Journal of Ecology — BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Evidence for divergence in phenology over morphology in response to limiting similarity in montane communities of *Rhododendron*

Qin Li[1,2] | Ji Wang[3] | Ryan Fuller[4] | Yaowu Xing[5] | Jianquan Liu[3] | Richard H. Ree[1,2]

[1]Grainger Bioinformatics Center, Field Museum, Chicago, Illinois, USA

[2]Department of Science and Education, Field Museum, Chicago, Illinois, USA

[3]College of Life Sciences, Sichuan University, Chengdu, China

[4]Committee on Evolutionary Biology, University of Chicago, Chicago, Illinois, USA

[5]CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, China

Correspondence
Qin Li
Email: qli@fieldmuseum.org
Richard H. Ree
Email: rree@fieldmuseum.org

Abstract

1. The coexistence of closely related species is key to understanding the nature of biodiversity hotspots where in situ diversification has yielded rich communities of close relatives. Limiting similarity predicts that co-occurring species are differentiated in their niches; identifying the axes of differentiation in sympatric close relatives can thus help reveal the eco-evolutionary dynamics of community assembly. For flowering plants, these axes may be temporal (related to reproductive phenology) or morphological (related to functional traits).

2. We collected fine-scale data on abundance, morphology and phenology over a flowering season for 34 species of *Rhododendron* (Ericaceae) spanning a 2700 m elevation gradient in a nature reserve in the eastern Hengduan Mountains, China. We used null models to test for patterns of clustering versus overdispersion in species' abundances, phylogenetic relatedness and functional traits across sites, and applied joint distribution models to examine the correlates of pairwise associations.

3. We found that species tended to be spatially aggregated, indicating that communities are not strongly structured by competitive exclusion. At higher elevation sites, species tended to be vegetatively more similar (clustered) and closely related. Environmental variables, including climate and topography, were strong predictors of species' ranges. No evidence of niche differentiation was detected along spatial or morphological (functional) axes, but along the temporal axis, the phenology of co-occurring species showed significant divergence, and was less phylogenetically conserved compared to morphological traits.

4. *Synthesis*. Local communities of *Rhododendron* in its centre of diversity are structured by environmental filtering and the effects of limiting similarity. Evidence for the latter is apparent in the pervasive phenological divergence of co-occurring species, likely driven by reproductive interference from shared pollinators. The evolutionary lability of flowering time appears to render it the quickest path to coexistence for recently diverged species that experience secondary contact in this biodiversity hotspot.

1 | INTRODUCTION

The coexistence of closely related species is a topic of enduring interest, with intertwined considerations of ecology, evolution and biogeography (Weber & Strauss, 2016). How do species originate and come to be co-distributed? How do they interact, and with what long-term population dynamics? Darwin famously hypothesized that recently diverged species are both more likely to co-occur, due to common geographical origins, as well as interfere with each other, due to inherited ecological similarities (Darwin, 1859). Recently diverged species would thus seem particularly susceptible to limiting similarity, the idea that if niche overlap is too great, coexistence is unstable (Burns & Strauss, 2011; Levine & HilleRisLambers, 2009; but see Godoy et al., 2014). So when close relatives are observed to co-occur, it is natural to wonder how their niches diverged, acknowledging the possibility of alternative explanations based on non-equilibrium dynamics, stochastic effects and ecological neutrality (Adler et al., 2007; Chesson, 2000; Hart, Schreiber, et al., 2016; Rees et al., 2001), and the challenges associated with inferring process from pattern.

The question of how close relatives coexist in sympatry is especially pertinent to regions of high species richness characterized by recent in situ diversification, where co-occurrence of close relatives is prevalent. One such region is the Hengduan Mountains of south-central China, a temperate hotspot of biodiversity where numerous clades of flowering plants have radiated extensively since the Miocene (Xing & Ree, 2017). Prominent among these is the genus *Rhododendron* (Ericaceae), of which about 272 out of more than 1000 species worldwide are native to the Hengduan flora

(D. E. Boufford, unpublished data; Geng, 2014; Wu et al., 2005). Here, we study a 'mini-hotspot' of *Rhododendron* diversity in the Gongga Mountain National Nature Reserve in western Sichuan, where more than 60 species are recorded (Zhou & Jiang, 2016). Our objective is to investigate the patterns of co-occurrence and infer potential processes facilitating coexistence of *Rhododendron* species in this local area, as this might ultimately help us understand the exceptional diversity of the broader Hengduan region.

We take a niche-based perspective, in which the strength of negative ecological interactions between species is expected to be positively related to their joint overlap along spatial, temporal (phenological) and functional (morphological) axes (Figure 1). A key hypothesis is that species that co-occur spatially are more likely to exhibit ecological differences that reduce their negative interactions; we wish to investigate the nature of those differences. To illustrate the basic framework, consider a hypothetical pair of sister species immediately after their divergence in allopatry. They are spatially segregated, but owing to their recent common ancestry, share similar environmental tolerances, habitat requirements and pollinators, such that if they were to co-occur at this early stage, their ecological similarities would be limiting. Stable coexistence of the pair after secondary contact would require niche divergence, manifested as evolved differences in functional traits. This simple trade-off between spatial co-occurrence and functional trait divergence might apply to competitive interactions (hereafter broadly referring to negative plant–plant interactions) that cannot be reduced by differences in phenology, such as abiotic resource competition (Figure 1a). By contrast, the negative effects of reproductive interference caused by heterospecific
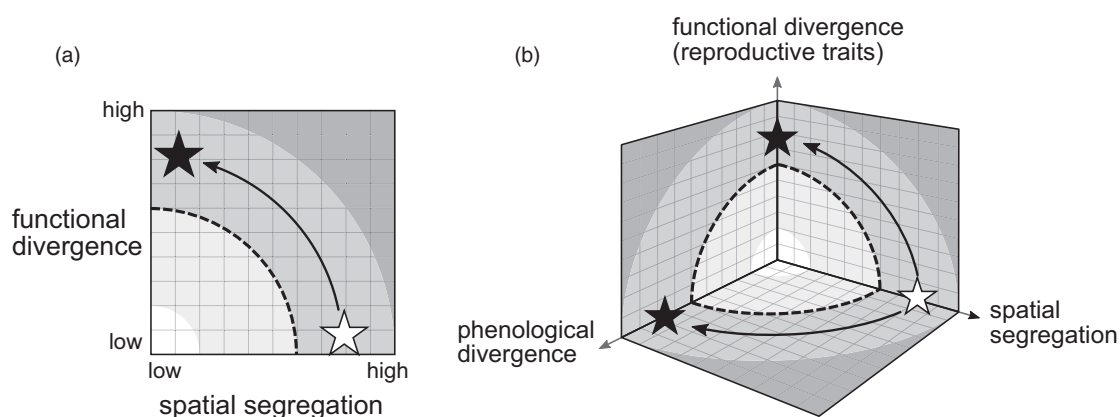

FIGURE 1 The relationship between spatial segregation, niche divergence and the expected intensity of negative interactions for cases when interactions (a) can be reduced by differences in functional traits but not phenology, such as abiotic resource competition and (b) when they can be reduced by differences in both factors, for example, reproductive interference caused by shared pollinators. Negative interactions are most intense (light shading) where spatial segregation and ecological divergence are lowest. Zones of limiting similarity, in which negative interactions prohibit stable coexistence, are indicated by the dashed lines. For sister species that originate allopatrically (open stars), stable coexistence in sympatry (filled stars) requires evolutionary divergence along one or more available niche axes. For reproductive interference, this could be realized through divergence in functional traits or phenology.

pollination via shared pollinators could be reduced in two ways: functional trait divergence (e.g. relating to pollinator attraction) and phenological divergence (*PD*) in flowering time; both are potential means of reducing the probability of pollen transfer between co-occurring species (Figure 1b). If one type of divergence is more easily evolved than the other, we would expect it to be more often associated with spatial co-occurrence of close relatives.

