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# APPLICATION

# phylospatial: An R package for spatial phylogenetic analysis with quantitative community data

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### Abstract

- 1. Spatial phylogenetic approaches enhance biodiversity analyses by incorporating information about species' evolutionary similarity. However, existing software packages for analysing spatial phylogenetic diversity (PD) patterns only provide full support for binary (presence-absence) community data. A major gap exists in support for occurrence probabilities (such as from species distribution models), a common and valuable data type that captures spatial uncertainty and habitat suitability gradients. While abundance data are partially supported by existing PD tools, these lack features such as geospatial data integration and flexible null model analysis. These gaps limit PD research on quantitative features of species distributions and can introduce imprecision and bias if continuous biodiversity data are thresholded to work with existing tools.
- 2. Here I present phylospatial, a new R package that fully supports probability, abundance, and binary community data across a range of spatial PD analyses. The package processes all three data types in a common framework, while handling them in distinct ways at key points in the analysis pipeline. It also integrates with raster and vector data formats, providing efficient workflows for geospatial data.
- 3. phylospatial provides an integrated framework for performing various types of analyses, including calculating alpha PD and endemism, testing significance using community null models, identifying beta-PD patterns including biogeographic regions, and conducting spatial conservation prioritization. I illustrate the package's functionality with worked examples using a dataset comprising a phylogeny and modelled occurrence probabilities for 5200 species of California plants.
- 4. By facilitating spatial phylogenetic analysis of quantitative data types that more accurately represent the reality of species distributions, these methods and tools help broaden the range of questions and applications that can be addressed, and can help to increase the detail and statistical rigour of these studies.

### KEYWORDS

biodiversity, Community Ecology, phylogenetic diversity, R package, spatial phylogenetics

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# 1 | INTRODUCTION

Understanding biodiversity patterns is fundamental to ecological theory and conservation planning. Phylogenetic diversity (PD) metrics, which incorporate evolutionary relationships into biodiversity analyses, reveal patterns that species-based methods cannot detect (Faith, 1992; Graham & Fine, 2008; Isaac et al., 2007). These metrics have been widely used to compare evolutionary heritage across ecological communities, delineate phylogenetically informed biogeographic regions, characterize areas of neo- and paleo-endemism, optimize the preservation of evolutionary diversity in conservation planning, and study community assembly and ecosystem function

(Cadotte & Davies, 2016; Daru et al., 2020; Kling et al., 2019; Mishler et al., 2014; Rosauer et al., 2009).

While biodiversity studies like these have traditionally relied on binary presence-absence data, there is growing potential to leverage data on quantitative attributes of species occurrence and abundance (Hartig et al., 2024; Peterson et al., 2015). Data on occurrence probabilities across landscapes, which reflect inherent uncertainty in species occurrences and habitat suitability gradients, are increasingly available from species distribution and occupancy models. Similarly, data on absolute or relative abundance, which provide rich quantitative measures of ecological communities, are increasingly available from sources including remote sensing, environmental DNA, camera traps, and acoustic sampling.

TABLE 1 Comparison of R packages for phylogenetic diversity analysis. This table only includes packages that compute alpha and/or beta phylogenetic diversity (PD) measures; it does not cover the many packages focused exclusively on other aspects of biogeographic or community phylogenetic analysis. An 'X' indicates a capability while a dash ('--') indicates no capability, with respect specifically to PD calculations. While some designations were unavoidably subjective, efforts were made at consistent assessment across packages.

	Community data types			Spatial integration		
Package	Probability data	Abundance data	Binary data	Raster support	Vector support	Endemism metrics
adiv (Pavoine, 2020)	-	Х	Х	-	-	-
BAT (Cardoso et al., 2015)	_	Х	Х	-	-	-
betapart (Baselga & Orme, 2012)	-	Х	Х	-	-	-
canaper (Nitta et al., 2023)	-	_	Х	_	_	Х
dispRity (Guillerme, 2018)	-	Х	Х	-	-	-
entropart (Marcon & Hérault, 2015)	-	Х	Х	-	-	-
hillR (Li, 2018)	_	х	Х	-	-	-
pez (Pearse et al., 2015)	_	Х	Х	-	-	-
PhyloMeasures (Tsirogiannis & Sandel, 2016)	_	-	Х	-	-	_
phylocomr (Ooms, 2018)	-	-	Х	_	-	_
phyloraster (Alves-Ferreira et al., 2024)	_	-	Х	Х	-	Х
phyloregion (Daru et al., 2020)	-	-	Х	Х	Х	Х
phylospatial (Kling, 2025b)	Х	Х	Х	Х	Х	Х
phyr (Li et al., 2020)	-	Х	Х	-	-	-
picante (Kembel et al., 2010)	_	Х	Х	-	-	-
TPD (Galán-Acedo et al., 2022)	-	Х	Х	-	-	-

