Ecological uniqueness of species assemblages and their determinants in forest communities

Jie Yao¹,² | Jihong Huang¹,² | Yi Ding¹,² | Yue Xu¹,² | Han Xu³ | Runguo Zang¹,²

¹Institute of Forest Ecology, Environment and Nature Conservation, Chinese Academy of Forestry, Key Laboratory of Forest Ecology and Environment of National Forestry and Grassland Administration, Beijing, China
²Co-Innovation Center for Sustainable Forestry in Southern China, Nanjing Forestry University, Nanjing, China
³Research Institute of Tropical Forestry, Chinese Academy of Forestry, Guangzhou, China

Correspondence
Runguo Zang, Institute of Forest Ecology, Environment and Nature Conservation, Key Laboratory of Forest Ecology and Environment of National Forestry and Grassland Administration, Beijing 100091, China
Email: zangrung@caf.ac.cn

Abstract

Aim: Beta diversity can be partitioned into the contributions of individual sampling units to overall beta diversity, which are comparative indicators of the ecological uniqueness of species assemblages in the sampling units. Yet, what determines ecological uniqueness has rarely been examined. Here, we investigated the determinants of ecological uniqueness in species assemblages in forest communities.

Location: China.

Methods: We used tree census data, combined with spatially explicit environmental variables collected from forest dynamics plots across tropical, subtropical and temperate forests in China. We computed beta diversity as the total variation of the community data, and a site-based approach was used to determine whether ecological uniqueness is related to local environmental conditions and/or community characteristics.

Results: Ecological uniqueness was explained by both local environment and community characteristics, but their relative importance varied across the four forest types. We provide direct evidence that the relationship between ecological uniqueness and species richness (EUSRR) is related to the percentage of rare species in the community. Local environmental factors affecting ecological uniqueness and beta diversity were inconsistent, indicating that focusing simultaneously on beta diversity and ecological uniqueness with regard to local environmental conditions is likely to be the appropriate approach to study forest community assembly.

Main conclusions: Although the EUSRR was negative in some cases, indicating high species richness, this does not necessarily imply high ecological uniqueness. Thus, for biological conservation, species-rich sites and unique low-richness sites should be valued more. The higher degree of ecological uniqueness indicates unique species compositions, which provides insight into finding such quadrats and taking measures for protection, restoration or management. We propose that focusing simultaneously on the beta diversity, species richness and ecological uniqueness of individual quadrats is likely to be a valuable approach for biodiversity conservation programmes.

[Correction added on 10 January 2022, after first online publication: first affiliation and correspondence section have been corrected in this version.]
Understanding the mechanisms that determine the spatial distribution of species and species diversity is a central theme in ecology (Chave, 2004; Chesson, 2000; Hutchinson, 1961; Ricklefs, 1990). For community ecologists, the interest to investigate beta diversity is that it can provide fundamental insights into the processes that determine the spatial patterns of species assemblages (Legendre & De Cáceres, 2013; Myers et al., 2013). Legendre and De Cáceres (2013) suggested that the total beta diversity can be partitioned into local contributions to beta diversity (LCBD), which are comparative indicators of the ecological uniqueness of species assemblages in sampling units (hereafter abbreviated as ecological uniqueness). Calculations of LCBD are suitable for quantifying which sites contribute more (or less) to beta diversity than the mean and, thereby, for evaluating the ecological uniqueness of species assemblages at each site in a community (Sor et al., 2018).

A high degree of ecological uniqueness (i.e. high LCBD values) may also be linked to unusual habitat conditions and the presence of newcomers or exotic species (Vilmi et al., 2017). Previous studies have indicated that biodiversity conservation programmes that apply this practical and heuristic approach show a high potential for better planning and monitoring to achieve their conservation goals (Legendre & De Cáceres, 2013; Legendre & Gauthier, 2014; Tonkin et al., 2016; Vilmi et al., 2017).

Some recent studies have applied LCBD approaches to partition total beta diversity. The majority of existing studies, however, mainly focus on freshwater ecosystems and the organisms therein, such as stream insects (Heino & Grönnroos, 2017), urban pond insects (Heino et al., 2017), fish in flood-pulse systems (Kong et al., 2017), lake zooplankton (Lopes et al., 2014), organisms in bomb crater ponds (Vad et al., 2017) and diatoms in streams and lakes (Vilmi et al., 2017). Very few studies have focused on other organisms and ecological systems (e.g. forest ecosystems; Legendre & Gauthier, 2014; Qiao et al., 2015; Yao et al., 2019). Validating the applicability of their findings in an ecosystem other than an aquatic one will indeed be welcome. Moreover, studies that investigate general patterns with regard to ecological uniqueness and their determinants in different ecosystems and organism groups are urgently needed.