In the present study, our primary goal is to infer the axes of ecological divergence associated with local community assembly of *Rhododendron* species. Specifically, we wish to assess (1) whether species in the Gongga Reserve spatially co-occur more or less frequently than expected by chance, (2) the degree to which co-occurrence is related to environmental and phylogenetic factors and (3) whether co-occurring species are more ecologically diverged along temporal or functional axes.

2 | MATERIALS AND METHODS

2.1 | The study region and community surveys

Between 25 April and 28 June 2019, we censused *Rhododendron* species in the Gongga Mountain National Nature Reserve (29°10′–30°10′N, 101°10′–102°10′E, an area ca. 1×10^4 km²) in western Sichuan province, China (Figure 2a). In several major valleys surrounding Mt. Gongga, we surveyed 128 sites spaced at intervals of approximately 100 m change in elevation, or distances > 1 km in the absence of elevation change. The sites spanned elevations from 1790 to 4580 m (Table S1), with habitats ranging from deciduous and mixed forests to alpine shrublands and meadows (Liu, 1985; Zu et al., 2019). We conducted four censuses, each involving a circuit of visits to all 128 sites, at intervals of 10–17 days over the fieldwork period. We identified species in the field using morphological keys (Geng, 2014; Wu et al., 2005), and deposited voucher specimens at Field Museum (F) and Sichuan University Herbarium (SZ).

We estimated the population densities of *Rhododendron* species using variable area transects (Parker, 1979), an efficient and robust method suitable for dense populations used in previous studies of *Rhododendron* (Hart & Salick, 2018). For each species at a site, we measured population density once by setting up two transects ($n = 2$) from different random starting points within the boundaries of their occurrence, each with a fixed width ($\omega = 1.5$ m). The transect length (x) was recorded as the distance to the fourth individual encountered ($r = 4$). Density was estimated using the formula $(nr - 1) / (\omega \sum_{i=1}^{n} x_i)$ (Parker, 1979). We translated densities to abundances by multiplying by a constant factor of 100 m². We then constructed a species abundance-by-site matrix and a
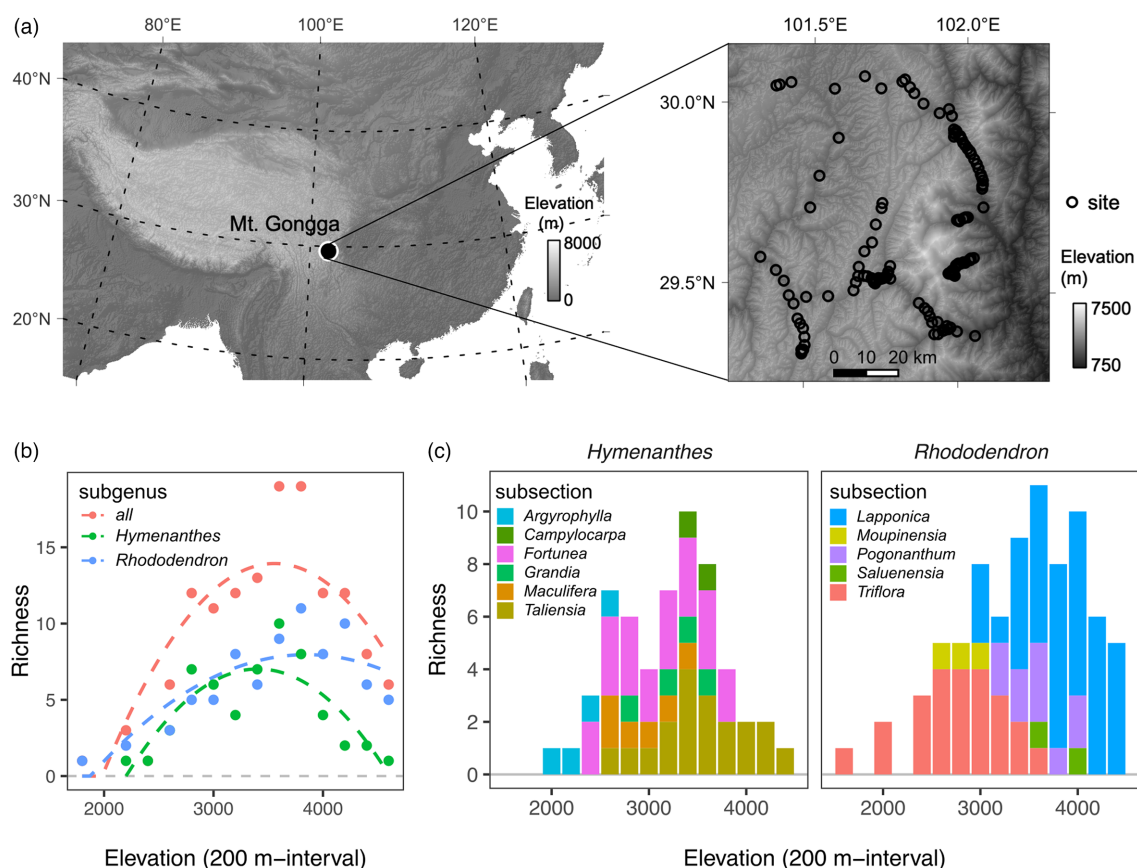

FIGURE 2 (a) Overview of the study region and surveyed sites, (b) *Rhododendron* richness along 200 m elevation intervals for all species and for each subgenus, with dashed lines fitted with generalized additive models, and (c) histograms of richness stacked by subsections along 200 m elevation intervals for subgen. *Hymenanthes* and subgen. *Rhododendron* separately.

corresponding binary presence–absence matrix. At each visit, we recorded the phenological phase of each species by visual estimation of the proportion of flowering inflorescences out of the total inflorescences across 10–20 individuals. These values were later normalized by the peak value observed for the species over the duration of the census.

To assess functional variation related to growth, stress tolerance and pollination, we measured three vegetative traits and six floral traits. Plant height and leaf area are indicators of light acquisition ability and correlate to overall plant biomass; specific leaf area (SLA) is a measure of photosynthetic capacity and leaf longevity, commonly used to quantify species response to environmental resources (Pérez-Harguindeguy et al., 2013). We collected mature leaves from three individuals per species per site in sealed plastic bags to maintain freshness, and later the same day scanned them on a flatbed scanner (Epson Perfection V19) and dried them in silica gel. We measured leaf area from the scans using ImageJ (Schneider et al., 2012), and measured leaf mass by an electronic analytical scale after oven-drying at 70°C for 24 h. Flower size and shape are pollination-related traits that influence the potential for reproductive interference via heterospecific pollen transfer. We measured corolla tube length and width, corolla lobe length and width, stamen length and style length on fully opened flowers of three individuals per species chosen randomly from representative sites (86 in total, ranging 1–10 sites per species, median = 4). All data involved in the study are deposited on Dryad (Li et al., 2022).

