Effects of Net Diversification Rate and Evolutionary Time on Inter-Familial Differences in Species Diversity in Saxifragales (Postprint)

Authors: Gu Jiahao, Zhang Lihao, Zhang Haoyu, Wu Tianqing, Huang Linqing, Ruijing Cheng, Xu Ying, Wang Qinggang, Xu Xiaoting

Date: 2022-05-21T20:03:12+00:00

Abstract

Different biological groups often exhibit substantial differences in species richness, a phenomenon commonly observed in ecological and biological research. However, the causes underlying this phenomenon remain an unresolved mystery. From a macroevolutionary perspective, the evolutionary time hypothesis and the diversification rate hypothesis are two prominent hypotheses. The evolutionary time hypothesis posits that the longer the evolutionary history of a group, the higher its accumulated species richness; whereas the diversification rate hypothesis suggests that the faster the net diversification rate of a group, the greater its species richness. To test these two hypotheses, this study utilized a fossil-calibrated phylogenetic tree of Saxifragales comprising 1,539 species as a foundation, obtained speciation and extinction rates for 15 families within Saxifragales through macroevolutionary analysis, and calculated the average diversification rate for each family. The results indicate: (1) Saxifragales exhibits an increasing trend in species diversification rates, and this increase occurs primarily in temperate and alpine groups, such as Grossulariaceae, Crassulaceae, and Paeoniaceae. (2) Results from phylogenetic generalized least squares models and linear regression models demonstrate that species richness in the 15 families of Saxifragales shows no significant correlation with family divergence time or the age of the most recent common ancestor of species within each family, but is significantly positively correlated with net diversification rate ($R2 = 0.38$, $P<0.01$). This study supports the diversification rate hypothesis, suggesting that differences in net diversification rates among families constitute one of the primary causes for inter-familial variation in species numbers within Saxifragales. Global climate cooling may have provided opportunities for range expansion and rapid species diversification in groups capable of adapting to cold environments, such as herbaceous plants, deciduous trees, and shrubs within Saxifragales. This study suggests that in temperate and alpine expanding groups, species net diversification rate may be the primary factor driving differences in species numbers among different groups.

Full Text

Influence of Net Diversification Rate and Evolutionary Time on Differences in Species Richness Among Families of the Order Saxifragales

GU Jiahao[1,2], ZHANG Lihao[1,2], ZHANG Haoyu[1,2], WU Tianqing[1], HUANG Linqing[3], CHENG Ruijing[1,2], XU Ying[1,2], WANG Qinggang[4], XU Xiaoting[1,2]*

[1]College of Life Sciences, Sichuan University, Chengdu 610065, China
[2]Key Laboratory of Biological Resources and Ecological Environment, Ministry of Education, Sichuan University, Chengdu 610065, China
[3]College of Biomedical Engineering, Sichuan University, Chengdu 610065, China
[4]College of Resources and Environmental Sciences, China Agricultural University, Beijing 100083, China

Abstract: Differences in species richness among biological groups are a widespread phenomenon in ecological and biological research, yet the underlying mechanisms remain unresolved. From a macroevolutionary perspective, the time-for-speciation hypothesis and the diversification rate hypothesis represent two leading explanations. The time-for-speciation hypothesis posits that older clades accumulate greater species richness over time, whereas the diversification rate hypothesis suggests that clades with higher net diversification rates produce more species. To test these hypotheses, we analyzed a fossil-calibrated phylogenetic tree comprising 1,539 species across 15 families of Saxifragales, estimating speciation and extinction rates for each family and calculating their average diversification rates. Our results reveal: (1) Saxifragales exhibits an increasing trend in diversification rates, particularly pronounced in temperate and alpine groups such as Grossulariaceae, Crassulaceae, and Paeoniaceae. (2) Phylogenetic generalized least squares and linear regression models show no significant relationship between species richness and either family crown age or stem age, but demonstrate a significant positive correlation with net diversification rate ($R^2 = 0.38$, $P < 0.01$). These findings support the diversification rate hypothesis, indicating that variation in net diversification rates among families is a primary driver of species richness differences within Saxifragales. Global climate cooling likely provided opportunities for range expansion and rapid diversification in herbaceous, deciduous, and shrub lineages adapted to cold environments. Our study demonstrates that in temperate and alpine radiating groups, net diversification rate may be the main factor causing differences in species numbers among clades.

