BIODIVERSITY STUDIES

Biodiversty Studies (BiSt)
2025, 4(2): 27-37
https://doi.org/10.56494/dnbgt.2025.25

RESEARCH PAPER

Reconstructing Evolutionary Histories: A Comprehensive Review of RASP for Historical Biogeography and Trait Evolution

Mevlüde Alev ATEŞ[1*] , **Tuğba ÇEVİRME**[1], **Berkan ÇEVİRME**[1]
[1]*Department of Agricultural Biotechnology, Faculty of Agriculture, Kırsehir Ahi Evran University, 40200 Kırsehir, Türkiye*

How to cite: Ateş, M. A., Çevirme, T., & Çevirme, B. (2025). Reconstructing evolutionary histories: A comprehensive review of RASP for historical biogeography and trait evolution. *Biodiversity Studies (BiSt)*, , *4*(2): 27-37.

*** Corresponding Author**
E-mail: malev.ates@ahievran.edu.tr
https://orcid.org/0000-0002-2141-5438
https://orcid.org/0009-0002-0286-813X
https://orcid.org/0009-0006-1792-4519

Article History:
Received: 09.11.2025
Accepted: 23.12.2025
First online: 25.12.2025

Keywords
RASP, evolution, biogeography

Abstract

Understanding how species originate, diversify, and change across geographic landscapes is a major topic in evolutionary biology. The rapid increase in phylogenetic and biogeographic datasets has driven need for integrative analytical platforms capable of reconstructing ancestral states while accommodating ambiguity. RASP (Reconstruct Ancestral State in Phylogenies) has developed as a frequently utilized tool for historical biogeography, enabling users to apply likelihood-based models, Bayesian frameworks, and parsimony approaches within a unified graphical environment. RASP 4 includes considerable developments, including generalized statistical integration across posterior trees, parallel computing capabilities, phylogenetic signal assessment, continuous and discrete trait evolution tools, and tree-comparison metrics. This paper synthesizes the theoretical underpinning, methodological framework, and practical functioning of RASP, stressing its implementation of BioGeoBEARS models (DEC, DIVALIKE, BAYAREALIKE), Bayesian Binary MCMC, and S-DIVA. Applications across plants, animals, fungi, and vertebrates indicate its capacity to infer biogeographic history, discover vicariance and dispersal mechanisms, and clarify evolutionary patterns under difficult topography or ecological circumstances. Case studies with Turkish *Astragalus* and *Gundelia* taxa indicate RASP's usefulness in places with significant endemism and environmental variation, while examples from Malagasy lizards and fungal infections highlight its versatility in addressing phylogenetic and ecological concerns. Although RASP enables sophisticated visualization, model testing, and uncertainty integration, its output remains subject to geographic coding accuracy and model assumptions. Nevertheless, expanding genomic datasets and developing evolutionary models assure that RASP will continue to function as a crucial tool in biogeography, trait evolution, and macroevolutionary study.

INTRODUCTION

Understanding the mechanisms by which species originate, evolve, and disperse across geographical landscapes is a fundamental objective in evolutionary biology. The increased accessibility of molecular, morphological, ecological, and biogeographic datasets, along with substantial progress in phylogenetic methodologies, has enabled effective techniques for deducing ancestral character states, including ancestral geographic distributions. RASP (Reconstruct Ancestral State in Phylogenies) has become a significant software platform in historical biogeography and trait evolution studies. RASP integrates various ancestral area reconstruction methodologies into a unified graphical interface, enabling researchers to assess phylogenetic uncertainty, compare distinct evolutionary models, and visualize reconstruction results. The incorporation of BioGeoBEARS models, Bayesian Binary, Markov Chain Monte Carlo-MCMC (BBM), parsimony-based methods, and trait evolution tools makes it highly suitable for current biogeographic analysis.

This review outlines the conceptual framework of RASP, clarifies its methodological components, highlights the advancements in RASP 4, and synthesizes its applications across various taxa, including plants, animals, and fungi.

OVERVIEW AND DEVELOPMENT OF RASP

RASP was originally developed to facilitate the implementation of Statistical Dispersal–Vicariance Analysis (S-DIVA) within a graphical user interface (Yu et al., 2015). Since its initial release, RASP has evolved into a comprehensive analytical platform that integrates multiple biogeographic and evolutionary approaches, including BioGeoBEARS models such as DEC, DIVALIKE, and BAYAREALIKE (Matzke, 2014), Bayesian Binary MCMC (BBM) analyses, parsimony-based ancestral state reconstructions, trait evolution and phylogenetic signal analyses, as well as tree comparison metrics and clustering tools.

Major Improvements in RASP 4 (Yu et al., 2015)

The latest version, RASP 4, includes several important advancements:

- A generalized statistical method that integrates ancestral reconstructions across multiple posterior trees
- Compatibility with phylogenomic, transcriptomic, proteomic, and morphological datasets
- Parallel computing capabilities to handle large datasets efficiently
- Expanded toolkits for:
  - Measuring phylogenetic signal (Moran's I, Abouheif's Cmean, Pagel's λ, Blomberg's K)
  - Inferring ancestral states for discrete and continuous traits
  - Comparing trees using distance metrics such as Robinson–Foulds and BHV

These developments position RASP as a versatile platform for both biogeographic and trait-based evolutionary analyses (Pagel, 1999; Blomberg et al., 2003; Joy et al.,2016).

METHODOLOGICAL FRAMEWORK

BioGeoBEARS Models in RASP

RASP implements widely used BioGeoBEARS models, each reflecting different assumptions about range evolution (Matzke, 2014; Yu et al., 2015) :

- DEC (Dispersal–Extinction–Cladogenesis): A likelihood-based model describing range evolution through dispersal and local extinction.
- DIVALIKE: A likelihood approximation of DIVA emphasizing vicariance.
- BAYAREALIKE: A Bayesian framework that optionally incorporates founder-event speciation.