2.2 | Site-based null model tests for overlap in space, time and traits

We used null models to test for non-random patterns of overlap in space, time and traits across *Rhododendron* communities. To test whether species are more spatially segregated or aggregated than expected by chance, we measured covariance in the species abundance-by-site matrix using two indices: an abundance analogue of the checkerboard score (CA), and a matrix-wide Morisita index of similarity (MA) (see equations (3) and (7) in Ulrich & Gotelli, 2010). High values of CA and low values of MA indicate negative covariation in abundances, that is, spatial segregation. The null distribution was generated from 1000 replicates of the *quasiswap_count* randomization algorithm implemented in the R package VEGAN (Oksanen et al., 2020), in which total counts per species, the total counts per site and the number of non-zero cells in the matrix are maintained. We used standardized effect size (SES) to measure the degree of which the observed value deviated from the null distribution, calculated as z-transformed scores, $z = (I_{obs} - I_{null}) / \sigma_{null}$, where I_{obs} is the estimate based on the observed matrix, and I_{null} and σ_{null} are the mean and standard deviation based on 1000 randomizations. Statistical significance was determined as I_{obs} above the 97.5th or below the 2.5th percentiles of randomized estimates (i.e. outside of the central 95% reference interval). To account for turnover and variation in richness in the species pool across elevation (Figure 2b), we

used a moving-window approach to test subsets of the matrix within elevational bands. We applied five window sizes (w_size = 200, 400, 600, 800, 1000 m), with a step size of 100 m. To complement the abundance-based tests of spatial segregation, we also tested binary presence–absence null models with the checkerboard score, standardized by the product of numbers of sites in which species occur separately (scaled C-score) (Gotelli, 2000). We calculated SES of the scaled C-score with 1000 randomizations by a fixed row-fixed column randomization algorithm, in which richness per site and species occurrences are maintained.

To test whether co-occurring species flower more or less synchronously than expected by chance, we quantified the phenology of each species as the flowering proportion averaged across sites for each of the four circuits of site visits. This effectively divided the surveyed flowering season into four periods of approximately 15 days, T1–T4. We conducted two tests on *PD*. The first is based on measurements of niche divergence between two species using the modified formula of Schoener's Index (Schoener, 1970), $PD_{pr} = \frac{1}{2} \sum_{k=1}^{n} |p_{ik} - p_{jk}|$, where p_{ik} and p_{jk} are the flowering proportions (standardized over four periods, summing up to 1) of species i and species j in the kth time period, and n is the total number of periods, calculated in the R package PHILENTROPY (Drost, 2018). The second test of *PD* used an abundance-weighted measure of dissimilarity in flowering between two species by a modified Bray–Curtis index, $PD_{ab} = 1 - 2 \sum_{k=1}^{n} \min(S_{ik}, S_{jk}) / \sum_{k=1}^{n} (S_{ik} + S_{jk})$, where S_{ik} and S_{jk} are counts of flowering individuals in the kth time period for species i and j, respectively, in the R package VEGAN. For both tests, the overall *PD* was calculated as the average pairwise divergence, and null models compared the observed *PD* with null distributions with 1000 randomizations. The randomization procedure involved keeping the temporal sequence of flowering states from T1 to T4 per species per site, and shuffling such fixed sequences among species and among sites. As with the spatial tests, we carried out the same moving-window analysis of *PD* across elevation, to account for the expectation that populations at higher elevations will tend to have a shorter and later flowering season.

We quantified the synchronicity of phenological change between species as similarity of change in the flowering proportion between consecutive time periods for pairs of species, using the formula $1 - \frac{1}{2} \sum_{k=1}^{n} |\Delta p_{ik} - \Delta p_{jk}|$, where Δp_{ik} and Δp_{jk} are changes in flowering proportion for species i and j between the $(k-1)$th and kth visits (Mahoro, 2002). We calculated average pairwise synchronicity across sites and average within-site synchronicity across species pairs, and their standard deviations. Then we built simple linear regressions between elevation and each of the above four types of synchronicity estimates, and tested their significance using a null distribution based on random permutations of flowering sequences.

We applied null models to test for clustering versus overdispersion (evenness) patterns for functional traits and evolutionary relatedness for sites with more than one species (108 sites). Trait measurements were averaged for each species per site, log-transformed and input into principal component analysis (PCA), separately for vegetative and floral traits, from which the first two

axes were used for downstream analyses. We used subgeneric taxonomic membership to subgenus and subsection (Table S2) as a proxy for evolutionary relatedness, because molecular evidence to date indicates that despite considerable gene-tree discordance, many of these subgeneric taxa are supported as monophyletic (Fu et al., 2022; Khan et al., 2020), whereas relationships within and between them are less well resolved. In addition, several species of subgenus *Rhododendron* in our sample are polyploid (R. Fuller, unpublished data), possibly with hybrid origins, calling into question the validity of using a bifurcating phylogeny to quantify relatedness. We coded the phylogenetic distance between two species from the same subsection as 1 (close), from the same subgenus but from different subsections as 2 (medium), from two different subgenera as 4 (distant). With these datasets, we evaluated abundance-weighted functional and phylogenetic structure by null models with two indices: mean pairwise dissimilarity (MPD) and mean nearest taxon distance (MNTD) (Tucker et al., 2017; Webb et al., 2002) separately, via the R package PICANTE (Kembel et al., 2010). MPD and MNTD are commonly used to assess the signal of deterministic assembly processes while controlling for species richness (Chao et al., 2014). Null distributions were constructed by randomly permuting trait values among species.

2.3 | Species-based pairwise associations and divergence

To analyse species associations regarding abundance covariance while accounting for environmental influences on range limits, we used joint species distribution models (JSDMs) implemented as generalized linear latent variable models (GLLVMs) in the R package GLLVM (Niku et al., 2019). JSDMs can jointly estimate abundance responses of multiple species to various environmental predictors to capture the environmental filtering process. Meanwhile, abundance covariance across sites that is not explained by the environment can be captured by latent (i.e. unobserved) variables, and a residual species-to-species correlation matrix is returned to depict pairwise associations at a scale of −1 (negative) to 1 (positive) (Ovaskainen et al., 2017; Pollock et al., 2014; Warton et al., 2015). Species that share similar responses to these latent variables show positive associations with the same sign in the correlation matrix, indicating possible facilitation. While negative associations suggest two species respond in different ways that lead to opposite signs, indicating possible competition (Niku et al., 2019).

We obtained six environmental predictors related to climatic and topographical heterogeneity, including annual mean temperature, temperature seasonality, annual precipitation, precipitation seasonality, topographical surface roughness and slope aspect. These climatic variables have been shown to affect plant distribution in this region (Zu et al., 2021), and topographical variables are assumed to affect microhabitat conditions. Climatic variables were downloaded from Worldclim at 30-s resolution (Fick & Hijmans, 2017). Roughness was calculated as the standard deviation of elevation in a ca 1-km^2

buffer centred at each site based on digital elevation model at 90 m-resolution (https://cgiarcsi.community). Slope aspect was recorded in the field by a compass and converted to values scaled between −1 (north-facing) and 1 (south-facing), discarding the east–west component. We conducted PCA on these six environmental predictors and input PC1–PC6 into GLLVMs with the abundance-by-site matrix for species with more than three occurrences (28 species in total; ranging from 4 to 33, median = 11 occurrences), assuming negative binomial distributions. We used the Akaike information criterion (AIC) to determine the suitable number of latent variables (1–5) in a maximum likelihood framework. We also applied GLLVMs to the binary presence–absence matrix.

Preliminary analyses of the GLLVMs with environmental predictors yielded non-significant associations between species from the residual correlation matrix, indicating that patterns of species co-occurrence and abundance covariance can be adequately explained by abiotic filtering (see Section 3). This prompted us to run a GLLVM without any environmental predictors to obtain a species association matrix based simply on ordination, and it showed that pairwise associations clearly fell into three categories: positive, random and negative (see Section 3). With these categories, we tested whether pairs of combinations of abundance associations (positive vs. negative) and evolutionary relatedness (close vs. medium vs. distant) show significant differences along individual distance axes. These included environmental divergence, geographical distance, elevational distance, divergence of vegetative and floral traits, and *PD*. Environmental, vegetative and floral trait divergence were calculated as the average pairwise Euclidean distances in PC space, whereas geographical and elevational distances were calculated as average pairwise distances in two- or one-dimensional geographical spaces, respectively. We used pairwise PD_{pr} as *PD* (highly correlated with PD_{ab}, $r = 0.88$). Additionally, we ran Mantel tests (with 1000 permutations) between pairwise trait dissimilarity and evolutionary relatedness, for both vegetative and floral traits, as well as *PD*, as an approximation of phylogenetic signal via the R package VEGAN.