Patterns in ecological uniqueness can be correlated with the local environmental conditions at sampling sites (e.g. characteristics of the topography and soil); thus, they can be examined using site-based approaches (Heino & Grönnroos, 2017; Legendre & De Cáceres, 2013). The relationships between ecological uniqueness and local environmental conditions have previously been studied in different ecosystems and have yielded unclear results. Sor et al. (2018) and da Silva et al. (2018) found that variations in ecological uniqueness are well-explained by local environmental variables in macroinvertebrate and dung beetle communities, respectively, whereas Heino and Grönnroos (2017) and Tonkin et al. (2016) found that ecological uniqueness is weakly related to environmental factors in stream invertebrate assemblages. In forest ecosystems, the relationship between the ecological uniqueness of species assemblages and the local environmental conditions has not been fully verified, and relevant results are quite scarce (but see Legendre & Gauthier, 2014; Qiao et al., 2015). Previous studies have shown that community characteristics (e.g. species richness, abundance and the basal area of each quadrat) also affect ecological uniqueness (da Silva et al., 2018; Sor et al., 2018; Vilmi et al., 2017). In particular, the relationship between ecological uniqueness and species richness is of great significance for biodiversity conservation or restoration (Legendre & De Cáceres, 2013). Similarly, there is a lack of consensus on the relationship between ecological uniqueness and species richness. Existing studies have shown that the ecological uniqueness–species richness relationship (EUSRR) can be negative (e.g. Heino et al., 2017; Legendre & De Cáceres, 2013; da Silva et al., 2018) or positive (e.g. Kong et al., 2017). It is assumed that the proportions of rare and common species in the assemblages may determine the degree to which the EUSRR is negative, positive or non-significant (da Silva et al., 2018). A negative EUSRR seems to occur when the proportion of common species is dominant, whereas it is positive when rare species are dominant in a community (Qiao et al., 2015; da Silva et al., 2018). Moreover, the generality of the EUSRR needs to be further verified in other ecosystems and organism groups (e.g. forest ecosystems). However, regardless of whether the EUSRR is positive or negative, the degree of ecological uniqueness may relate to species-rich or species-poor sites. Hence, linking environmental characteristics to sites with high ecological uniqueness may help identify which type of environment should be given more attention from a conservation context (Legendre & Gauthier, 2014; da Silva et al., 2018).

The forest dynamics plots (FDPs) in the present study include the tropical rainforests in southern China, subtropical evergreen and deciduous broadleaved mixed forests in central China, warm temperate deciduous forests found along the geographical dividing line between North and South China and temperate coniferous forests in north-western China. Here, we investigate the patterns of ecological uniqueness in species assemblages as well as their determinants, and test whether these patterns vary across tropical, subtropical and temperate forests. Specifically, the aim of this study was to test whether the degree of ecological uniqueness in species assemblages can be predicted by community characteristics and/or local environmental conditions. Additionally, we provided insight into whether the local environmental factors that affect ecological uniqueness can be linked to the factors that affect the variations in species composition (i.e. beta diversity).
Study areas and FDPs

The study was conducted in four 6-ha FDPs, which we refer to as Hnjfl, Hbmlz, Gsxl, and Xjk FDPs across tropical, subtropical and temperate forests. The Hnjfl FDP is located in the Jianfengling National Nature Reserve (18°23′–18°50′N, 108°36′–109°05′E) in the southwestern region of Hainan Island, China. A 60-ha (1,000 × 600 m) FDP within a vast area of continuous old-growth tropical montane rainforest (TMRF) in the core area of the reserve was established from March 2009 to November 2012 (Xu et al., 2015; Zang et al., 2019). In the present study, we used data collected from a continuous 6-ha (300 × 200 m) area (i.e., the Hnjfl FDP) in the north-western corner of the 60-ha FDP. The Hbmlz FDP (300 × 200 m) is located in the Mullinzi National Nature Reserve, southwest Hubei Province, Central China (29°55′59″–30°10′47″N, 110°17′58″E), which represents an old-growth subtropical evergreen and deciduous broadleaf mixed forest (SEDBMF, Feng et al., 2018). The Gsxl FDP is located in the Xiaolong Mountain National Nature Reserve (33°35′12″–33°45′11″N, 106°13′10″–106°33′06″E) in the west of Qinling Mountain, south-eastern Gansu Province, China, and it represents an old-growth warm temperate deciduous forest (WTDF). The Xjk FDP (300 × 200 m) is located in the western Tianshan Mountain National Natural Reserve (43°03′–43°15′N, 82°51′–83°06′E), Xinjiang Uygur Autonomous Region, north-western China, within an old-growth temperate coniferous forest (TCF, Ding et al., 2019). The forest represents the most well-conserved spruce forest in north-western China (Zang et al., 2011).