To integrate uncertainty across phylogenetic trees, RASP consolidates ancestral estimates using:

$$p(x_n) = \frac{\sum_{t \in T} w(x_n)_t}{g(n)}$$

where $p(xn)$= denotes the posterior probability of ancestral state x at node n n, calculated as the weighted frequency of that state across posterior trees, normalized by the occurrence of the node among those trees.

T = set of posterior trees,
w(xn) = weight of ancestral state x at node n,
g(n) = frequency of the node among trees.

S-DIVA

S-DIVA (Statistical Dispersal–Vicariance Analysis) is an extension of the classical DIVA framework that incorporates phylogenetic uncertainty by evaluating ancestral area reconstructions across bootstrap replicates or posterior distributions of trees. Unlike traditional DIVA, which relies on a single optimal topology, S-DIVA averages reconstructions across multiple trees, generating probabilistic estimates of ancestral ranges. This statistical integration provides a more robust depiction of vicariance- and dispersal- driven evolutionary processes, especially in groups where phylogenetic relationships are weakly supported or highly complex. Due to its intuitive conceptual basis and computational efficiency, S-DIVA remains one of the most widely used approaches for inferring historical biogeography within RASP (Yu et al., 2015).

Bayesian Binary MCMC (BBM)

Bayesian Binary MCMC (BBM) is a Bayesian approach for reconstructing ancestral geographic ranges by estimating posterior probabilities through Markov chain Monte Carlo sampling (Yu et al., 2015). Unlike parsimony-based methods, BBM explicitly models uncertainty by sampling ancestral states across thousands of MCMC iterations, yielding probability distributions rather than single-point estimates. This makes BBM particularly effective for taxa with ambiguous or polymorphic distributions and for datasets with sparse sampling. By integrating branch lengths, model parameters, and stochastic character evolution, BBM provides a flexible framework for inferring historical dispersal and vicariance patterns while fully incorporating phylogenetic and geographic uncertainty. As a result, BBM remains one of the most widely used components of RASP for probabilistic ancestral-area estimation (De Oliveira Martins et al, 2008;2016).

Comparison with Alternative Platforms

While RASP incorporates various models for ancestral range reconstruction, it is not the only platform for biogeographic inference. Software like as BioGeoBEARS (standalone), BayesTraits, RevBayes, BEAST add-ons, and Mesquite provide implementations for dispersal–extinction processes, trait evolution, and state transition modeling. The advantage of RASP is its cohesive visual interface and post-tree integration statistics, while command-line solutions like RevBayes offer significant flexibility in model programming but necessitate advanced computing proficiency. Likewise, BioGeoBEARS standalone accommodates founder-event speciation (+J parameter) with explicit probability testing, however it does not offer the graphical visualization efficiencies seen in RASP. Consequently, RASP occupies an intermediary niche—accessible to novices while being enough robust for sophisticated phylogenetic datasets. Future evaluations of platforms should focus on model equivalence, uncertainty management, and computing efficiency, rather than solely on output similarity.

PHYLOGENETIC SIGNAL AND TRAIT EVOLUTION TOOLS

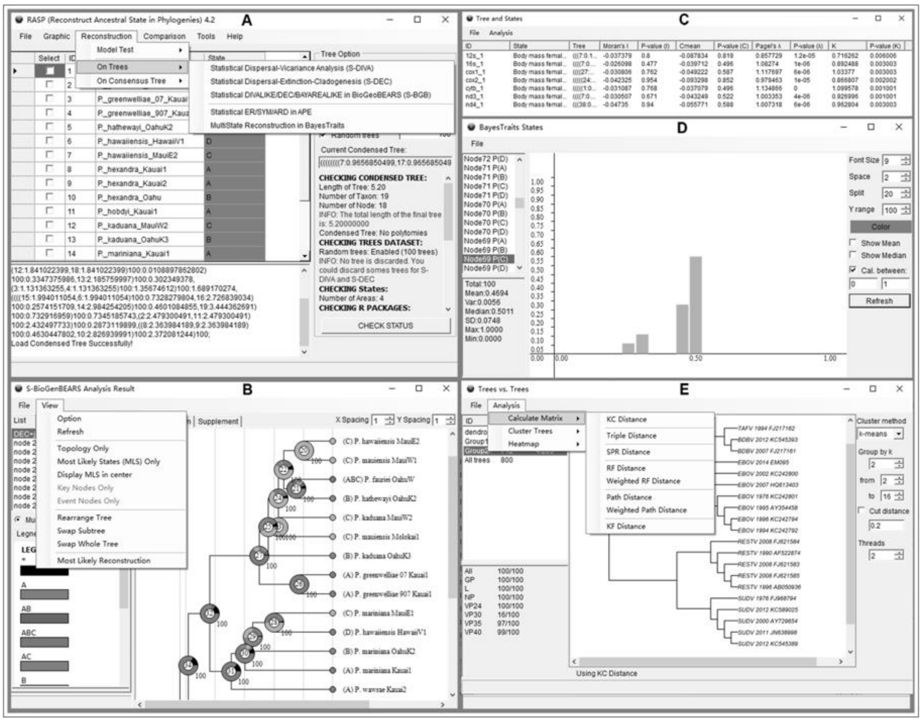
RASP incorporates an extensive array of techniques for evaluating phylogenetic signal and reconstructing trait evolution. The software employs various accepted measures to assess whether morphological or ecological features demonstrate non-random evolutionary organization. Moran's I (Moran, 1948, 1950) and Abouheif's C mean (Abouheif, 1999) are employed to identify autocorrelation patterns among species, whereas Pagel's λ (Pagel, 1999) and Blomberg's K (Blomberg, Garland, & Ives, 2003) measure the intensity of phylogenetic signal in continuous variables. RASP employs likelihood ratio tests for discrete features to assess various evolutionary models and automatically manages taxa with multiple states by creating all possible combinations of their character states. These analytical instruments are crucial for ascertaining if traits adhere to a phylogenetically ordered evolutionary pattern, a vital need for reliable ancestral state reconstruction. Besides trait-based analyses, RASP enables users to calculate tree distance metrics, as outlined by Sand et al. (2014), offering a formal approach to compare alternative topologies obtained from various genetic markers or inference methods, thereby facilitating the identification of phylogenetic congruence or conflict among datasets.