3 | RESULTS

3.1 | Site-based patterns of spatial, temporal and functional overlap

3.1.1 | Spatial co-occurrence patterns

In total, we collected data on 34 *Rhododendron* species, representing three sections and 11 subsections in the two largest subgenera, *Hymenanthes* and *Rhododendron* (Table S2; Figure S2). Across the Gongga Reserve, species of *Rhododendron* showed peak richness at middle elevations (ca. 3500 m; Figure 2b). This unimodal pattern was consistent across the two subgenera, with the peak at a higher elevation for subgen. *Rhododendron* than that for subgen. *Hymenanthes*. Elevational ranges vary across subsections in both subgenera (Figure 2c), and across species (Figure S1). In the moving-window tests with abundance

data, positive covariation in abundance (i.e. aggregation pattern) by the CA index was consistent across most elevational windows with a size of 600 m (Figure 3a). Similar patterns held with larger window sizes (800 and 1000 m), while more non-significant patterns appeared with smaller window sizes (200 and 400 m) at middle to high elevations (Figure S3a). Similar patterns also held when partitioning co-occurrence patterns by subgenus (*Hymenanthes* and *Rhododendron*; Figure S4a,b), but with more non-significant cases in subgen. *Rhododendron*. The alternative MA index showed a decreasing signal of aggregation from low to high elevations (Figure S3a), which was similar in subgen. *Rhododendron*, while consistent aggregation patterns were observed in subgen. *Hymenanthes* (Figure S4a,b). By the scaled C-score with binary data, most results returned random patterns along elevation, except a few windows with segregation pattern for all species at middle elevation and a trend of segregation to aggregation for subgen. *Hymenanthes* with increasing elevation (Figure S5). The abundance data thus appear to be more informative than the presence–absence data. Null models of abundance data across the whole elevational gradient yielded overall nonsignificant patterns of spatial covariance by both CA and MA (Figure S6a,b), as did the test by the scaled C-score using presence–absence data (Figure S6c). In tests conducted for individual subgenera, subgen. *Hymenanthes* showed significant aggregation, whereas for subgen. *Rhododendron* the signal of aggregation was close to but short of significance (but see the opposite with the scaled C-score; Figure S6a,c).

3.1.2 | Phenological divergence and synchronicity

Six species had started flowering by the start of our census and four were still flowering at the end, representing a potential source of error in our analyses of *PD* and synchronicity, but our phenological sampling captured the peak of flowering in most species surveyed (Figure S1), so we expect this error to be minor. The standard deviation in flowering proportion was 0–0.45 across sites, species

and periods. In contrast to the spatial patterns, a significant pattern of divergence in phenology was detected by PD_{pr} with the moving-window approach (a size of 600 m; Figure 3b), as well as by the alternative divergence index (PD_{ab} and other window sizes, Figure S3b), although the strength of divergence varied across elevation. This pattern was further confirmed by tests including the whole elevational range (Figure S6d,e). Similar results were obtained from tests of individual subgenera (Figure S4c,d). Changes in phenological stage occurred with higher synchronicity between species at higher elevations, with the observed regression slope being larger than all null estimates (Figure S7a). A similar pattern was also found with models based on pairwise or within-site synchronicity (Figure S7b,d), but not for within-site averages (Figure S7c).

3.1.3 | Functional and phylogenetic structure along elevation

Interspecific variation far exceeded intraspecific variation in functional traits (Table S3), with standard deviations of trait PCs being 0.76–2.27 and 0.22–0.28, respectively. In functional trait spaces, the first two PC axes explained 97.2% of the variation in vegetative traits (74.8% and 22.4%, respectively), and 95.1% in floral traits (84.1% and 11%), and in both cases the two subgenera were clearly separated (Figure S8). For vegetative traits, PC1 was generally associated with size (plant height and leaf size), and PC2 was mostly related to SLA. For floral traits, PC1 was also closely related with flower size and PC2 was related to flower shape (broadly funnel-form to campanulate or tubular). These PC axes showed significant relationships with elevation (Figure S9). Null model tests with abundance-weighted MPD yielded most random patterns but significant clustering patterns at 10 sites for vegetative traits (9.3%) and at 12 sites for relatedness (11.1%), often simultaneously for sites at high elevations (Figure 4a,c). Floral traits showed significant patterns
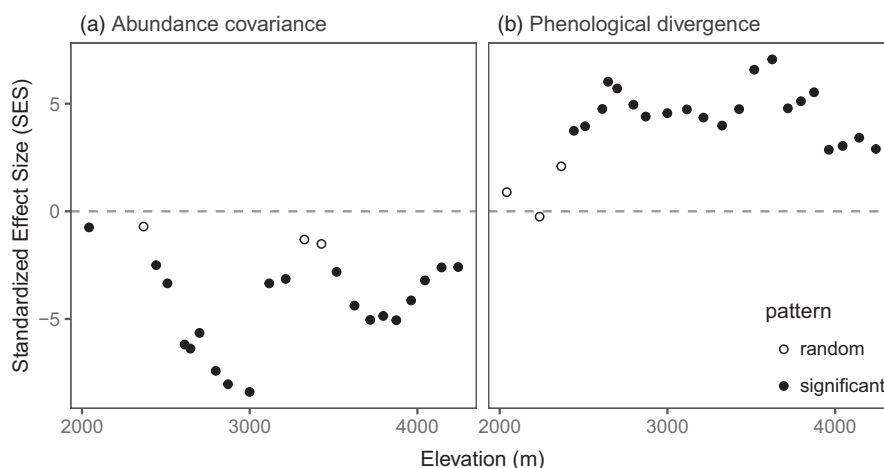

FIGURE 3 Elevational patterns quantified by standardized effect size (SES) with a moving-window approach: (a) abundance covariation in space by CA, and (b) phenological divergence in flowering time by PD_{pr}. Solid points indicate significant non-random patterns within elevational windows (meaning the observed value is outside of the central 95% reference interval based on the null model test) and open points indicate nonsignificant patterns. The window size is 600 m (see Figure S3 for a full set of window sizes and alternative indices).

at fewer sites, with clustering in only six sites (5.5%) and overdispersion in one site (0.9%) at middle to high elevations (Figure 4b). Similar results were obtained with abundance-weighted MNTD (Figure S10) and with both indices based on presence–absence data (but with more sites with significant patterns; Figure S11).

3.2 | Species pair-based tests of covariation and divergence along niche axes

A GLLVM with six environmental PCs (Figure S12) and one latent variable was selected based on AIC (Table S4). Values in the residual

correlation matrix were nearly all close to zero (Figure S13), indicating that covariation in species' abundances is well explained by their responses to environmental conditions across sites (Figure S14). By contrast, a GLLVM-based ordination without environmental predictors showed that variation in pairwise association fell into three discrete categories: positive, random and negative associations (Figure 5). GLLVMs with presence–absence data yielded similar pairwise associations (Figures S15 and S16).