Keywords: Saxifragales, species diversity, phylogeny, diversification rate,

macroevolution

Introduction

Differences in total species numbers among biological groups are ubiquitous in nature, yet the mechanisms generating these patterns remain an unresolved puzzle (Li & Wiens, 2019). From a macroevolutionary perspective, the time-for-speciation hypothesis and the diversification rate hypothesis represent two core explanations for inter-clade variation in species diversity (Scholl & Wiens, 2016; Li & Wiens, 2019). The time-for-speciation hypothesis proposes that greater evolutionary time allows for higher species accumulation, making temporal differences the primary cause of diversity disparities among groups. In other words, ancient lineages should contain more species than recently originated groups simply by virtue of their longer evolutionary history. Conversely, the diversification rate hypothesis argues that dynamic variation in speciation and extinction rates across lineages, resulting in differences in net diversification rates, drives changes in species diversity (Scholl & Wiens, 2016). Under this scenario, clades with high speciation rates and low extinction rates—thus exhibiting high net diversification rates—should possess greater species richness.

The relative importance of these two hypotheses in shaping species diversity patterns remains contentious. The time-for-speciation hypothesis assumes negligible differences in net diversification rates among clades, yet accumulating evidence reveals substantial rate variation across groups. This is particularly evident in lineages that have experienced major extinction events, where species numbers can plummet abruptly, causing sudden losses of diversity. For example, Rabosky et al. (2012) found no significant relationship between clade age (stem age) and species richness across 1,397 major eukaryotic lineages, thereby rejecting the time-for-speciation hypothesis. Pyron & Wiens (2013) similarly observed that many ancient amphibian lineages harbor low species diversity while some younger clades contain numerous species, though their study did not directly test the relationship between diversity and diversification rates. In contrast, McPeek & Brown (2007) identified clade age as a determinant of species diversity in animal groups, and Marin & Hedges (2016) reported significant positive correlations between crown age and species richness in amphibians, birds, and mammals. To further evaluate these hypotheses, Scholl & Wiens (2016) analyzed species diversity patterns across different taxonomic levels using the tree of life, finding that diversity at levels from phyla to families is primarily determined by diversification rates rather than evolutionary time, with some cases even showing negative correlations. They suggested that ancient clades may have low diversification rates while younger clades exhibit high rates, potentially obscuring relationships between diversification rates and species richness. Overall, the roles of evolutionary time and diversification rates in generating species diversity patterns remain debated.

Saxifragales comprises approximately 3,000 species across 15 families, encompassing diverse life forms including trees, shrubs, perennial and annual herbs, succulents, and aquatic plants distributed globally across various ecosystems (Soltis et al., 2013). The families within Saxifragales diverged from the Late Cretaceous to the Early Tertiary, yet exhibit dramatic variation in species numbers. The largest family, Crassulaceae, contains about 1,600 species, while Cynomoriaceae, Tetracarpaeaceae, and Aphanopetalaceae each have fewer than 10 species. The molecular phylogenetics of Saxifragales are well-established, with a robust phylogenetic framework based on 301 nuclear genes that resolved inter-familial relationships and divergence times (Folk et al., 2019). Folk et al. (2019) further constructed a species-level phylogeny using multiple gene fragments, achieving over 70% coverage of recognized species and providing a solid foundation for accurate diversification rate estimation. Consequently, Saxifragales represents an ideal system for investigating inter-familial variation in species richness and testing the time-for-speciation and diversification rate hypotheses. Using phylogenetic generalized least squares (PGLS) models, we analyzed relationships between species diversity and family crown age, stem age, and diversification rates. We found significant positive correlations between species diversity and diversification rates, but no significant relationships with evolutionary time. Moreover, the combined effects of evolutionary time and diversification rates provided stronger explanatory power for richness differences. These results highlight the importance of diversification rates in shaping Saxifragales diversity patterns, supporting the diversification rate hypothesis while also acknowledging the combined effects of time and rate.