Experimental design and data collection

All the FDPs in the present study were established according to the standards set by the Centre for Tropical Forest Science (http://www.ctfs.si.edu/), the main features of which are summarized in Table 1. A census methodology was identical for all FDPs: all woody stems with a diameter at breast height (dbh) of 1 cm or larger were spatially mapped, measured and identified to the species level, and tagged. Each FDP was divided into 150 (20 m × 20 m) subplots, hereafter called quadrats. Data on specific topographic and soil variables were also collected for each quadrat. Four topographic variables (mean elevation, convexity, slope and aspect) were calculated for each quadrat following the recommendation of Harms et al. (2001) and Yamakura et al. (1995). In brief, the mean elevation is the mean elevation value at the four corners of each subplot. The slope is the mean inclination angle of the four triangular planes composed of any three quadrat corners. The slope aspect was from 0° to 360°, measured in degrees from north, indicating the azimuth. The convexity was calculated as the mean elevation of the focal quadrat minus the mean elevation of its eight surrounding quadrats (Ding et al., 2019). At the central point of each subplot, a soil sample (0–20 cm in depth) was collected. The soil samples were air-dried and transported to the soil laboratory for chemical analysis. Six soil environmental and nutrient variables, including soil pH, the amount of organic matter (OM) and their total amounts, as well as the available amounts of nitrogen (N) and phosphorus (P), were measured.

2.3 Statistical analyses

2.3.1 Beta diversity and the ecological uniqueness of species assemblages

We applied the index proposed by Legendre et al. (2005) and Legendre and De Cáceres (2013) to compute beta diversity (\(BD_{\text{total}}\)) as the variance of the community data (i.e. variation in species composition among all quadrats within each FDP):

\[
BD_{\text{total}} = \text{Var} (Y) = SS (Y) / (n - 1)
\]

where \(Y = [y_{ij}]_{n×p}\) is the Hellinger transformed cell-by-species data table (each \(y_{ij}\) element represents the number of individuals of species \(j\) in quadrat \(i\)). The total sum of squares, \(SS(Y)\), is the sum of all species and
all quadrats of the squared deviations from the species means. $n$ is the number of quadrats. Following Legendre and De Cáceres (2013), the local contributions to beta diversity of a sampling unit $i$ (LCBD$_i$) represent the relative contributions of that sampling unit to the total beta diversity. LCBD$_i$ indicates how exceptional the composition of site $i$ is compared with the centroid of all points, which would represent a theoretical site with the average species composition of all the sampling units (Yao et al., 2019). The ecological uniqueness of each quadrat $i$ (LCBD$_i$) in terms of community composition can be calculated as:

$$\text{LCBD}_i = \sum_{j=1}^{p} \frac{s_{ij}}{SS(Y)}$$

where $s_{ij}$ is the square of the difference between the $y_{ij}$ value and the mean value of the corresponding $j$th species; the LCBD indices are scaled to add up to one. We used the function ‘beta.div’ in the adespatial R package (Dray et al., 2018), available on CRAN (https://CRAN.R-project.org/package=adespatial), to calculate the BD$_{Total}$ and LCBD indices. LCBD indices can be tested for significance using the same function and R package (Legendre & De Cáceres, 2013).