Wilcoxon rank sum tests showed that negatively associated pairs exhibited greater divergence than positively associated pairs along all axes ($p < 0.001$; Table S5): environment, geography, elevation, phenological, floral and vegetative traits (Figure S17a–f). Distantly
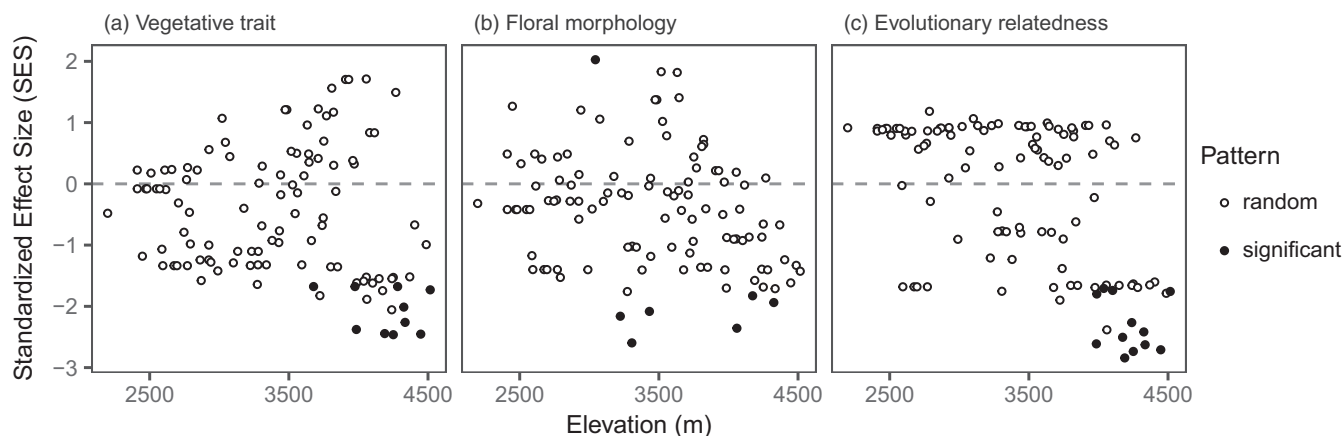

FIGURE 4 Abundance-weighted functional and phylogenetic structure as indicated by standardized effect size (SES) of the mean pairwise distance metric (MPD): (a) vegetative traits, (b) floral traits and (c) evolutionary relatedness. Negative values indicate the tendency of clustering, while positive values indicate the tendency of overdispersion. Open circles depict random results, while solid points depict significant results.
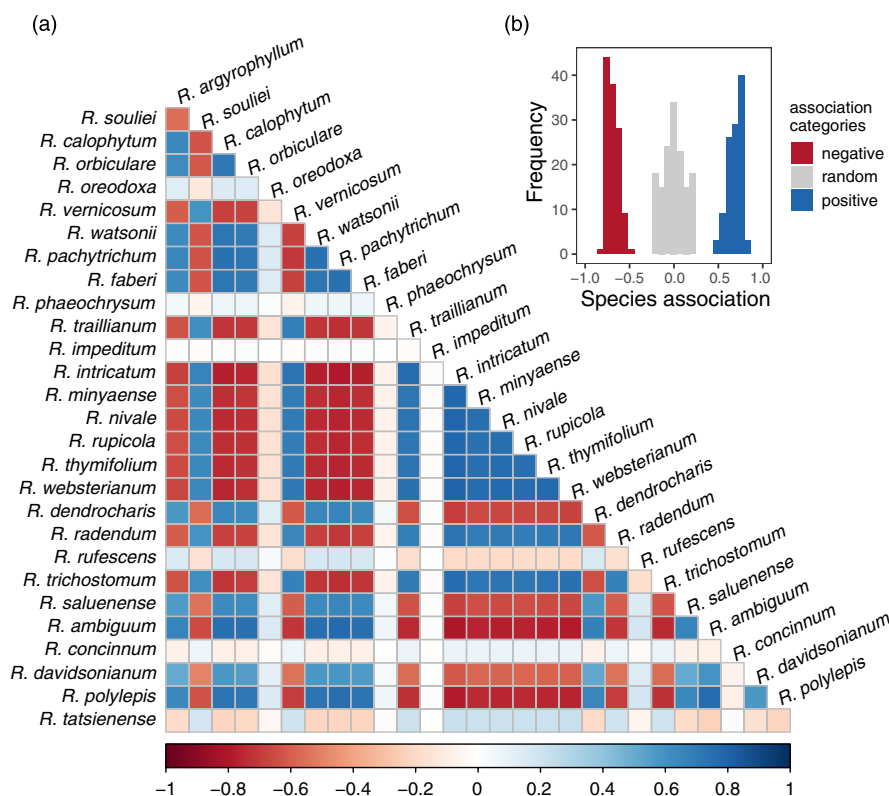

FIGURE 5 Pairwise species associations inferred by the residual species-to-species correlation matrix from a GLLVM without any environmental predictors in (a). Red cells indicate negative associations, while blue cells depict positive associations. The nested histogram (b) shows how the residuals fall into three discrete categories: Negative (red), random (grey) and positive (blue).
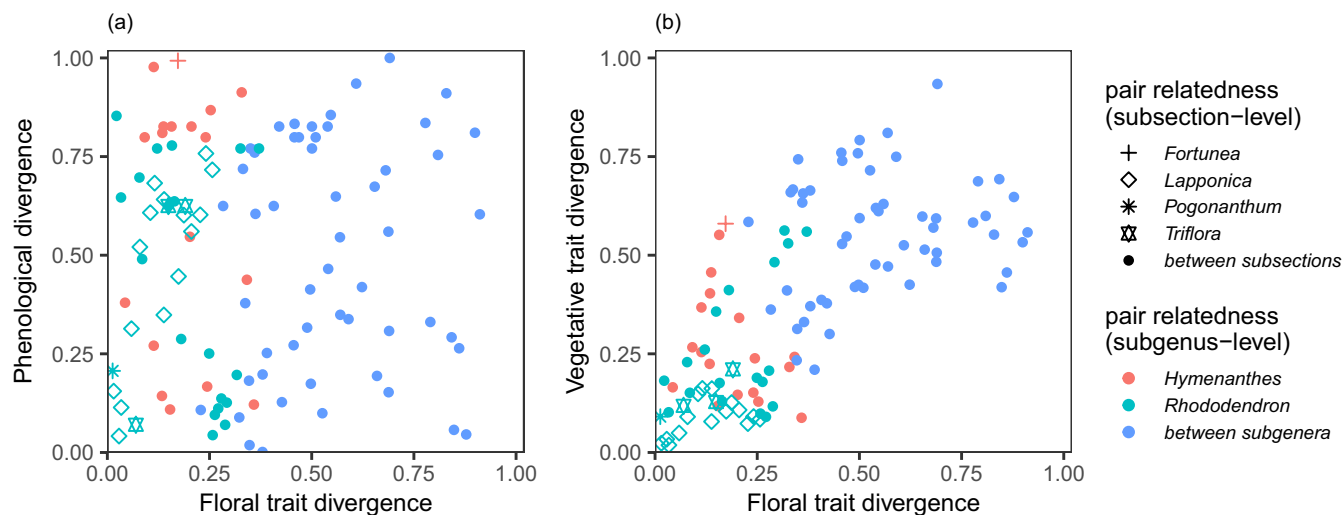
FIGURE 6 Covariation (a) between phenological divergence and floral trait divergence and (b) between vegetative and floral trait divergence, in positively associated species pairs.

related species pairs showed greater divergence than closely related pairs along axes of environment, elevation, floral and vegetative traits, indicating phylogenetic conservatism ($p < 0.01$; Table S6). Along axes of geographical distance and PD, there was no significant difference between distantly and closely related pairs. However, closely related pairs were more divergent than distantly related pairs in terms of the ratio of phenological to floral trait divergence (Wilcoxon rank sum test: z-score = −5.89, $p < 0.001$; Figure S18d,e).

Mantel tests gave similar results to those from rank sum tests. Distantly related species were more dissimilar in vegetative traits ($r = 1$, $p < 0.001$) and floral traits ($r = 0.631$, $p < 0.001$) compared to closely related species, indicating phylogenetic signal. By contrast, PD was not correlated with phylogenetic relatedness ($r = 0.032$, $p = 0.226$). For positively associated species pairs, PD was unrelated to floral divergence, whereas vegetative divergence was positively correlated with floral divergence ($p = 0.04$, $R^2 = 0.61$). The decoupling of PD from phylogenetic relatedness is evident in the excess of phenologically divergent but closely related species pairs (Figure 6).