Materials and Methods

1.1 Phylogenetic Tree of Saxifragales

Our phylogenetic tree was primarily based on the Saxifragales phylogeny published by Folk et al. (2019) and the *Saxifraga* phylogeny constructed by Xu et al. (2021). Folk et al. (2019) first built a phylogeny of major Saxifragales lineages using 301 nuclear gene sequences from 627 species, calibrating divergence times with fossils and molecular clock methods. They then constructed a phylogenetic tree comprising 1,455 species across 15 families using nuclear ITS regions and 24 chloroplast gene fragments (including *matK*) downloaded from GenBank. The phylogeny by Xu et al. (2021) included 353 *Saxifraga* species, covering all *Saxifraga* taxa present in the Folk et al. (2019) tree, with consistent divergence times. We integrated these two trees by replacing the *Saxifraga* clade in the Folk et al. (2019) tree with the more comprehensive *Saxifraga* phylogeny from Xu et al. (2021) using R (Bininda & Olaf, 2004; Gordon, 1986). The final integrated phylogeny contained 1,539 species, representing all families within Saxifragales.

1.2 Species Diversity of Families

Species counts for each family were compiled from the Catalogue of Life database (COL, https://www.catalogueoflife.org/, accessed May 2021), following accepted species names. Subspecific taxa (varieties and subspecies) and hybrids were excluded. Because species richness data did not follow a normal distribution, we $\log_{10}$-transformed the counts to improve model fit, following Rabosky et al. (2012).

1.3 Calculation of Crown and Stem Ages

Crown age and stem age represent two distinct concepts for measuring clade age in phylogenetic trees (Fig. 1). Crown age denotes the age of the most recent common ancestor (MRCA) of all extant members of a clade, while stem age represents the age of the MRCA shared between the clade and its sister group. Some researchers argue that crown age is more appropriate for statistical analyses when sampling is adequate, as it eliminates the effects of long branches resulting from evolutionary stasis or extinction events (Sanchez-Reyes et al., 2017). To comprehensively assess the relationship between evolutionary time and species richness, we analyzed both crown and stem ages for each family.

We extracted crown and stem ages using the `ape` package in R (R Core Team, 2021; Paradis & Schliep, 2019). The `getMRCA()` function identified the node representing the MRCA of each family's species (crown age), and its parent node (stem age). Node ages were extracted using the `branching.times()` function, and node labels were obtained with `getMRCA()`. This process yielded crown and stem ages for all 15 families.

1.4 Diversification Rates of Families

We estimated diversification rates using Bayesian Analysis of Macroevolutionary Mixtures (BAMM) via the `BAMMtools` package in R (Rabosky et al., 2014). Markov chain Monte Carlo (MCMC) analyses ran for 10 million generations, sampling every 1,000 generations. Convergence and effective sample sizes (ESS) were assessed using the `coda` package; ESS values >200 indicated adequate independent samples for reliable parameter estimation. Family-level speciation and extinction rates were extracted as branch-length-weighted averages using the `getCladeRates()` function in `BAMMtools`. Net diversification rate was calculated as the difference between speciation and extinction rates. Due to high uncertainty in extinction rate estimates, we analyzed both speciation and net diversification rates in relation to species richness.

To examine rate variation between temperate and evergreen tree lineages, we partitioned the Saxifragales phylogeny using the `drop.tip()` function in `ape`. Evergreen tree families (Peridiscaceae, Daphniphyllaceae, Iteaceae, and Altingiaceae) were separated from the remaining 11 temperate-adapted families. Rate-through-time plots were generated using `plot.bammdata()` in `BAMMtools`.

1.5 Relationships Between Species Richness, Diversification Rates, and Evolutionary Time

We employed both linear regression (LM) and phylogenetic generalized least squares (PGLS) models to analyze relationships between species richness and diversification rates or evolutionary time. To test the diversification rate hypothesis, we constructed univariate LM and PGLS models with speciation rate and net diversification rate as predictors. To test the time-for-speciation hypothesis, we built separate models with crown age and stem age as predictors. Recognizing that both factors may jointly influence richness, we also examined the interactive effects of diversification rates and evolutionary time (represented by crown age) on species diversity. LM analyses were performed using the base `lm()` function in R, while PGLS analyses used the `gls()` function in the `nlme` package. For PGLS, we used a family-level phylogeny constructed by pruning the species tree to retain a single representative species per family using `drop.tip()` in `ape`.