APPLICATIONS OF RASP IN BIOLOGICAL RESEARCH

RASP has been extensively utilized to reconstruct ancestral geographic distributions and evolutionary characteristics across a diverse range of organisms, including mammals, plants, fungi, and bacteria (Moore & Donoghue 2007; Blair et al., 2015; Yu et al., 2015; ; Bourguignon et al.,2018; Navaud et al., 2018; Sahal,2023). With the progression of sequencing technologies, phylogenomic datasets are increasingly incorporated into historical biogeographic analyses (Choi & Kim, 2017; Münkemüller et al., 2012), while ecological, morphological and distributional data have attained equal significance in thorough evolutionary investigations (Soltis & Soltis, 2016). RASP 4 (Figure 1) further augments these capabilities via its integrated statistical framework, enhanced visualization tools, and parallel computing functionality. In this environment, users can evaluate phylogenetic signal, rebuild ancestral states for discrete and continuous features, and examine topological discordance by calculating tree distance metrics. The ancestral state probabilities at each node are computed using the aforementioned generalized statistical procedure, which integrates estimates from posterior trees. Parallel computation alleviates the total analytical load by allocating tree partitions among various processing threads, facilitating the efficient management of extensive phylogenomic datasets.

The Study: Astragalus L. (Fabaceae) of Türkiye (Ates et al, 2025)

Astragalus is the most extensive genus in Türkiye, encompassing around 493 species categorized into 63 sections, exhibiting a notably high endemism rate of approximately 42%. The genus demonstrates significant morphological convergence and ecological specialization, rendering morphology-based taxonomy inadequate for delineating sectional borders. Thus, molecular phylogenetic methods employing nuclear ITS and other cpDNA markers *(trnL–F, matK)* have proven crucial for clarifying relationships among Turkish taxa. A detailed dataset comprising 152 samples from 30 species across six sections was examined utilizing ITS and cpDNA regions, thereafter undergoing ancestral range reconstruction in RASP. Phylogenetic analysis identified two major clades that match broadly to known sectional groupings (Figure 2). The *Macrophyllium* species



Select	ID		State
☐	3	P_greenwelliae_07_Kauai	
☐	4	P_greenwelliae_907_Kaua	
☐	5	P_hathewayi_OahuK2	
☐	6	P_hawaiiensis_HawaiiV1	D
☐	7	P_hawaiiensis_MauiE2	C
☐	8	P_hexandra_Kauai1	A
☐	9	P_hexandra_Kauai2	A
☐	10	P_hexandra_Oahu	B
☐	11	P_hobdyi_Kauai1	A
☐	12	P_kaduana_MauiW2	C
☐	13	P_kaduana_OahuK3	B
☐	14	P_mariniana_Kauai1	A

```
(12:1.841022399,18:1.841022399)100:0.0108897862802)
100:0.3347375986,13:2.185759997)100:0.302349378,
(3:1.131363255,4:1.131363255)100:1.35674612)100:1.689170274,
((((15:1.994011054,6:1.994011054)100:0.7328279804,16:2.726839034)
100:0.2574151709,14:2.984254205)100:0.4601084855,19:3.444362691)
100:0.732916959)100:0.7345185743,(2:2.479300491,11:2.479300491)
100:2.432497733)100:0.2873119899,((8:2.363984189,9:2.363984189)
100:0.4630447802,10:2.826939991)100:2.372081244)100;
Load Condensed Tree Successfully!
```

Current Condensed Tree:

```
(((((((7:0.9656850499,17:0.965685049
```

CHECKING CONDENSED TREE:
Length of Tree: 5.20
Number of Taxon: 19
Number of Node: 18
INFO: The total length of the final tree is: 5.20000000
Condensed Tree: No polytomies
CHECKING TREES DATASET:
Random trees: Enabled (100 trees)
INFO: No tree is discarded. You could discard somes trees for S-DIVA and S-DEC
CHECKING States:
Number of Areas: 4
CHECKING R PACKAGES:

Figure 1. Screenshots from RASP 4. The sample data and tutorials can be found on the RASP website. (A) The main screen of RASP. The expanded menu shows the ancestral state reconstruction methods implemented in RASP. (B) The tree view interface of RASP. The graphic shows the results of using the DIVAlike model in BioGeoBears. The expanded menu shows the operations that can be performed on the results. (C) The Trees and States tool. The list shows the results of phylogenetic signal for three states. (D) Graphical interface showing ancestral state reconstruction results from BayesTraits (Meade and Pagel 2018). (E) The Trees versus Trees tool. The expanded menu shows the supported distance methods. (Yu et al. 2020)