### 2.3.2 Predictors of ecological uniqueness in species assemblages

To determine whether the ecological uniqueness of species assemblages in quadrats is related to local environmental conditions, or results from community characteristics, we modelled the degree of ecological uniqueness (i.e. LCBD indices) as a function of local environmental variables (i.e. topographic and soil variables) and community characteristics (i.e. species richness, abundance, and
total basal area), using beta regression with the logit link function (Cribari-Neto & Zeileis, 2010). We implemented the best-subset selection for beta regression based on genetic algorithms using the function ‘kofnGA’ in the package [kofnGA] (Wolters, 2015). For all continuous explanatory variables, the values were $z$-transformed by subtracting the mean value of the variable (across all 150 quadrats) and then dividing by one standard deviation. This allows for a direct comparison of the effect of explanatory variables (Gelman & Hill, 2006). Finally, to explore whether the proportions of rare species in the assemblages determined the EUSR, we first calculated the Spearman rank correlation coefficient to measure the EUSR. Then, the relationship between the Spearman rank correlation coefficient and the percentage of rare species (%) was investigated. Here, we defined rarity using species occupancy (i.e. the number of quadrats within which a species occurred). Following De Cáceres et al. (2012), we defined the percentage of rare species (%) as the proportion of species occurring in fewer than 40% of the 20 m × 20 m quadrats.

We conducted an additional analysis to identify the factors driving the observed variation in species composition (i.e. beta diversity), as shown in the Supporting Information. To test whether the local environmental factors that affected ecological uniqueness were necessarily linked to factors that affected the variation in species composition, the individual contributions of the 10 environmental variables were also estimated. Specifically, we derived canonical axes from a redundancy analysis (Legendre et al., 2009; Punchi-Manage et al., 2014; Rao, 1964). We then calculated the correlation coefficients between the first canonical axis of the environmental variables of species composition with single environmental variables.

### RESULTS

#### 3.1 Beta diversity and ecological uniqueness of species assemblages

Total beta diversity was 0.391, 0.398, 0.352 and 0.096 in Hnjfl, Hbmlz, Gsxls and Xjk FDPs, respectively. The highest species richness was found in Hnjfl, followed by Hbmlz, Gsxls and Xjk FDPs (Table 1). The degree of ecological uniqueness (LCBD indices) was in the range of 0.004–0.014, 0.003–0.014, 0.003–0.015 and 0.001–0.115 in Hnjfl, Hbmlz, Gsxls and Xjk FDPs, respectively. However, there was substantial variation within each FDP in the degree of ecological uniqueness of species assemblages in the quadrats (Figure 1). The quadrats that had significantly higher ecological uniqueness (i.e. LCBDs denoted by black circles in Figure 1) showed a certain degree of aggregated distribution in Hnjfl, Hbmlz and Gsxls FDPs. The degree of ecological uniqueness of eight quadrats (black circles) was several orders of magnitude larger than that of the others in the Xjk FDP (Figure 1d).

#### 3.2 Determinants of ecological uniqueness

Local environmental factors that affect ecological uniqueness varied significantly among plots (Figure 2). The mean elevation and aspect affected ecological uniqueness only in the Xjk FDP. Slope and convexity were the most important topographical factors in determining the degree of ecological uniqueness in the quadrats (Figure 2). Soil pH determined the ecological uniqueness only in Gsxls, whereas OM
content affected the ecological uniqueness only in Hbmlz. Nitrogen content (total and available) had a significant impact on the ecological uniqueness of Hnjfl, Hbmlz and Gsxs.

The degree of ecological uniqueness in the quadrats was also strongly influenced by community characteristics (Figure 2). However, the community characteristics (species richness, abundance and basal area) were strongly linked to the degree of ecological uniqueness in the quadrats, meaning that the strength and direction of their influence varied among FDPs. Negative EUSRR values were observed in Hnjfl ($r = -0.66$) and Gsxs ($r = -0.35$), whereas positive values were noted in Xjk ($r = 0.85$) and Hbmlz ($r = 0.10$). Importantly, the strength and direction of EUSRR were strongly related to the percentage of rare species in the species assemblages (Figure 3). The EUSRR was negative when common species predominated, whereas it was positive when rare species were more dominant (Figure 3). Ecological uniqueness was significantly and positively related to abundance in Hnjfl but was negatively related in Xjk. The relationship between basal area and ecological uniqueness was consistently negative in Hnjfl and Hbmlz.

The total variation explained by the first canonical axes of the environmental variables decreased from tropical through subtropical to temperate forests (Table 2). Additionally, the first canonical axis of the environmental variables was strongly correlated with convexity in Hnjfl ($R^2_{adj} = 0.56$), mean elevation in Hbmlz ($R^2_{adj} = 0.58$) and Gsxs ($R^2_{adj} = 0.68$). The edaphic variables showed a weak correlation with the first canonical axis in Hnjfl but showed moderate correlation in Hbmlz (Table 2). All environmental variables were weakly correlated with the first canonical axis in Xjk. These results indicated that local environmental factors that affect ecological uniqueness and beta diversity were not completely consistent.