Results

2.1 Relationships Between Crown Age, Stem Age, and Species Richness in Saxifragales Families

Crown and stem ages varied substantially among the 15 Saxifragales families. The youngest family, Cercidiphyllaceae, had a crown age of only 3 million years (Myr), while the oldest, Peridiscaceae, exceeded 80 Myr (Table 1), demonstrating considerable temporal heterogeneity within the order.

Linear regression explained 26.1% of variation in species richness using crown age, but only 16.4% using stem age (Fig. 2). PGLS results were consistent: the slope for crown age ($\beta = 0.015$) was slightly lower than for stem age ($\beta = 0.019$). However, neither crown nor stem age showed significant effects on species richness ($P > 0.05$). These results indicate that species richness among Saxifragales families is not significantly correlated with evolutionary time, suggesting that temporal differences are not the primary driver of inter-familial diversity variation.

2.2 Relationships Between Diversification Rates and Species Richness in Saxifragales Families

Families with high net diversification rates were predominantly temperate and alpine groups, concentrated within the herbaceous clade of Saxifragales. Grossulariaceae, Haloragaceae, and Crassulaceae exhibited relatively high speciation and net diversification rates (Table 1, Fig. 3), with notable increases over the past 15 million years (Fig. 3, Fig. 4). In contrast, families composed primarily of evergreen trees showed lower speciation and net diversification rates (Table 1, Fig. 3, Fig. 4).

Both LM and PGLS analyses revealed positive relationships between speciation rate and species richness, though significance varied between methods (LM: $R^2 = 0.280$, $\beta = 7.319$, $P < 0.05$; PGLS: $\beta = 6.425$, $P < 0.05$). Net diversification rate showed consistently significant positive correlations with species richness across both methods (PGLS: $\beta = 9.790$, $P = 0.031$; LM: $R^2 = 0.380$, $\beta = 11.791$, $P < 0.05$).

2.3 Combined Effects of Evolutionary Time and Diversification Rates on Family Species Richness

The interactive effects of evolutionary time and net diversification rate on species richness were significant in both LM and PGLS models (LM: $R^2 = 0.603$, $\beta = 0.297$, $P < 0.05$; PGLS: $\beta = 0.287$, $P < 0.05$) (Fig. 6). The LM model explained 60% of diversity variation through this interaction, with PGLS slopes exceeding those from single-variable models. These results support the importance of combined evolutionary time and diversification rate effects on inter-familial richness differences in Saxifragales, with the interaction providing greater explanatory power than diversification rate alone.

Discussion and Conclusion

Our PGLS analyses demonstrate a significant positive relationship between species richness and net diversification rate across 15 Saxifragales families, while no significant correlation exists with crown age. Linear regression models show that net diversification rate alone explains 38% of variation in species richness. Building on Scholl & Wiens (2016), who suggested that interactions between diversification rates and age may drive diversity differences, we tested the interaction between net diversification rate and crown age, finding that it explains 60% of richness variation. We therefore conclude that differences in net diversification rates are the primary determinant of species diversity variation, while the combined effects of evolutionary time and diversification rates play a secondary role.

Our findings do not support the time-for-speciation hypothesis, consistent with Rabosky et al. (2012) and Scholl & Wiens (2016), who demonstrated that richness differences among clades are not driven by evolutionary time. Although Pyron & Wiens (2013) found significant positive relationships between diversity and crown age in tropical amphibians, they also reported strong positive correlations between diversity and net diversification rate, linking diversification rates to net primary productivity and area. They concluded that rapid niche evolution, high speciation, and low extinction in tropical families, combined with the persistence of ancient lineages, explain high tropical diversity. In Saxifragales, herbaceous and shrub families adapted to temperate environments exhibit higher speciation and net diversification rates, which likely drives the observed positive correlation between richness and net diversification rate. Folk et al. (2019) reconstructed ancestral niches showing that common ancestors of temperate-adapted families like Crassulaceae, Saxifragaceae, and Grossulariaceae could tolerate relatively dry and cold conditions as early as 80 million years ago. During Oligocene global cooling, these lineages already showed higher diversification rates than woody families such as Altingiaceae. After the Miocene, as global climate cooled further, diversification rates in these temperate groups increased rapidly. The strong adaptation of herbaceous and shrub lineages to cold environments likely facilitated their rapid diversification during global cooling. For example, Haloragaceae experienced substantial range expansion and diversification rate increases during the Eocene-Oligocene cooling and aridification (Moody & Garcia, 2021).