4 | DISCUSSION

In this study, we investigated whether locally co-occurring species of *Rhododendron* exhibited patterns of ecological divergence consistent with limiting similarity, while accounting for the possible effects of environmental filtering and phylogenetic conservatism. We expected that negative interactions between congeners could result from competition for abiotic resources and/or shared pollinators (reproductive interference), and thus influence community structure. We found no evidence that competitive exclusion has led to spatial segregation of species among sites; instead, species show a tendency towards spatial aggregation within the bounds of their apparent environmental tolerances. At higher elevations, communities were assembled by more closely related, morphologically similar

species. We detected significant temporal divergence in flowering phenology, especially among closely related species, consistent with the expectation of limiting similarity driven by reproductive interference. This suggests that divergence in phenology is evolved more easily than divergence in morphological functional traits, and for these species, has been the path of lesser resistance towards stable coexistence following speciation and secondary contact.

Studies of *Rhododendron* co-occurrence in relation to phenology, traits and relatedness have been carried out at sites elsewhere in the Hengduan Mountains (Hart & Salick, 2018; Zou et al., 2021) and the eastern Himalaya (Basnett et al., 2021; Basnett, Ganesan, et al., 2019; Basnett, Nagaraju, et al., 2019). While the methods of these studies varied and differed from ours, some pertinent comparisons can be made. Particularly noteworthy is that for communities of *Rhododendron* in the Kyongnosla Alpine Sanctuary in Sikkim, overlap in flowering time among species was found to be negatively related to overlap in their pollinators (Basnett et al., 2021). This supports the idea that pollinator sharing results in reproductive interference that is reduced through differences in flowering phenology. For the species of *Rhododendron* occurring on Mt. Yulong in northern Yunnan, flowering times and elevational range were found to overlap significantly less than expected by chance (Hart & Salick, 2018), suggesting that both PD and spatial segregation may reduce limiting similarity in those communities.

A common pattern across previous studies and ours is that at higher elevations, alpine species of *Rhododendron* tend to be more synchronized in their flowering (Hart & Salick, 2018) and more similar in morphology, for example, have smaller leaves (Zou et al., 2021). These patterns likely reflect the shorter flowering season and environmental filtering of harsher alpine climates. In our study, alpine communities also tended to have higher relatedness, due to the prevalence of species of *R.* subsection *Lapponica*, a group largely restricted to the Hengduan Mountains (Geng, 2014; Wang et al., 1994; Wu, 2008; Wu et al., 2005). Nevertheless, within the bounds of these environmental

and phylogenetic constraints, the signal of *PD* at the highest elevations remains clear (Figure 3b), with positively associated species of *Lapponica* in particular exhibiting high pairwise divergence in phenology relative to their divergence in floral traits (Figure 6).

The ecological and evolutionary significance of *PD* in flowering time may extend beyond reproductive interference and competition for shared pollinators, and include avoidance of hybridization (Hart & Salick, 2018; Milne & Abbott, 2008; Zheng et al., 2021). The ability of *Rhododendron* species to produce fertile hybrids, long exploited in horticulture, has been documented in field studies of hybrid zones and introgression in natural populations across the world (Kron et al., 1993; Marczewski et al., 2015; Milne et al., 2003; Tagane et al., 2008; Yan et al., 2017). More recently, genomic evidence has mounted that reticulation, including hybrid speciation, has been pervasive throughout the phylogenetic history of *Rhododendron*, mostly within subgenera (Milne et al., 2010; Xia et al., 2022). Our own phylogenomic investigations of the species sampled from Mt. Gongga and subsection *Lapponica* show extensive gene-tree discordance suggestive of hybridization (R. Fuller, unpublished data). Clearly, *PD* (and other potential isolating mechanisms, such as polyploidy) have not prevented hybridization; however, they may still be important in reducing it at early stages of lineage diversification when genomic compatibility is highest, where the balance of gene flow between recently diverged species may be tipped away from one lineage absorbing the other, towards the persistence of both (Milne & Abbott, 2008; Zha et al., 2008; Zheng et al., 2021).

In our analyses, we made efforts to account for environmental filtering, that is, the potential effect of abiotic variables such as elevation on species ranges. However, we did not directly evaluate these effects, for example, through common garden or reciprocal transplant experiments. Environmental correlates of species turnover, such as the dominance of subsection *Lapponica* at higher elevations, may be driven in part by contemporary biotic interactions such as competitive exclusion (Kraft et al., 2015). But those effects, if present, should not invalidate our inferences about niche divergence in co-occurring species.

Confirmation of our results across multiple flowering seasons and sites is a priority for future research. In the meantime, they contribute to a broader understanding of the eco-evolutionary processes underlying the rich biodiversity of the Hengduan Mountains. *Rhododendron* is among the many species-rich genera in the flora that underwent extensive in situ diversification in the region (Xing & Ree, 2017) as the climate cooled, summer monsoon intensified and tectonic activity contributed to mountain-building throughout the Neogene (Spicer et al., 2020). In this deeply incised region, where climatic fluctuations would have caused recurrent fragmentation and fusion of elevationally zoned habitats (Spicer et al., 2020), allopatric speciation followed by secondary contact was likely a common driver of situ diversification across many resident clades (Muellner-Riehl, 2019). However, the responses of individual clades to secondary contact of close relatives appear to be more idiosyncratic, even across animal-pollinated plants that presumably faced similar pressures from reproductive interference and interspecific gene flow caused by shared pollinators.

For example, in communities of synchronously flowering species of *Pedicularis* (Orobanchaceae) in the Hengduan Mountains, converging lines of evidence suggest that floral trait differences, functioning to segregate heterospecific pollen placement on shared pollinators (Huang & Shi, 2013), evolved recurrently and facilitated sympatric coexistence (Eaton et al., 2012). By contrast, our study of *Rhododendron* suggests that flowering phenology is more labile than floral traits, and that divergence in flowering time has played an important role in the clade's success in the region. Indeed, *Rhododendron* is conspicuous in the Hengduan Mountains for its broad range of flowering times, that begins early and largely precedes the main peak of flowering in June–August that characterizes most of the flora (Geng, 2014; Hart, Georgian, et al., 2016; Wang et al., 1994).

How other species-rich taxa in the Hengduan flora responded to secondary contact following in situ diversification is a fertile area for future research. We predict varied paths towards coexistence among clades, with a common theme: that community assembly of close relatives will be positively related to divergence in ecological traits with greatest evolutionary lability.

AUTHOR CONTRIBUTIONS

Qin Li and Richard H. Ree conceived the ideas and designed methodology of this study. Qin Li, J. Wang and Ryan Fuller conducted the field surveys. Qin Li performed the data analyses with critical inputs from other authors. Qin Li and Richard H. Ree led the writing, and all authors contributed to revisions and gave final approval for publication.

ACKNOWLEDGEMENTS

CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/1365-2745.14002.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.pnvx0k6rb (Li et al., 2022).