**FIGURE 3** The Spearman correlation coefficient between ecological uniqueness and species richness (EUSRR) plotted against the percentage of rare species. Spearman’s rank correlation coefficient was used to measure the EUSRR. Percentage of rare species (%) was measured as the proportion of species occurring in fewer than 40% of the 20 m × 20 m quadrats

4 | DISCUSSION

LCBDs are comparative indicators of site uniqueness; hence, large LCBD values indicate sites with significantly different species compositions (Legendre & De Cáceres, 2013). A high LCBD index plays the role of a light flashing atop some sites on the map. Investigating beta diversity can answer precise ecological questions and test hypotheses about the origin and maintenance of community assemblages in ecosystems. Here, we explored the determinants of beta diversity and of ecological uniqueness (i.e., LCBD, the contributions of sampling units to total beta diversity). Our findings indicated that the ecological uniqueness was explained by both local environment and community characteristics. LCBD may be an effective approach if ecological uniqueness is a conservation goal. At the same time, we emphasize the need to explore the determinants of ecological uniqueness in forest ecosystems. On the one hand, our results indicated that the ecological uniqueness did not show the same patterns as beta diversity with regard to local environmental variables. On the other hand, the negative ecological uniqueness–species richness relationship (EUSRR) indicated that sites with low numbers of species are usually those with greater ecological uniqueness. Researchers and conservation agencies can then examine in detail what happened at the unique sites using the data at hand or by revisiting the sites to determine what can be done.

We found that the ecological uniqueness of forest quadrats was strongly associated with local environmental variables. Our results are consistent with those of Sor et al. (2018) and da Silva et al. (2018), who found that the variation in ecological uniqueness is well-explained by local environmental variables in macroinvertebrate and dung beetle communities, respectively. However, our results contrast with those reported by Heino and Grönroos (2017) and Heino et al. (2017), who found that ecological uniqueness is weakly related to environmental factors in stream insect and urban pond insect assemblages, respectively. This discrepancy may have partially resulted from the different biological groups and ecosystems that were the focus of these studies. As few previous studies have focused on forest ecosystems, our results shorten the gap in the correlation between ecological uniqueness and local environmental conditions in forest ecosystems.

It is notable that the local environmental variables that affect ecological uniqueness vary significantly among forest plots (Figure 2). A striking finding from our study is that the effect of environmental factors on ecological uniqueness gradually weakens from tropical (Hnjfl) to subtropical to temperate (Xjk) forests. This result suggests that environmental control is more important in shaping the community assembly of tropical forests (Figures S1 and S2). The environmental conditions are more homogeneous in Xjk than in Hnjfl (Ding et al., 2019). It is supposed that species are more climatically tolerant in high latitudes than in low latitudes. Lower climatic tolerance may further lead to narrower niche breadths in tropical forests than in temperate forests (Chen et al., 2016). We thus hypothesize that the species distribution in Hnjfl is more sensitive to heterogeneous environmental conditions than that in Xjk. According
to the environmental filtering hypothesis, there is a negative relationship between habitat heterogeneity and latitude (Pianka, 1966) and the higher beta diversity at lower latitudes is caused by stronger environmental filtering (Qian & Ricklefs, 2007; Ricklefs, 1977). Therefore, different processes may shape ecological communities, producing different relationships between ecological uniqueness and local environmental conditions.

We found that ecological uniqueness did not show the same pattern as beta diversity regarding local environmental variables (Table 2 and Figure 2). An important finding from our study is that the local environmental factors that affect ecological uniqueness and beta diversity were not completely consistent, which illustrates that the local environmental factors that affect ecological uniqueness are not necessarily linked to factors that affect the variation in species composition (i.e. beta diversity). Hence, in practice, focusing simultaneously on variations in species composition (i.e. beta diversity) and ecological uniqueness with regard to local environmental conditions is likely an appropriate approach to study forest community assembly.