Geological events reshape topography and alter regional climates, thereby influencing biological evolution (Tang & Fang, 2004; Antonelli et al., 2018). Mountain uplift promotes population isolation and divergence while creating complex habitats and diverse niches that drive rapid evolution in alpine plants, a process closely linked to accelerated diversification in multiple Saxifragales families (Zhang et al., 2014a; Liu et al., 2017; Moody & Garcia, 2021). Rapid adaptation and divergence of montane herbaceous groups have made the Qinghai-Tibet Plateau, western North American mountains, and European Alps major centers of alpine diversity in Saxifragales (Zhang et al., 2008; Zhang et al., 2014b; Ebersbach et al., 2017; Xing et al., 2017; Stubbs et al., 2020). Following plateau uplift, many plant lineages diversified rapidly, including cold-adapted Saxifragales such as *Saxifraga* and *Rhodiola* (Zhang et al., 2014a; Ebersbach et al., 2017; Folk et al., 2019). Consequently, rapid diversification of alpine groups in Saxifragales has produced the observed positive correlation between species richness and net diversification rate.

Studies of rosids have found that diversification rates in Saxifragales and other orders increased with global cooling and show latitudinal gradients, with higher rates at higher latitudes (Sun et al., 2020). Igea et al. (2020) reported similar patterns across angiosperms, where temperate and boreal lineages often diversify faster than tropical groups. These findings suggest that temperate lineages have accumulated diversity during global cooling. Although high-latitude regions currently harbor lower diversity due to severe glacial impacts, temperate clades have experienced higher diversification rates than tropical clades. Therefore, beyond Saxifragales, similar patterns may exist across angiosperm families, where inter-familial richness differences correlate positively with net diversification rates.

Researchers have proposed that multiple factors likely contribute to diversity differences, with both clade age and diversification rates playing important roles (Valente et al., 2011; Bloom et al., 2014; Yan et al., 2018). Recent discussions have shifted from testing which hypothesis is “correct” toward examining interactions among these factors and developing more sophisticated statistical models (Pontarp et al., 2019). Although our study shows high explanatory power for the interaction between net diversification rate and age, whether this conclusion applies to other groups requires further validation. This question remains open for debate, and future research should employ more complex statistical methods and comprehensive datasets across plants and animals.

Nuclear genes have synonymous substitution rates five times higher than chloroplast genes and twenty times higher than mitochondrial genes, with multiple independent loci and biparental inheritance (Small et al., 2004). Consequently, nuclear gene phylogenies provide more comprehensive and objective resolution of relationships than those based on small DNA fragments. Our study utilized the phylogeny from Folk et al. (2019), which combined 301 nuclear genes for major lineages with chloroplast genome fragments and ITS sequences to improve species coverage. This approach yielded familial relationships consistent with APG IV (Chase et al., 2016). However, low taxon sampling can substantially affect diversification analyses (Chang et al., 2020), and nuclear genomic data remain limited by sampling difficulties and high costs. Combining genomic and small-fragment data represents one solution, though small fragments may lack sufficient informative sites for accurate resolution of recent relationships and could affect branch length estimation, thereby influencing diversification rate inference. As chloroplast genome sequencing becomes more affordable and analytical methods mature, increasing chloroplast genome coverage may provide a more economical and efficient approach for resolving relationships among closely related species.

References

ANTONELLI A, KISSLING WD, FLANTUA S, et al., 2018. Geological and climatic influences on mountain biodiversity [J]. Nat Geosci, 11(10): 718-725.

ANGIOSPERM PHYLOGENY GROUP, CHASE MW, CHRISTENHUSZ MJM, et al., 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV[J]. Bot J Linn Soc, 181(1): 1-20.

BARRACLOUGH TG, HARVEY PH, NEE S, 1996. Rate of rbcL gene sequence evolution and species diversification in flowering plants (Angiosperms) [J]. Proc Roy Soc London Ser A, 263(1370): 589-591.