ORCID

Qin Li https://orcid.org/0000-0001-9976-8236
Ji Wang https://orcid.org/0000-0003-4309-7087
Ryan Fuller https://orcid.org/0000-0003-2457-0975
Yaowu Xing https://orcid.org/0000-0001-6709-4492
Jianquan Liu https://orcid.org/0000-0002-4237-7418
Richard H. Ree https://orcid.org/0000-0003-1898-3335

REFERENCES

Adler, P. B., HilleRisLambers, J., & Levine, J. M. (2007). A niche for neutrality. *Ecology Letters*, 10(2), 95–104. https://doi.org/10.1111/j.1461-0248.2006.00996.x

Basnett, S., Ganesan, R., & Devy, S. M. (2019). Floral traits determine pollinator visitation in *Rhododendron* species across an elevation gradient in the Sikkim Himalaya. *Alpine Botany*, 129(2), 81–94. https://doi.org/10.1007/s00035-019-00225-3

Basnett, S., Nagaraju, S. K., Hart, R., & Devy, S. M. (2021). Floral traits and community phylogenetic structure shape plant-pollinator interactions in co-occurring Rhododendrons in the Himalaya. *Perspectives in Plant Ecology, Evolution and Systematics*, 53, 125646. https://doi.org/10.1016/j.ppees.2021.125646

Basnett, S., Nagaraju, S. K., Ravikanth, G., & Devy, S. M. (2019). Influence of phylogeny and abiotic factors varies across early and late reproductive phenology of Himalayan *Rhododendrons*. *Ecosphere*, 10(1), e02581. https://doi.org/10.1002/ecs2.2581

Burns, J. H., & Strauss, S. Y. (2011). More closely related species are more ecologically similar in an experimental test. *Proceedings of the National Academy of Sciences of the United States of America*, 108(13), 5302–5307. https://doi.org/10.1073/pnas.1013003108

Chao, A., Chiu, C. H., & Jost, L. (2014). Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through hill numbers. *Annual Review of Ecology, Evolution, and Systematics*, 45, 297–324. https://doi.org/10.1146/annurev-ecolsys-120213-091540

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, 31(1), 343–366. https://doi.org/10.1146/annurev.ecolsys.31.1.343

Darwin, C. (1859). *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. John Murray.

Drost, H. (2018). Philentropy: Information theory and distance quantification with R. *Journal of Open Source Software*, 3(26), 765. https://doi.org/10.21105/joss.00765

Eaton, D. A., Fenster, C. B., Hereford, J., Huang, S. Q., & Ree, R. H. (2012). Floral diversity and community structure in *Pedicularis* (Orobanchaceae). *Ecology*, 93(sp8), S182–S194. https://doi.org/10.1890/11-0501.1

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37(12), 4302–4315. https://doi.org/10.1002/joc.5086

Fu, C. N., Mo, Z. Q., Yang, J. B., Cai, J., Ye, L. J., Zou, J. Y., Qin, H. T., Zheng, W., Hollingsworth, P. M., Li, D. Z., & Gao, L. M. (2022). Testing genome skimming for species discrimination in the large and taxonomically difficult genus *Rhododendron*. *Molecular Ecology Resources*, 22(1), 404–414. https://doi.org/10.1111/1755-0998.13479

Geng, Y. (2014). *The genus Rhododendron of China*. Shanghai Scientific and Technical Publishers.

Godoy, O., Kraft, N. J., & Levine, J. M. (2014). Phylogenetic relatedness and the determinants of competitive outcomes. *Ecology Letters*, 17(7), 836–844. https://doi.org/10.1111/ele.12289

Gotelli, N. J. (2000). Null model analysis of species co-occurrence patterns. *Ecology*, 81(9), 2606–2621. https://doi.org/10.1890/0012-9658(2000)081[2606,NMAOSC]2.0.C0;2

Hart, R., Georgian, E. M., & Salick, J. (2016). Fast and cheap in the fall: Phylogenetic determinants of late flowering phenologies in Himalayan *Rhododendron*. *American Journal of Botany*, 103(2), 198–206. https://doi.org/10.3732/ajb.1500440

Hart, R., & Salick, J. (2018). Vulnerability of phenological progressions over season and elevation to climate change: *Rhododendrons* of Mt. Yulong. *Perspectives in Plant Ecology, Evolution and Systematics*, 34, 129–139. https://doi.org/10.1016/j.ppees.2018.09.001

Hart, S. P., Schreiber, S. J., & Levine, J. M. (2016). How variation between individuals affects species coexistence. *Ecology Letters*, 19(8), 825–838. https://doi.org/10.1111/ele.12618

Huang, S. Q., & Shi, X. Q. (2013). Floral isolation in *Pedicularis*: How do congeners with shared pollinators minimize reproductive interference? *New Phytologist*, 199(3), 858–865. https://doi.org/10.1111/nph.12327

Kembel, S., Cowan, P., Helmus, M., Cornwell, W., Morlon, H., Ackerly, D., Blomberg, S., & Webb, C. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, 26, 1463–1464. https://doi.org/10.1093/bioinformatics/btq166

Khan, G., Nolzen, J., Schepker, H., & Albach, D. C. (2020). Incongruent phylogenies and its implications for the study of diversification, taxonomy and genome size evolution of *Rhododendron* (Ericaceae). *bioRxiv*. https://doi.org/10.1002/ajb2.1747

Kraft, N. J., Adler, P. B., Godoy, O., James, E. C., Fuller, S., & Levine, J. M. (2015). Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology*, 29(5), 592–599. https://doi.org/10.1111/1365-2435.12345

Kron, K. A., Gawen, L. M., & Chase, M. W. (1993). Evidence for introgression in azaleas (*Rhododendron*; Ericaceae): Chloroplast DNA and morphological variation in a hybrid swarm on Stone Mountain, Georgia. *American Journal of Botany*, 80(9), 1095–1099. https://doi.org/10.1002/j.1537-2197.1993.tb15335.x

Levine, J. M., & HilleRisLambers, J. (2009). The importance of niches for the maintenance of species diversity. *Nature*, 461(7261), 254–257. https://doi.org/10.1038/nature08251

Li, Q., Wang, J., Fuller, R., Xing, Y., Liu, J., & Ree, R. H. (2022). Data from: Evidence for divergence in phenology over morphology in response to limiting similarity in montane communities of *Rhododendron*. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.pnvx0k6rb

Liu, Z. (1985). *Vegetation of Gongga Mountain*. Sichuan Science & Technology Press. (in Chinese).

Mahoro, S. (2002). Individual flowering schedule, fruit set, and flower and seed predation in *Vaccinium hirtum* Thunb. (Ericaceae). *Canadian Journal of Botany*, 80(1), 82–92. https://doi.org/10.1139/b01-136

Marczewski, T., Chamberlain, D. F., & Milne, R. I. (2015). Hybridization in closely related *Rhododendron* species: Half of all species-differentiating markers experience serious transmission ratio distortion. *Ecology and Evolution*, 5(15), 3003–3022. https://doi.org/10.1002/ece3.1570

Milne, R. I., & Abbott, R. J. (2008). Reproductive isolation among two interfertile *Rhododendron* species: Low frequency of post-F_1 hybrid genotypes in alpine hybrid zones. *Molecular Ecology*, 17(4), 1108–1121. https://doi.org/10.1111/j.1365-294x.2007.03643.x

Milne, R. I., Davies, C., Prickett, R., Inns, L. H., & Chamberlain, D. F. (2010). Phylogeny of *Rhododendron* subgenus *Hymenanthes* based on chloroplast DNA markers: Between-lineage hybridisation during adaptive radiation? *Plant Systematics and Evolution*, 285(3), 233–244. https://doi.org/10.1007/s00606-010-0269-2

Milne, R. I., Terzioglu, S., & Abbott, R. (2003). A hybrid zone dominated by fertile F1s: Maintenance of species barriers in *Rhododendron*. *Molecular Ecology*, 12(10), 2719–2729. https://doi.org/10.1046/j.1365-294x.2003.01942.x

Muellner-Riehl, A. N. (2019). Mountains as evolutionary arenas: Patterns, emerging approaches, paradigm shifts, and their implications for plant phylogeographic research in the Tibeto-Himalayan region. *Frontiers in Plant Science*, 195. https://doi.org/10.3389/fpls.2019.00195

Niku, J., Hui, F. K., Taskinen, S., & Warton, D. I. (2019). Gllvm: Fast analysis of multivariate abundance data with generalized linear latent variable models in R. *Methods in Ecology and Evolution*, 10(12), 2173–2182. https://doi.org/10.1111/2041-210X.13303

