate variation in phylogenetic diversity (Chao et al., 2010; Pavoine and Bonsall, 2011; Tucker and Cadotte, 2013). Relatively few, but more common species contribute more to patterns of diversity (Heegaard et al., 2013; Lennon et al., 2004). As a result, few species with frequent lineages can have greater phylogenetic diversity, which caused our observed logarithmic relationship between taxonomic and phylogenetic diversity. The evergreen needleleaf community deviated the most from the other vegetation types in this relationship, having the steepest slope. This was the community that was also the most phylogenetically over-dispersed, leading to a much steeper slope in the relationship between taxonomic and phylogenetic diversity when common species are weighted more heavily (Tucker et al., 2017; Webb et al., 2002). In phylogenetically more over-dispersed communities, phylogenetic diversity of common species varied disproportionately to taxonomic diversity, which caused a weak correlation between them. Therefore, the strength of the correlation between taxonomic and phylogenetic diversity of common species covaried with phylogenetic relatedness. Index of species diversity can be adapted, to measure phylogenetic diversity (Pavoine and Ricotta, 2019), while it could be more reliable in phylogenetically related communities.

4.3. Environmental drivers of community structure

When we examined geographical and environmental factors correlated with both taxonomic and phylogenetic diversity across different weightings of common versus rare species ($q = 0, q = 1, q = 2$), we found several important patterns. In all cases, we found important evidence for geographic, soil and climate-related factors in underlying patterns of diversity. In a few cases, the important variables were consistent across biodiversity facets and metrics that differentially weight common

species (e.g., longitude, total nitrogen in the soil), suggesting these variables might have an overriding importance underlying diversity measure. In other cases, the importance of underlying variables strongly flip-flopped between biodiversity metrics and different abundance weighting, emphasizing the nuance that can often emerge in biodiversity patterns along broad gradients, but also allowing a deeper consideration of the reasons underlying that nuance.

Firstly, we found that the longitude of the site was consistently ranked in the top two variables explaining patterns of every measure of diversity we analyzed. A likely reason for the different structuring roles of longitude underlying patterns of diversity is the difference in characteristics of floras between eastern and western China (Lu et al., 2018). The flora in eastern China shows higher diversity than in western China, and consequently, both taxonomic and phylogenetic diversity of shrubland positively correlated with longitude. This suggests that, at least in part, historical biogeography plays a role in underlying patterns of shrubland biodiversity across the broad geographic extent of China.

Second, we found that total nitrogen in the soil was also among the most important explanatory variables for every diversity metric we analyzed, while soil carbon was strongly associated with most measures of diversity (other than phylogenetic diversity when $q = 2$). Specifically, patterns of diversity typically increased with increasing soil fertility, which could be related to the ability of more species of plants to partition resources with higher availability, stronger plant-soil feedbacks enhancing coexistence, and/or with higher microsite heterogeneity in nutrients with higher total soil nutrient s (Reynolds and Haubensak, 2009; Tilman and Pacala, 1993). Indeed, plant diversity is known to increase along spatial gradients of increasing soil fertility in many parts of the world (Homeier et al., 2010; Laurance et al., 2010), even though anthropogenic nitrogen deposition can lead to losses of species at a given site (Simkin et al., 2016; Staudé et al., 2020). Other variables associated with at least some aspects of diversity also likely influence soil nutrient availability, such as temperature and precipitation and their associations with geography (e.g., altitude, latitude), also influence microbial processes that regulate plant nutrient supply from the soil (Sundqvist et al., 2013).

Third, we found that aspects of climate, including precipitation (e.g., PWM) and temperature (e.g., Isothermality) were associated with almost all diversity metrics, again except phylogenetic diversity when weighted towards the most common species ($q = 2$). Both temperature and precipitation are well known to influence multiple patterns of diversity (Francis and Currie, 2003; Keil and Chase, 2019; O'Brien et al., 2000), primarily through a combination of increasing energy and resource availability, as well as the total numbers of individuals, which can allow more species to coexist locally via both deterministic and stochastic means (Evans et al., 2005; Hawkins et al., 2003; Simova et al., 2011).