Our results revealed that the ecological uniqueness of forest quadrats is better explained by various community characteristics, such as species richness, abundance and basal area, which is consistent with the findings of most previous studies (Heino et al., 2017; da Silva et al., 2018; Sor et al., 2018; Vilmi et al., 2017). However, our results indicated that species richness was strongly linked to the degree of ecological uniqueness, meaning that the strength and direction of their influence varied among FDPs. A negative EUSRR (e.g. Hnjfl and Gsxls) indicated that quadrats with a high degree of ecological uniqueness (i.e. large LCBD indices) harboured low species richness. A positive EUSRR (e.g. Xjk) indicated that quadrats with unique species compositions (high ecological uniqueness) harboured high species richness. A negative EUSRR has been reported in most previous studies for different biological groups (e.g. Heino et al., 2017; Heino & Grönroos, 2017; Legendre & De Cáceres, 2013; Qiao et al., 2015; da Silva & Hernández, 2014). However, a positive EUSRR was reported only by Kong et al. (2017), who investigated spatiotemporal patterns in fish assemblages. We, therefore, infer that the relationship between ecological uniqueness and richness is related to the ecosystems and biological groups targeted.

Furthermore, we have provided direct evidence that the strength and direction of EUSRR were strongly related to the percentage of rare species in a community (Figure 3). Therefore, our results support the assumption that the proportions of rare and common species in the species assemblages may determine whether the EUSRR is negative, non-significant or positive (da Silva et al., 2018). It is supposed that species-rich quadrats exhibit low ecological uniqueness (i.e. negative EUSRR) owing to the greater chance of sharing species with other quadrats (Maloufi et al., 2016) when a community harbours a comparatively high proportion of common species. Recent studies on freshwater ecosystems have indicated that the relationship between ecological uniqueness and species richness is of great significance for biodiversity conservation or restoration (Legendre & De Cáceres, 2013; da Silva et al., 2018; Sor et al., 2018; Vilmi et al., 2017). From a conservation biology viewpoint, for instance, a negative EUSRR suggests that it is not enough to preserve sites with high species richness because high-richness sites are not necessarily the most unique ecologically. Moreover, species-poor sites may harbour rare or exotic species; thus, these sites contribute strongly to overall beta diversity and are worth studying in more detail in terms of biodiversity conservation. In practice, limited resources do not allow us to conserve all sites. Our results show that ecological uniqueness and the relationship between species richness and ecological uniqueness could be used to prioritize biodiversity conservation.

**ACKNOWLEDGEMENTS**

We gratefully acknowledge the numerous scientists, graduate and undergraduate students, and research technicians for their contributions to this research. This work was supported by the Fundamental Research Funds for the Central Non-Profit Research Institution.
CONFLICT OF INTEREST
The authors declare no conflict of interest.

PEER REVIEW
The peer review history for this article is available at https://publo n/10.1111/ddi.13205.

DATA AVAILABILITY STATEMENT
The JFL 60-ha plot (1,000 × 600 m) data are belonging to Jianfengling National Key Field Research Station for Tropical Forest Ecosystem, Hainan Island, China, and also a member of CTFS-ForestGEO net-work: https://doi.org/10.3974/geodb.2017.02.05.V1 (Li et al., 2017).

Data available from the Dryad Digital Repository.

ORCID
Jie Yao https://orcid.org/0000-0002-8606-8158
Jihong Huang https://orcid.org/0000-0001-7668-3010
Yi Ding https://orcid.org/0000-0002-3649-0211
Yue Xu https://orcid.org/0000-0003-2414-0000
Han Xu https://orcid.org/0000-0002-1085-3344
Runguo Zang https://orcid.org/0000-0001-5392-8193

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**BIOSKETCH**

Jie Yao is currently a post-doctor in the Key Laboratory of Forest Ecology and Environment, the State Forestry and Grassland Administration, Research Institute of Forest Ecology, Environment and Protection, Chinese Academy of Forestry. His main research interests focus on the ecology of forest trees, mostly based on field data from the temperate and tropical forests in China, and more particularly on understanding the processes that both generate and maintain diversity in the identity, characteristics and abundances of species that are found together in forest communities.

Author contributions: J.Y. and R.Z. conceived the ideas and designed methodology; J.H., Y.D., Y.X. and H.X. collected the data; J.Y. and R.Z. led the writing together in forest communities.

**How to cite this article**: Yao J, Huang J, Ding Y, Xu Y, Xu H, Zang R. Ecological uniqueness of species assemblages and their determinants in forest communities. *Divers Distrib*. 2021;27:454–462. https://doi.org/10.1111/ddi.13205

**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.