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However, there is limited support for these quantitative community data types across the ecosystem of R packages focused on spatial PD analysis (Table 1). Most critically, I am not aware of any tools that support probability data in PD analyses. While various phylogenetic packages do support abundance data (e.g. adiv– Pavoine, 2020 and hillR–Li, 2018), they lack statistical features like null model analysis of abundance-weighted PD, as well as spatial features like calculation of endemism-weighted metrics and integration with geospatial raster and vector data formats. The existing PD tools that do offer these features require binary presence-absence data (e.g. biodiverse–Laffan et al., 2010, canaper–Nitta et al., 2023, PhyloMeasures–Tsirogiannis & Sandel, 2016, phyloraster–Alves-Ferreira et al., 2024 and phyloregion–Daru et al., 2020). These limitations can force researchers to threshold continuous data before conducting spatial phylogenetic analyses, resulting in information loss that reduces statistical power and affects biological interpretation. They also make some scientific questions impossible to address with existing tools.

Here I present phylospatial, an R package that implements a range of spatial phylogenetic analyses for probability, abundance, and binary data. phylospatial aims to be a flexible toolkit for spatial PD studies. In addition to supporting these three key community data types, it is compatible with raster and vector spatial data formats. And unlike some packages, it works with both ultrametric and non-ultrametric trees, so alternative branch-length variables can be used to analyse different facets of PD, including

Alpha diversity dimensions			าร	Other capabilities						
	Richness	Divergence	Evenness	Null model analysis	Beta diversity analysis	Conservation optimization	Trait integration	Comp. performance focus	Special features	
	Х	Х	Х	_	Х	_	Х	_	Comprehensive diversity measures	
	Х	-	-	-	Х	-	Х	-	Integrated functional and phylogenetic diversity	
	_	-	_	_	х	_	_	-	Specialized in turnover/ nestedness components	
	Х	Х	-	х	-	-	-	_	Specialized for categorical analysis of neo- and paleo- endemism analysis	
	Х	Х	_	Х	_	-	Х	-	Focuses on morphological disparity	
	Х	Х	-	Х	х	-	-	-	Entropy decomposition, partitioning	
	Х	Х	Х	_	Х	_	-	_	Hill numbers framework for diversity	
	Х	Х	Х	Х	Х	_	Х	-	Integrates phylo and trait analysis	
	Х	Х	_	Х	_	-	-	Х	Fast computation for large datasets	
	Х	Х	-	Х	Х	-	-	-	R interface to Phylocom	
	Х	-	_	_	_	_	-	Х	Optimized for large raster datasets	
	Х	-	-	-	Х	-	-	Х	Biogeographic regionalization	
	Х	Х	Х	Х	Х	Х	-	_	Integrated framework supporting continuous data	
	Х	Х	-	-	-	-	Х	х	Fast phylogenetic regression methods	
	Х	Х	_	х	Х	_	Х	_	Legacy package for phylo. community analysis	
	Х	-	-	-	-	-	Х	-	Integrated trait and phylogenetic diversity	



**FIGURE 1** Graphical comparison of functions for using terminal occurrences to calculate clade occurrence values—which are necessary for computing phylogenetic diversity (PD) and related metrics—for different community data types. Black lines illustrate phylogenetic relationships among species found in a hypothetical community. The weight given to each lineage in PD calculations is represented by the area of the coloured rectangles, which is a product of the clade's occurrence value in that site (rectangle width; black numeric labels) and the length of the clade's unique branch segment (rectangle height). Terminals are illustrated with uniform weights for clarity, but these would vary in real datasets. (a) Traditional binary spatial phylogenetic methods use the function any(x) to calculate clade occurrence values. (b) Probability models—which are not currently implemented in other R packages—use the function 1 - prod(1 - x) to calculate the probability that at least one terminal is present. (c) Abundance or proportion data use the function sum(x) to calculate the number of individuals in a clade.

divergence, diversification, and survival time (Kling et al., 2019). It also implements traditional non-phylogenetic biodiversity analyses when a phylogeny is not provided. phylospatial currently includes functions that calculate alpha PD and endemism metrics; use null models to test statistical significance; quantify phylogenetic beta diversity patterns such as biogeographic regions; and perform spatial to inform conservation planning. It encompasses much of the functionality that is currently spread across existing packages, as well as enabling probability-based PD analyses not possible with other tools (Table 1).