Although we found a few key variables associated with geography (longitude), soil (total nitrogen and carbon) and climate (PWM and Isothermality) played an important role in most diversity metrics, other variables had a more nuanced relationship with variation in diversity. For example, by comparing patterns of taxonomic diversity with different weighting, we found that metrics that were more strongly influenced by the presence of rarer species in the community (i.e., $q = 0$) tended to be more associated with seasonal/monthly climate patterns, whereas those of more common species (when $q = 1, q = 2$) were more associated with annual features of climate (e.g. annual mean temperature and precipitation). A possible reason for the discrepancy in the response of common and rare species to environmental factors is that rare species can be more sensitive to fluctuations in environmental conditions (Liu and van Kleunen, 2017). In addition, several features of temperature variation were associated with diversity measures that weighted common species more, possibly due to the important role of temperature variation in influencing the distributional range and abundance of species (Steinbauer et al., 2018; Wang et al., 2009).

By comparing patterns of phylogenetic diversity and its correlates

with those of taxonomic diversity, we were able to identify important deviations that could help to identify possible mechanisms underlying the patterns. For example, altitude was an important factor underlying variation in taxonomic diversity for all weightings of common and rare species, as has been shown previously in China (Wang et al., 2011). However, altitude played no significant role in underlying variation in phylogenetic diversity for $q = 0$ and $q = 2$. One possible reason for this discrepancy in the explanatory power of altitude for taxonomic versus phylogenetic diversity could be if patterns of taxonomic diversity with altitude were underlain by species that are phylogenetically similar (i.e., species replacements from among closely related species along an altitudinal gradient) (Humphries et al., 2017).

Based on a dataset derived from an extensive survey of shrubland communities spanning a large geographical extent, our results highlight the importance of considering multiple facets of diversity (i.e., taxonomic and phylogenetic) as well as multiple weightings of common versus rare species (i.e., Hill Numbers) in order to gain a deeper understanding of the patterns, and potential processes, influencing broad biodiversity gradients. Nevertheless, further work is needed to fully understand the mechanisms driving biodiversity. For example, future analyses can include trait information in addition to phylogenetic information, and more deeply consider the roles of the phylogeography of the underlying species. In addition, as global change continues to alter vegetation communities and their interactions, the next challenge will be to integrate eco-evolutionary feedback more explicitly into biodiversity studies. Despite this, our results that incorporate multiple diversity measures, multiple potential drivers and large spatial extents provide a step advance for our understanding of biodiversity patterns and their underlying variation that has not been detected previously. Such information will be essential as we continue to develop a more nuanced perspective of the patterns, and drivers, of different facets of biodiversity and the role of these measures to capture the full complexity of diversity in conservation studies.

CRedit authorship contribution statement

Dongdong Chen: Conceptualization, Data curation, Formal analysis, Funding acquisition, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Li Li:** Conceptualization, Data curation, Formal analysis, Investigation, Writing – review & editing. **Jonathan M. Chase:** Conceptualization, Methodology, Writing – original draft, Writing – review & editing. **Jun Hu:** Data curation, Investigation. **Huajun Yin:** Data curation, Investigation. **Chunzhang Zhao:** Conceptualization, Data curation, Investigation, Methodology. **Guozhen Shen:** Data curation, Investigation. **Chengyang Zheng:** Data curation, Investigation. **Ting Li:** Data curation, Investigation. **Xinying Cheng:** Conceptualization, Data curation, Investigation. **Wenhong Ma:** Data curation, Investigation. **Weihua Guo:** Data curation, Investigation. **Feng Zhang:** Data curation, Investigation. **GuoYing Zhou:** Data curation, Investigation. **Lin Zhang:** Data curation, Investigation. **Anwar Mohammad:** Data curation, Investigation. **Yunxiang Li:** Data curation, Investigation. **Gaoming Xiong:** Data curation, Investigation. **Xiao Liu:** Data curation, Investigation. **Hede Gong:** Data curation, Investigation. **Fangqing Chen:** Data curation, Investigation. **Yuelin Li:** Data curation, Investigation. **Yaozhan Xu:** Data curation, Investigation. **Xiaocheng Yang:** Data curation, Investigation. **Xinrong Liao:** Conceptualization, Data curation, Investigation. **Xin Huang:** Data curation, Investigation. **Qiurong Liu:** Data curation, Investigation. **Yao Luo:** Data curation, Investigation. **Qing Liu:** Data curation, Investigation.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Qing Liu reports financial support was provided by Special Foundation for National Science and Technology Basic Research Program of China.

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Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2024.111559>.

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