BARRACLOUGH TG, SAVOLAINEN V, 2010. Evolutionary rates and species diversity in flowering plants [J]. Evolution, 55(4): 677-683.

BININDA-EMONDS ORP, 2004. The evolution of supertrees [J]. Trend Ecol Evol, 19(6): 315-322.

BLOOM DD, MARTIN F, SHORT A, et al., 2014. Clade age and diversification rate variation explain disparity in species richness among water scavenger beetle (Hydrophilidae) Lineages [J]. PLoS ONE, 9(6): e98430.

CHANG J, RABOSKY DL, ALFARO ME, 2020. Estimating diversification rates on incompletely sampled phylogenies: theoretical concerns and practical solutions[J]. Syst Biol, 69(3): 602-611.

EBERSBACH J, MUELLNER-RIEHL AN, MICHALAK I, et al., 2017. In and out of the Qinghai-Tibet Plateau: divergence time estimation and historical biogeography of the large arctic-alpine genus Saxifraga L [J]. J Biogeogr, 44(4): 900-910.

FOLK RA, STUBBS RL, MORT ME, et al., 2019. Rates of niche and phenotype evolution lag behind diversification in a temperate radiation [J]. Proc Natl Acad Sci USA, 116(22): 11074-11079.

GORDON AD, 1986. Consensus supertrees: The synthesis of rooted trees containing overlapping sets of labeled leaves [J]. J Classif, 3(2): 335-348.

IGEA J, TANENTZAP AJ, 2020. Angiosperm speciation cools down in the tropics [J]. Ecol Lett, 23(4): 692-700.

JIAN S, SOLTIS PS, GITZENDANNER MA, et al., 2008. Resolving an ancient, rapid radiation in Saxifragales [J]. Syst Biol, 57(1): 38-57.

LI H, WIENS JJ, 2019. Time explains regional richness patterns within clades more often than diversification rates or area [J]. Amer Nat, 193(4): 514-529.

LIU J, LUO YH, LI DZ, et al., 2017. Evolution and maintenance mechanisms of plant diversity in the Qinghai-Tibet Plateau and adjacent regions: retrospect and prospect [J]. Biodivers Sci, 25(2): 163-174.

MACHAC A, 2020. The dynamics of bird diversity in the New World [J]. Syst Biol, 69(6): 1180-1194.

MARIN J, HEDGES SB, 2016. Time best explains global variation in species richness of amphibians, birds and mammals [J]. J Biogeogr, 43(6): 1069-1079.

MARIN J, RAPACCIUOLO G, COSTA GC, et al., 2018. Evolutionary time drives global tetrapod diversity [J]. Proc Roy Soc B-Biol Sci, 285(1872): 20172378.

MCPEEK MA, BROWN JM, 2007. Clade age and not diversification rate explains species richness among animal taxa [J]. Amer Nat, 169(4): 97-106.

MOODY ML, GARCIA M, 2021. Post-Oligocene diversification in Australia: Phylogeography, systematics and new species of Gonocarpus (Haloragaceae)[J]. Taxon, 70(4): 761-777.

MORALES-BARBERO J, GOUVEIA SF, MARTINEZ PA, 2021. Historical climatic instability predicts the inverse latitudinal pattern in speciation rate of modern mammalian biota [J]. J Evol Biol, 34(2): 339-351.

MOREAU CS, BELL CD, 2013. Testing the museum versus cradle tropical biological diversity hypothesis: phylogeny, diversification, and ancestral biogeographic range evolution of the ants [J]. Evolution, 67(8): 2240-2257.

PARADIS E, SCHLIEP K, 2019. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R[J]. Bioinformatics, 35(3): 526-528.

PONTARP M, BUNNEFELD L, CABRAL JS, et al., 2018. The latitudinal diversity gradient: novel understanding through mechanistic eco-evolutionary models [J]. Trends Ecol Evol, 34(3): 211-223.

PYRON RA, WIENS JJ, 2013. Large-scale phylogenetic analyses reveal the causes of high tropical amphibian diversity [J]. Proc Roy Soc B: Biol Sci, 280(1770): 20131622.

RABOSKY DL, 2010. Ecological limits and diversification rate: alternative paradigms to explain the variation in species richness among clades and regions [J]. Ecol Lett, 12(8): 735-743.