The use of continuous data requires several modifications to traditional binary methods. First, occurrence quantities for the terminal nodes present in each site must be summarized to calculate occurrence quantities for each internal node (which represent the contemporary geographic distributions of all the individuals in each clade, not ancestral state reconstructions of lineages' historic ranges). Importantly, different data types require different summary methods (Figure 1), which means that existing abundance-weighting methods cannot be used to compute probability-based PD. For binary data, a clade is considered present if any constituent terminal is present (Faith, 1992); for probability data, a clade's occurrence probability is the probability that at least one constituent terminal is present (Kling et al., 2019); and for abundance data, a clade's abundance is the sum of the abundances of its constituent terminals (Chao et al., 2010). Continuous quantities for every node in the tree are then used as weights in all analyses, including when weighting lineages' presences in a given site for diversity metrics, when calculating their range sizes for endemism measures, and when assessing their protection levels for conservation prioritization. Finally, if using community null models for hypothesis testing, an appropriate randomization algorithm must be selected based on its support for binary, continuous (probability), or count (abundance) data (Gotelli & Ulrich, 2012).

### 2 | THE phylospatial R PACKAGE

phylospatial is implemented in R and available on CRAN, with development versions and source code hosted on GitHub. Detailed documentation and vignettes are available through standard R help systems. The package builds on existing tools including ape (Paradis & Schliep, 2019) for phylogenetic methods, vegan (Oksanen et al., 2022) for community analyses, and terra (Hijmans, 2023) and sf (Pebesma, 2018) for spatial operations.

Below I describe the package's core functionality, including data integration, alpha and beta diversity analyses, and conservation prioritization (Figure 2). Each topic is illustrated with worked examples using published data from Thornhill et al. (2017) and Kling et al. (2019) representing evolutionary relationships and modelled occurrence probabilities for the 5221 native vascular plant species of California. Select results are shown in Figure 3.

# install the package from CRAN, load it, and view vignettes
install.packages("phylospatial")
library(phylospatial)
browseVignettes("phylospatial")

# 2.1 | Data integration

All analyses in phylospatial are built around a core data structure that combines a community data matrix, a phylogenetic tree, and spatial metadata. The function phylospatial() constructs this dataset, an object of class phylospatial, from a user-supplied phylogeny and community data. These data structures serve as the input to all other major functions in the package.

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**FIGURE 2** Workflow and key functions of the phylospatial R package. All analyses involve constructing a dataset of class phylospatial, which can then be passed to functions implementing various analyses of alpha-diversity, beta-diversity, and conservation planning.

In addition to validating, cleaning, and restructuring the input data, this routine expands the input community dataset, adding occurrence data for each multi-terminal clade on the phylogeny. By default, phylospatial automatically detects the data type and selects the appropriate function for calculating clade occurrence quantities (Figure 1). Alternatively, users can specify a custom summary function (e.g. if species occurrence probabilities were known to be nonindependent, a function incorporating this could be used; in the extreme, this would be the max function). There is also an option to bypass automated clade construction if a user already has cladelevel community data, such as from fitting dedicated distribution models for every clade.

The code below demonstrates the creation of a phylospatial dataset, using species occurrence probabilities and a phylogeny for California plants.

# load data and build phylospatial data set sdm <- terra::rast("data/sdm.tif") tree <- ape::read.tree("data/chronogram.tree") d <- phylospatial(sdm, tree)</pre>

### 2.2 | Alpha diversity and significance testing

The package calculates a suite of alpha diversity metrics via the function ps\_diversity(). These include richness measures (PD, clade diversity, terminal diversity, Shannon PD, and Simpson PD), divergence measures (relative PD and mean pairwise distance), and regularity measures (variance in pairwise distances). Each of these metrics has been widely used in the literature (Cadotte et al., 2010; Chao et al., 2010; Tucker et al., 2017), though most have not previously been applied to all three community data types. In addition to the basic form, most metrics are also available in an endemism (rarity-weighted) form, in which each terminal's or clade's contribution is weighted by the inverse of the sum of its occurrence quantities across all communities in the dataset.