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2020). *Vegan: Community ecology package*. R package version 2.5-7. https://CRAN.R-project.org/package=vegan

Ovaskainen, O., Tikhonov, G., Norberg, A., Guillaume Blanchet, F., Duan, L., Dunson, D., Roslin, T., & Abrego, N. (2017). How to make more

out of community data? A conceptual framework and its implementation as models and software. *Ecology Letters*, 20(5), 561–576. https://doi.org/10.1111/ele.12757

Parker, K. R. (1979). Density estimation by variable area transect. *The Journal of Wildlife Management*, 484–492. https://doi.org/10.2307/3800359

Pérez-Harguindeguy, N., Díaz, S., Garnier Eric, L. S., Poorter, H., Jaureguiberry, P., Bret-Harte, M., Corn-Welf, W., Craine, J., Gurvich, D., Urcelay, C., Veneklaas, E. J., Reich, P. B., Poorter, L., Wright, I. J., Ray, P., Enrico, L., Pausas, J. G., de Vos, A. C., Buchmann, N., … Cornelissen, J. H. C. (2013). New handbook for standardized measurement of plant functional traits worldwide. *Australian Journal of Botany*, 61(3), 167–234. https://doi.org/10.1071/BT12225_CO

Pollock, L. J., Tingley, R., Morris, W. K., Golding, N., O'Hara, R. B., Parris, K. M., Vesk, P. A., & McCarthy, M. A. (2014). Understanding co-occurrence by modelling species simultaneously with a joint species distribution model (JSDM). *Methods in Ecology and Evolution*, 5(5), 397–406. https://doi.org/10.1111/2041-210X.12180

Rees, M., Condit, R., Crawley, M., Pacala, S., & Tilman, D. (2001). Long-term studies of vegetation dynamics. *Science*, 293(5530), 650–655. https://doi.org/10.1126/science.1062586

Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH image to ImageJ: 25 years of image analysis. *Nature Methods*, 9(7), 671–675. https://doi.org/10.1038/nmeth.2089

Schoener, T. W. (1970). Nonsynchronous spatial overlap of lizards in patchy habitats. *Ecology*, 51(3), 408–418. https://doi.org/10.2307/1935376

Spicer, R. A., Farnsworth, A., & Su, T. (2020). Cenozoic topography, monsoons and biodiversity conservation within the Tibetan region: An evolving story. *Plant Diversity*, 42(4), 229–254. https://doi.org/10.1016/j.pld.2020.06.011

Tagane, S., Hiramatsu, M., & Okubo, H. (2008). Hybridization and asymmetric introgression between *Rhododendron eriocarpum* and *R. indicum* on Yakushima Island, Southwest Japan. *Journal of Plant Research*, 121(4), 387–395. https://doi.org/10.1007/s10265-008-0167-7

Tucker, C. M., Cadotte, M. W., Carvalho, S. B., Davies, T. J., Ferrier, S., Fritz, S. A., Grenyer, R., Helmus, M. R., Jin, L. S., Mooers, A. O., Pavoine, S., Purschke, O., Redding, D. W., Rosauer, D. F., Winter, M., & Mazel, F. (2017). A guide to phylogenetic metrics for conservation, community ecology and macroecology. *Biological Reviews*, 92(2), 698–715. https://doi.org/10.1111/brv.12252

Ulrich, W., & Gotelli, N. J. (2010). Null model analysis of species associations using abundance data. *Ecology*, 91(11), 3384–3397. https://doi.org/10.1890/09-2157.1

Wang, W., Wu, S., Lang, K., Li, P., Pu, F., & Chen, S. (1994). *Vascular plants of the Hengduan Mountains* (Vol. 2). Science Press.

Warton, D. I., Blanchet, F. G., O'Hara, R. B., Ovaskainen, O., Taskinen, S., Walker, S. C., & Hui, F. K. (2015). So many variables: Joint modeling in community ecology. *Trends in Ecology & Evolution*, 30(12), 766–779. https://doi.org/10.1016/j.tree.2015.09.007

Webb, C. O., Ackerly, D. D., McPeek, M. A., & Donoghue, M. J. (2002). Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, 33(1), 475–505. https://doi.org/10.1146/annurev.ecolsys.33.010802.150448

Weber, M. G., & Strauss, S. Y. (2016). Coexistence in close relatives: Beyond competition and reproductive isolation in sister taxa. *Annual Review of Ecology, Evolution, and Systematics*, 47, 359–381. https://doi.org/10.1146/annurev-ecolsys-112414-054048

Wu, Y. (2008). *The vascular plants and their eco-geographical distribution of the Qinghai-Tibetan plateau*. Science Press.

Wu, Z. Y., Raven, P. H., & Hong, D. Y. (2005). *Flora of China. Vol. 14 (Apiaceae through Ericaceae)*. Science Press and Missouri Botanical Garden Press.

Xia, X. M., Yang, M. Q., Li, C. L., Huang, S. X., Jin, W. T., Shen, T. T., Wang, F., Li, X. H., Yoichi, W., Zhang, L. H., Zheng, Y., & Wang, X.-Q. (2022). Spatiotemporal evolution of the global species diversity of *Rhododendron*. *Molecular Biology and Evolution*, 39(1), msab314. https://doi.org/10.1093/molbev/msab314

Xing, Y., & Ree, R. H. (2017). Uplift-driven diversification in the Hengduan Mountains, a temperate biodiversity hotspot. *Proceedings of the National Academy of Sciences of the United States of America*, 114(17), E3444–E3451. https://doi.org/10.1073/pnas.1616063114

Yan, L. J., Burgess, K. S., Milne, R. I., Fu, C. N., Li, D. Z., & Gao, L. M. (2017). Asymmetrical natural hybridization varies among hybrid swarms between two diploid *Rhododendron* species. *Annals of Botany*, 120(1), 51–61. https://doi.org/10.1093/aob/mcx039

Zha, H. G., Milne, R. I., & Sun, H. (2008). Morphological and molecular evidence of natural hybridization between two distantly related *Rhododendron* species from the Sino-Himalaya. *Botanical Journal of the Linnean Society*, 156(1), 119–129. https://doi.org/10.1111/j.1095-8339.2007.00752.x

Zheng, W., Yan, L. J., Burgess, K. S., Luo, Y. H., Zou, J. Y., Qin, H. T., Wang, J. H., & Gao, L. M. (2021). Natural hybridization among three *Rhododendron* species (Ericaceae) revealed by morphological and genomic evidence. *BMC Plant Biology*, 21(1), 1–12. https://doi.org/10.1186/s12870-021-03312-y

Zhou, H., & Jiang, Y. (2016). *Rhododendrons in the Gongga reserve*. Sichuan Digital Publishing and Media Co. (in Chinese).

Zou, J. Y., Luo, Y. H., Burgess, K. S., Tan, S. L., Zheng, W., Fu, C. N., Xu, K., & Gao, L. M. (2021). Joint effect of phylogenetic relatedness and trait selection on the elevational distribution of *Rhododendron* species. *Journal of Systematics and Evolution*, 59(6), 1244–1255. https://doi.org/10.1111/jse.12690

Zu, K., Luo, A., Shrestha, N., Liu, B., Wang, Z., & Zhu, X. (2019). Altitudinal biodiversity patterns of seed plants along Gongga Mountain in the southeastern Qinghai–Tibetan plateau. *Ecology and Evolution*, 9(17), 9586–9596. https://doi.org/10.1002/ece3.5483

Zu, K., Wang, Z., Zhu, X., Lenoir, J., Shrestha, N., Lyu, T., Luo, A., Li, Y., Ji, C., Peng, S., Meng, J., & Zhou, J. (2021). Upward shift and elevational range contractions of subtropical mountain plants in response to climate change. *Science of the Total Environment*, 783, 146896. https://doi.org/10.1016/j.scitotenv.2021.146896

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.