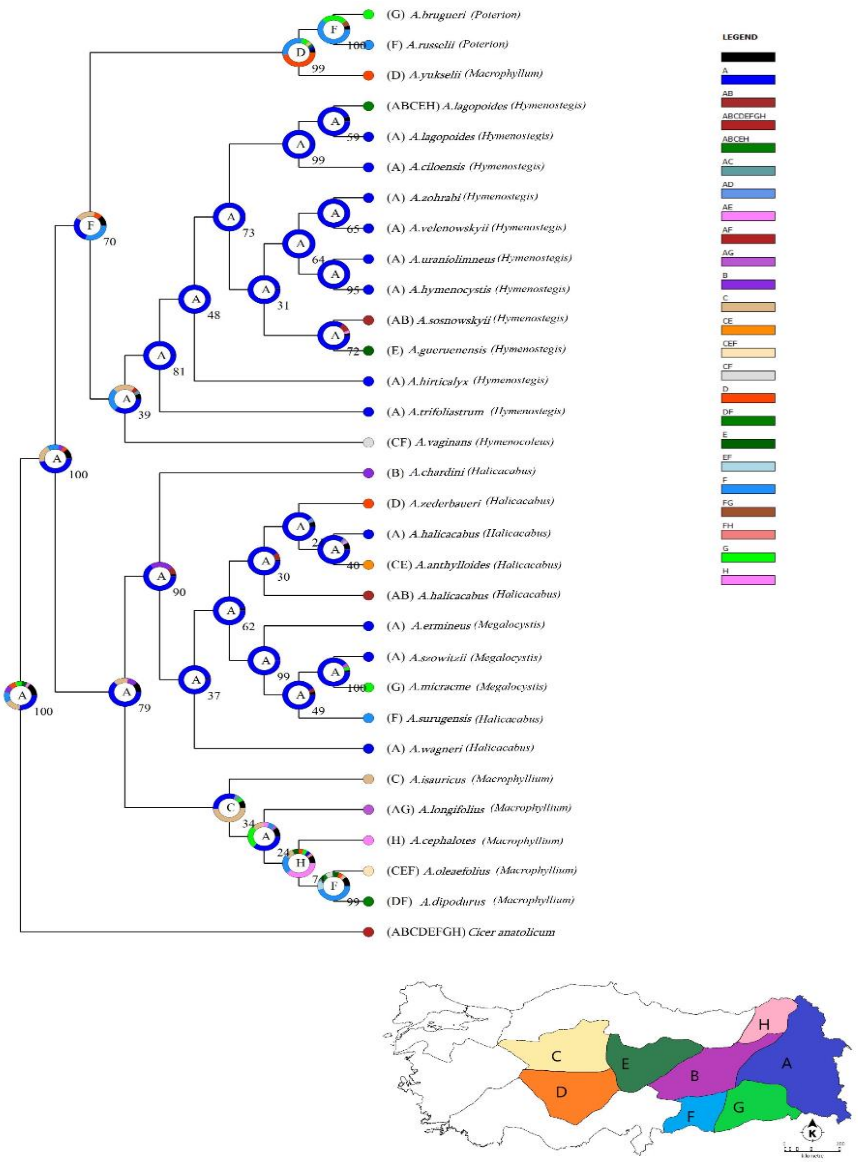


Figure 2. Tree output of S-DIVA analysis with MCMC runs (RASP program). Posterior probability values (PP) are shown over 100 and the most probable regions are shown with letters. Color legend refers to possible ancestral ranges at each node and biogeographical regions on the Türkiye map (Ateş, et al. 2025)ancestral state reconstruction results from BayesTraits (Meade and Pagel 2018). (E) The Trees versus Trees tool. The expanded menu shows the supported distance methods.(Yu et al. 2020)

constituted a discrete subclade, excluding *A. yukselii*, whereas the species of Halicacabus and Megalocystis clustered together with robust support. The only representative of sect. Hymenocoleus, *A. vaginans*, clustered with species of sect. Hymenostegis; however, its location exhibited diminished support values. To investigate the spatial aspects of diversification, species distributions were categorized using a geographic framework particular to Anatolia (regions A–H), which delineates subunits of the Eastern, Central, Southeastern Anatolian, and Black Sea regions. RASP analyses, namely S-DIVA, demonstrated that both vicariance and dispersal were pivotal in influencing the divergence of sectional lineages. Divergence episodes were predominantly deduced in central and eastern Anatolia, areas characterized by environmental complexity and intricate topography features. The Macrophyllium clade likely evolved in region C (Central Anatolia), while other clades exhibited divergence in eastern Anatolia (region A) or southeastern regions (region F). The *Astragalus* study illustrates that the integration of multilocus phylogenies with RASP-based biogeographic reconstruction offers a solid foundation for comprehending diversification in species characterized by significant endemism, morphological complexity, and pronounced ecological specialization.

The Study: Gundelia L. (Asteraceae) (Ateş et al,2021)

Gundelia has always been considered a monotypic genus, represented exclusively by *G. tournefortii*. Recent taxonomic research, grounded in comprehensive morphological analyses, has broadened the genus to encompass over 20 species found in the Eastern Mediterranean, Anatolia, Transcaucasia, Iran, and Afghanistan. Species delimitations have predominantly depended on variations in the number of cephaloid flower heads, their aggregation patterns, and corolla colors, despite the fact that these traits are known to be affected by environmental influences, necessitating validation via molecular systematics. Phylogenetic investigations utilizing ITS and ndhF markers, along with BEAST-based tree - inference and bootstrap support evaluations, established the foundation for an extensive biogeographic reconstruction in RASP. Model testing with BioGeoBEARS revealed that S-DEC in conjunction with Bayesian Binary MCMC was the most supported model (AICc), and this methodology was executed with 50,000 burn-in generations to estimate ancestral range probabilities. RASP analyses consistently indicated that the ancestral lineages of *Gundelia* emerged within the continental climatic zones of the Eastern Anatolian Diagonal and the Mesopotamian sectors of the Irano–Turanian region, with further corroboration for transitional zones between southeastern and eastern Türkiye (Figure 3). These regions align with well-documented biogeographic corridors distinguished by significant geographical and climatic variations. Numerous species demonstrated restricted endemism, especially in southeastern and eastern Anatolia, indicating localized environmental specialization. Conversely, species of Mediterranean origin, such as *G. cilicica* and *G. tournefortii*, seem to signify subsequent diffusion events into western and southern Anatolia.The present distribution patterns reinforce these historical conclusions: *G. anatolica* is confined to Central Anatolia; species like *G. purpurascens*, *G. mesopotamica*, and *G. siirtica* are typical of southeastern Turkey, but *G. dersim, G. colemerikensis, G. vitekii,* and *G. glabra* are primarily found in eastern Anatolia. Collectively, our findings underscore the significant impact of Anatolia's climatic corridors, elevational gradients, and biogeographic transition zones on lineage diversification in *Gundelia*. The amalgamation of multilocus phylogenies with RASP-based ancestral range reconstruction offers a cohesive framework for delineating species boundaries and comprehending the history biogeography of this morphologically intricate and regionally varied genus.