RABOSKY DL, ADAMS DC, 2012. Rates of morphological evolution are correlated with species richness in salamanders [J]. Evolution, 66(6): 1807-1818.

RABOSKY DL, GRUNDLER M, ANDERSON C, et al., 2014. BAMM tools: an R package for the analysis of evolutionary dynamics on phylogenetic trees [J]. Meth Ecol Evol, 5(7): 701-707.

RABOSKY DL, SLATER GJ, ALFARO ME, et al., 2012. Clade age and species richness are decoupled across the eukaryotic tree of life [J]. Plos Biol, 10(8): e1001381.

R CORE TEAM, 2021. R: A language and environment for statistical computing, R Foundation for Statistical Computing, Vienna, Austria [EB/OL]. URL http://www.R-project.org/.

RICKLEFS RE, RENNER SS, 1994. Species richness within families of flowering plants [J]. Evolution, 48(5): 1619-1636.

SÁNCHEZ-REYES LL, MORLON H, MAGALLÓN S, 2017. Uncovering higher-taxon diversification dynamics from clade age and species-richness data [J]. Syst Biol, 66(3): 367-378.

SCHOLL JP, WIENS JJ, 2016. Diversification rates and species richness across the tree of life [J]. Proc Roy Soc B: Biol Sci, 283(1838): 20161334.

SMALL RL, CRONN RC, WENDEL JF, 2004. Use of nuclear genes for phylogeny reconstruction in plants[J]. Aust Syst Bot, 17(2): 145-170.

SMITH SA, DONOGHUE MJ, 2008. Rates of molecular evolution are linked to life history in flowering plants [J]. Science, 322(5898): 86-89.

SOLTIS DE, MORT ME, LATVIS M, et al., 2013. Phylogenetic relationships and character evolution analysis of Saxifragales using a supermatrix approach [J]. Amer J Bot, 100(5): 916-929.

STUBBS RL, FOLK RA, SOLTIS DE, et al., 2020. Diversification in the Arctic: Biogeography and systematics of the North American Micranthes (Saxifragaceae) [J]. Syst Bot, 45(4): 802-813.

SUN M, FOLK RA, GITZENDANNER MA, et al., 2020. Recent accelerated diversification in rosids occurred outside the tropics [J]. Nat Commun, 11(1): 3333.

TANG ZY, FANG JY, 2004. A review on the elevational patterns of plant species diversity [J]. Biodivers Sci, 12(1): 20–28.

VALENTE LM, SAVOLAINEN V, VARGAS P, et al., 2011. Unparalleled rates of species diversification in Europe [J]. Proc Roy Soc B: Biol Sci, 278(1722): 3099-3106.

WIENS JJ, 2011. The causes of species richness patterns across space, time, and clades and the role of "Ecological Limits" [J]. Quart Rev Biol, 86(2): 75-96.

XING Y, REE RH, 2017. Uplift-driven diversification in the Hengduan Mountains, a temperate biodiversity hotspot [J]. Proc Natl Acad Sci USA, 114(17): 3444-3451.

XU Y, 2021. Speciation patterns of Saxifraga. L based on sister species [D]. Chengdu: Sichuan University:1-27.

YAN HF, ZHANG CY, ANDERBERG AA, et al., 2018. What explains high plant richness in East Asia? Time and diversification in the tribe Lysimachieae (Primulaceae) [J]. New Phytol, 219(1). doi: 10.1111/nph.15144.

ZHANG DJ, CHEN SY, GAO QB, et al., 2008. Circumscription and phylogeny of Saxifraga sect. Ciliatae: Evidence from nrDNA ITS sequences [J]. J Syst Evol, 46(5): 667-675.

ZHANG JQ, MENG SY, RAO GY, 2014a. Phylogeography of Rhodiola kirilowii (Crassulaceae): A story of miocene divergence and quaternary expansion [J]. PLoS ONE, 9(11): e112923.

ZHANG JQ, MENG SY, ALLEN GA, et al., 2014b. Rapid radiation and dispersal out of the Qinghai-Tibetan Plateau of an alpine plant lineage Rhodiola (Crassulaceae) [J]. Mol Phylogenet Evol, 77: 147-158.

Note: Figure translations are in progress. See original paper for figures.