The Study: Malagasy Plated Lizards (Zonosaurinae) (Blair, et al. 2015)

The diversity and historical biogeography of Malagasy plated lizards have been examined using a multilocus phylogenetic framework alongside geospatial analysis. Due of the inadequate support of several nodes in the maximum clade credibility (MCC) tree, ancestral range reconstruction was performed using 10000 posterior BEAST trees to explicitly account for phylogenetic uncertainty. The S-DIVA model utilized in RASP was employed to deduce ancestral distributions across Madagascar's primary biomes, classified into four main habitat types: dry forest, spiny forest, rainforest, and subhumid forest. RASP studies yielded high-resolution estimates of dispersal and extinction events, represented as blue and yellow nodes on the phylogeny, respectively. These reconstructions disclosed multiple colonization events across Madagascar's principal ecological zones (Figure 4). Spatial autoregression models (CAR and SAR) were employed using SAM v4.0 to investigate the relationships among lineage diversity, climatic stability, and topographic variation, therefore elucidating the factors influencing diversification. This study demonstrates RASP's efficacy in managing extensive posterior tree sets and highlights its significance in reconstructing biogeographic histories in environments characterized by substantial complexity and phylogenetic ambiguity.

The Study: Host Range Evolution in Sclerotiniaceae (Fungi) (Navaud et al. 2018)

The Sclerotiniaceae, a varied family of ascomycete fungi, has significant variety in host range and diversification trends.To clarify the evolutionary mechanisms responsible for these patterns, multilocus phylogenies were integrated

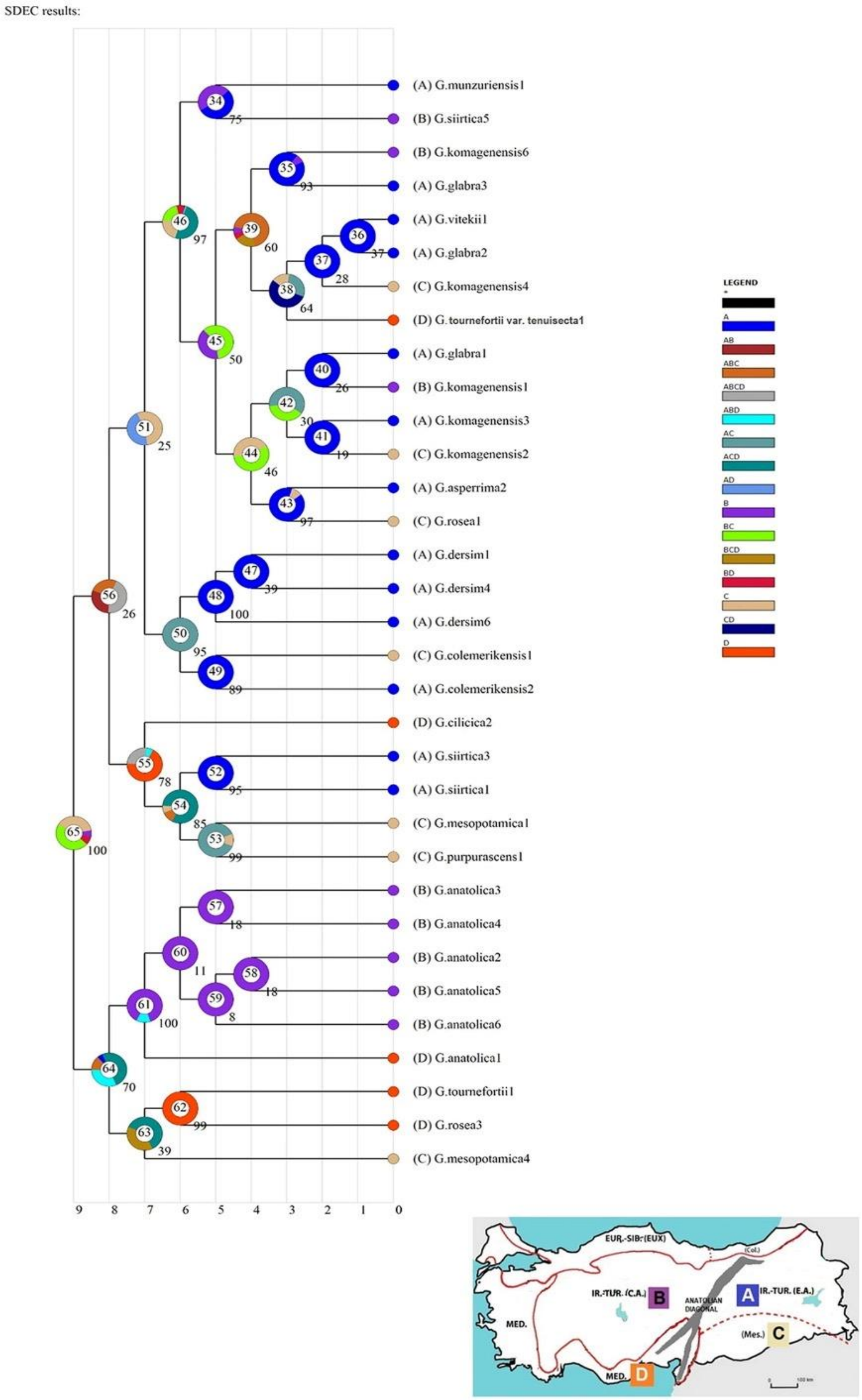


Figure 3. Tree output of RASP analysis with S-DEC & Bayes ian Traits with the ITS data. Bayesian Credibility values are shown above the pies and the most probable region was shown with color of the pies at each node. The color legend of the map indicates the possible ancestral ranges at the nodes shown above the tree and the phytogeographical regions from which the samples originated (Ateş et al., 2021)

with ancestral host reconstruction utilizing RASP (Yu et al., 2015) and supplementary analyses in PHYTOOLS (Revell, 2012). Both the S-DIVA and S-DEC models indicated Fabids as the most probable ancestral hosts for the family, with a relative probability of 100%, and random tree pruning in PHYTOOLS corroborated that this finding was resilient to sample biases. RASP further disclosed several host jump events throughout the Sclerotiniaceae lineage (Figure 5). Over 48% of species parasitize host lineages that emerged before the divergence of Fabids, signifying recurrent transitions to distantly related plant groups. Significant occurrences encompass:

- a transition to Malvids, succeeded by Monocots, at the base of the Botrytis genus (87% and 85% probability, respectively),
- a leap to Commelinids within Myriosclerotinia (91% probability),
- a transition to Ranunculales at the base of Sclerotinia (76% probability), and
- a shift to Asterids at the base of a prominent Monilinia clade (89% probability).

Host shifts were not arbitrarily allocated; rather, species with extensive host ranges were predominantly found in clades characterized by heightened diversification rates, while clades with diminished diversification rates displayed narrower host ranges and a higher incidence of duplication events. These trends indicate that the evolution of generalist fungal diseases within Sclerotiniaceae predominantly arises from recurrent host shifts, a phenomenon previously observed in other pathogen groups, including oomycetes. The amalgamation of RASP and PHYTOOLS illustrates that ancestral host range reconstruction yields insights akin to geographical analyses, underscoring RASP's extensive usefulness in ecology and trait evolution. These findings provide significant insights into the evolutionary dynamics of fungal infections and enhance comprehension of the mechanisms underlying emergent plant disease epidemics.

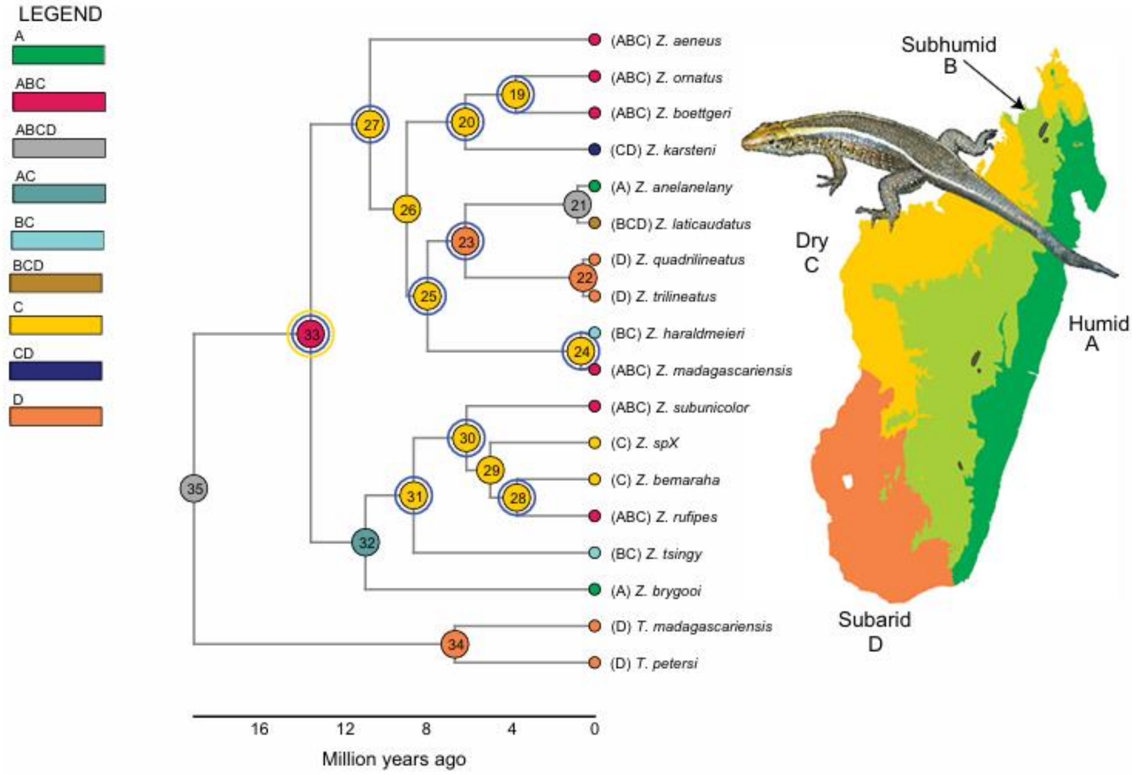


Figure 4. Biogeographic history for Malagasy zonosaurines inferred through the S-DIVA method in RASP. Ancestral states were inferred from 10 000 species trees from *BEAST to explicitly account for both biogeographic and phylogenetic uncertainty. Results are summarized on the *BEAST MCC tree. For clarity only the most likely ancestral states are shown. Blue circles surrounding nodes represent inferred dispersal events, whereas the yellow circle represents an extinction event. Coloured circles at tips represent present ranges for each species as inferred through our clipped species distribution models. Map is redrawn from Cornet (1974) (Blair, et al. 2015).

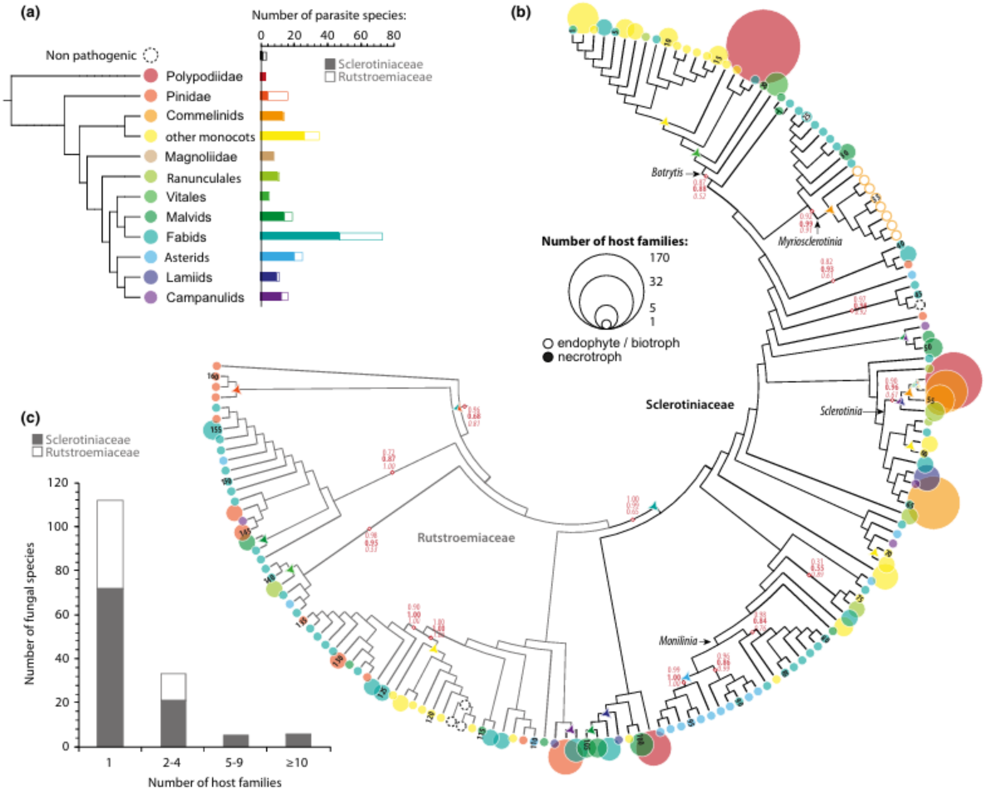


Figure 5. Multiple independent shift sand expansions of host range in the evolution of the Sclerotiniaceae. (a) Distribution of plant hosts of parasites from the Sclerotiniaceae and Rutstroemiaceae fungi. (b) Maximum-likelihood ITS phylogeny of 105 Sclerotiniaceae and 56 Rutstroemiaceae species showing host range information and ancestral host reconstruction (Navaud et al., 2018).

STRENGTHS AND LIMITATIONS of RASP

Benefits RASP offers several methodological advantages that have enabled its widespread application in historical biogeography. The program incorporates multiple reconstruction frameworks, including as S-DIVA, Bayesian Binary MCMC, and BioGeoBEARS likelihood models (Matzke 2014), enabling researchers to evaluate alternative evolutionary hypotheses inside a unified analytical structure. Its ability to include uncertainty across posterior tree distributions (Yu et al., 2015), along with a user-friendly interface and strong visualization features, enables the intuitive analysis of intricate data. Parallel computation support markedly enhances efficiency in managing large phylogenomic datasets. These attributes have made RASP beneficial for a diverse range of taxa and data types, including plants, fungi, vertebrates, and microbial lineages.

Despite these advantages, some limitations must be recognized when evaluating RASP findings. Ancestral area reconstructions are highly sensitive to the precision and intricacy of geographic coding, and overparameterization may occur when an excessive number of regions are defined relative to the dataset size. Furthermore, different BioGeoBEARS models (e.g., DEC versus DIVALIKE) may provide contrasting biogeographic outcomes, underscoring the importance of model validation and biological justification (Matzke 2014; Paradis & Schliep, 2019). The founder-event speciation (+J parameter), which can substantially influence reconstructions in island systems, is not included in all iterations of RASP. Ultimately, geographic assumptions—such as dispersal constraints or interregional connectivity—must be validated by genuine geological and biological evidence to avoid overstated results. Consequently, RASP is most effective when spatial coding is physiologically relevant and model assumptions are thoroughly assessed.

FUTURE DIRECTIONS AND RESEARCH PERSPECTIVES

The ongoing growth of genomic, ecological, and spatial datasets underscores various emerging methodological requirements for biogeographic software. The integration of founder-event speciation models across all RASP modules would enhance reconstructions for island-like systems, such as archipelagos and ecological micro-refugia. Secondly, simulation-based biogeography, which establishes null expectations for dispersal and vicariance frequency, has gained prominence in recent macroevolutionary studies and serves as a rational progression for future RASP development. Third, implementing automated sensitivity analyses that allow users to systematically vary region definitions or dispersal constraints would enhance the robustness of inferences and minimize user bias in geographic coding.

Enhancing compatibility with genomic data formats and high-performance computing frameworks would solidify RASP's role as a key analytical engine in phylogenomic biogeography. Adhering to these guidelines will guarantee that RASP retains methodological relevance and scientific impact as evolutionary datasets grow.

CONCLUSIONS

RASP serves as an essential tool for reconstructing ancestral states, especially geographic ranges, within a specified phylogenetic framework. The integration of likelihood-based biogeographic models, Bayesian inference, and trait-evolution methods provides a robust framework for addressing diverse evolutionary questions (Yu et al. 2015; Matzke 2014). Research on Turkish flora, illustrates its effectiveness in regions characterized by considerable topographic complexity, climatic variability, and high levels of endemism. These studies demonstrate how RASP can clarify historical processes, including vicariance, dispersion, and habitat specialization, in environmentally dynamic contexts.

The ongoing growth of genomic and phylogenomic datasets, coupled with advancements in models of range evolution, suggests that RASP will continue to be an essential tool in historical biogeography and trait-based evolutionary studies.The capacity to incorporate uncertainty, manage large datasets, and depict complex evolutionary scenarios ensures its ongoing relevance in research within systematics, ecology, and macroevolution. The integration of simulation-based biogeography, standardized sensitivity workflows, and founder-event modeling will significantly enhance RASP's inferential capabilities, solidifying its role as a crucial tool for analyzing evolutionary histories in complex landscapes. RASP functions not merely as a visualization tool but as a dynamic analytical platform that influences both conceptual and empirical developments in historical biogeography.

CONFLICT OF INTEREST

The authors declare that there is no conflict of interest regarding the publication of this manuscript. No financial or personal relationships exist that could have influenced the work reported in this paper.

ACKNOWLEDGEMENTS

We express our heartfelt gratitude to Göktürk ÇEVİRME for his meaningful encouragement and moral support throughout this study.

REFERENCES

Abouheif, E. (1999). A method for testing the assumption of phylogenetic independence in comparative data. *American Naturalist*, *154*(1), 140–153.

Ateş, M. A., Fırat, M., & Kaya, Z. (2021). Updated-extended molecular time and molecular phylogeny of *Gundelia* species native to Turkey. *Plant Systematics and Evolution*, *307*(4), 47.

Ateş, M. A., Karaman, S., Aytaç, Z., & Kaya, Z. (2025). Molecular insights into the diversification and biogeographic history of six *Astragalus* L. sections in the Turkish flora. *Plants, 14*(14), 2226.

Blair, C., Noonan, B., Brown, J., Raselimanana, A., Vences, M., & Yoder, A. (2015). Multilocus phylogenetic and geospatial analyses illuminate diversification patterns and the biogeographic history of Malagasy endemic plated lizards (Gerrhosauridae: Zonosaurinae). *Journal of Evolutionary Biology, 28*(2), 481–492.

Blair, C., Weigel, D. E., Balazik, M., Keeley, A. T., Walker, F. M., Landguth, E. L., ... & Murphy, M. A. (2015). A simulation-based evaluation of methods for inferring linear barriers to gene flow. *Molecular Ecology Resources, 15*(6), 121–129.

Blomberg, S. P., Garland, T., Jr., & Ives, A. R. (2003). Testing for phylogenetic signal in comparative data: Behavioral traits are more labile. *Evolution, 57*(4), 717–745.

Bourguignon, T., Lo, N., Cameron, S. L., Šobotník, J., Hayashi, Y., Shigenobu, S., ... & Evans, T. A. (2018). The evolutionary history of termites as inferred from 66 mitochondrial genomes. *Molecular Biology and Evolution, 32*(2), 406–421.

Choi, J., & Kim, S. H. (2017). A genome tree of life for the fungi kingdom. *Proceedings of the National Academy of Sciences, 114*(35), 9391–9396.

Cornet, A. (1974). *Essai de cartographie bioclimatique à Madagascar* (Notice explicative No. 55). ORSTOM.

De Oliveira Martins, L., Leal, E., & Kishino, H. (2008). Phylogenetic detection of recombination with a Bayesian prior on the distance between trees. *PLoS ONE, 3*(7), e2651.

De Oliveira Martins, L., Mallo, D., & Posada, D. (2016). A Bayesian supertree model for genome-wide species tree reconstruction. *Systematic Biology, 65*(3), 397–416.

Joy, J. B., Liang, R. H., McCloskey, R. M., Nguyen, T., & Poon, A. F. (2016). Ancestral reconstruction. *PLoS computational biology, 12*(7), e1004763.

Liu, L., Yu, L., & Edwards, S. V. (2010). A maximum pseudo-likelihood approach for estimating species trees under the coalescent model. *BMC Evolutionary Biology, 10*(1), 302.

Matzke, N. J. (2014). Model selection in historical biogeography reveals that founder-event speciation is a crucial process in island clades. *Systematic Biology, 63*(6), 951–970.

Meade, A., & Pagel, M. (2017). *BayesTraits: A computer package for analyses of trait evolution* (Version 3).

Moran, P. A. P. (1948). The interpretation of statistical maps. *Journal of the Royal Statistical Society. Series B (Methodological), 10*(2), 243–251.

Moran, P. A. P. (1950). Notes on continuous stochastic phenomena. *Biometrika, 37*(1–2), 17– 23.

Moore, B. R., & Donoghue, M. J. (2007). Correlates of diversification in the plant clade Dipsacales: geographic movement and evolutionary innovations. *the American Naturalist, 170*(S2), S28-S55.

Münkemüller, T., Lavergne, S., Bzeznik, B., Dray, S., Jombart, T., Schiffers, K., & Thuiller, W. (2012). How to measure and test phylogenetic signal. *Methods in Ecology and Evolution, 3*(4), 743–756.

Navaud, O., Barbacci, A., Taylor, A., Clarkson, J. P., & Raffaele, S. (2018). Shifts in diversification rates and host jumps shaped the diversity of host range among Sclerotiniaceae fungal plant pathogens. *Molecular Ecology, 27*(5), 1309–1323.

Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature, 401*(6756), 877–884.

Paradis, E., & Schliep, K. (2019). ape 5.0: An environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics, 35*(3), 526–528.

Pennell, M. W., Eastman, J. M., Slater, G. J., Brown, J. W., Uyeda, J. C., FitzJohn, R. G., ...& Harmon, L. J. (2014). geiger v2.0: An expanded suite of methods for fitting macroevolutionary models to phylogenetic trees. *Bioinformatics, 30*(15), 2216–2218.

Rangel, T. F., Diniz-Filho, J. A. F., & Bini, L. M. (2010). SAM: A comprehensive application for spatial analysis in macroecology. *Ecography, 33*(1), 46–50.

Revell, L. J. (2012). phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution, 3*(2), 217–223.

Sand, A., Holt, M. K., Johansen, J., Brodal, G., Mailund, T., & Pedersen, C. N. (2014). tqDist: A library for computing the quartet and triplet distances between binary or general trees. *Bioinformatics, 30*(14), 2079–2080.

Soltis, P. S., & Soltis, D. E. (2016). Mobilizing and integrating big data in studies of spatial and phylogenetic patterns of biodiversity. *Plant Diversity, 38*(6), 264–270.

Sahal, M. R. (2023). *Comparative genomics and phylogenomics of Mycobacterium tuberculosis with a special emphasis on Mycobacterium africanum* (Doctoral dissertation, Université Paris-Saclay).

Yan, H.-F., Zhang, C.-Y., Anderberg, A. A., Hao, G., Ge, X.-J., & Wiens, J. J. (2018). What explains high plant richness in East Asia? Time and diversification in the tribe Lysimachieae (Primulaceae). *New Phytologist, 219*(1), 436–448.

Yu, Y., Blair, C., & He, X. (2015). RASP (Reconstruct Ancestral State in Phylogenies): A tool for historical biogeography. *Molecular Phylogenetics and Evolution, 87*, 46–49.