The statistical significance of these diversity metrics can be analysed by using randomization algorithms to generate null distributions of each metric. phylospatial implements randomization analyses through the function ps\_rand(), which provides access to phylogenetic versions of a wide range of community null model algorithms specified in the R package vegan (Oksanen et al., 2022). A user's choice of



FIGURE 3 A subset of the results generated by the code examples analysing spatial phylogenetic patterns for the 5221 native vascular plant species of California. (a) Phylogenetic diversity (PD); values represent the fraction of total phylogenetic branch length represented in a given site. (b) Statistical significance of PD calculated using a randomization-based null model that controls for species richness; sites in dark green and dark purple are significantly high and low in PD, respectively. (c) Categorical analysis of neo- and paleo-endemism classification of communities with significant endemism characteristics; see Mishler et al. (2014) for descriptions of each category. (d) Phylogenetic community ordination mapped onto red-green-blue (RGB) colour space, with colour similarity representing plant community similarity. (e) Phylogenetic regions representing discrete areas that are relatively homogeneous and distinct from one another. (f) Priority sites for the creation of new protected areas for the conservation of California plants.

algorithm should be determined by the type of community data being analysed, and by which properties of the terminal-level community matrix they wish to be free versus fixed (Gotelli & Ulrich, 2012).

One particular application of randomization-based analysis is 'categorical analysis of neo- and paleo-endemism' (CANAPE; Mishler et al. (2014)), which highlights sites with significant concentrations of long- and short-branch taxa. The ps\_canape() function classifies communities into these endemism categories.

The following code demonstrates the calculation of basic PD metrics for the California flora (including PD; Figure 3a), the use of a null model to compute the significance of these diversity metrics (Figure 3b), and the classification of endemism significance data into CANAPE categories (Figure 3c).

# calculate alpha diversity, significance, and CANAPE div <- ps\_diversity(d) sig <- ps\_rand(d, n\_rand = 999) cnp <- ps\_canape(sig)</pre>

# 2.3 | Beta-diversity and biogeographic structure

Patterns of phylogenetic community turnover across sites can be analysed in a variety of ways to reveal biogeographic structure and study its ecological and evolutionary drivers. Three common categories of turnover analysis include pairwise regressions (e.g. generalized dissimilarity models, GDM—Rosauer et al., 2014 and Mantel tests—Swenson, 2011), community ordination (e.g. fuzzy weighting—Duarte et al., 2016 and distance-based approaches—Webb et al., 2008), and clustering analyses (e.g. phylogenetic regionalization, Carta et al., 2022; Daru et al., 2017). phylospatial includes functionality in each of these three areas.

Pairwise beta-diversity measures can be computed with ps\_dissim(), which implements phylogenetic versions of a wide variety of quantitative community dissimilarity metrics specified in the vegan R package (Oksanen et al., 2022). This includes frequently used measures such as phylogenetic Jaccard, Sorensen, and Canberra distances, as well as options for metrics partitioning beta diversity into its turnover and nestedness components (Baselga, 2010; Graham & Fine, 2008; Pavoine, 2016).

These pairwise distances can be used in GDM or Mantel analyses. They can also be passed to the functions ps\_ordinate() and ps\_rgb(), which offer several kinds of ordination to identify the dominant axes of phylogenetic compositional variation in a dataset. In addition, they can be used in the function ps\_regions() to perform a phylogenetic cluster analysis identifying a set of discrete biogeographic provinces.

The following code example calculates pairwise quantitative Sorensen's (a.k.a. Bray–Curtis) phylogenetic beta-diversity between grid cells. It then uses these dissimilarity data in an ordination embedding the data in three-dimensional colour space to visualize biogeographic structure (Figure 3d), and in a phylogenetic cluster analysis delineating eight floristic regions across California (Figure 3e).

# calculate pairwise dissimilarity; use for ordination & clustering d <- ps\_add\_dissim(d, method = "sorensen") rgb <- ps\_rgb(d, trans = rank) reg <- ps\_regions(d, k = 8, method = "kmeans")</pre>

### 2.4 | Spatial conservation prioritization

The final category of analysis addressed by the package is conservation prioritization. Spatial conservation planning is a diverse field, broadly focused on identifying key locations across a landscape where prospective conservation actions—often the creation of protected areas—could be implemented most efficiently to benefit biodiversity (Wilson et al., 2009). phylospatial utilizes a variant of the stepwise prioritization algorithm described by Kling et al. (2019), which identifies a nested ranking of priority sites for new reserves using data on species distributions, phylogeny, land cost, and existing protected areas. The framework also offers a probabilistic method that relaxes the assumption that sites will be protected in the optimal order. In addition to quantitative community data, it can handle continuous protection levels, which enables a more nuanced representation of landscape conservation status than the typical protected-unprotected classification used in conservation optimizations.

The example code below demonstrates a conservation prioritization for California plants. In addition to the phylospatial object, the analysis incorporates raster data on existing protected areas Methods in Ecology and Evolution

and on population density, which is often used as a proxy for land cost (Naidoo et al., 2006). The results identify high-priority sites that, relative to their cost, contain a large fraction of the geographic distribution of many long-branch taxa that are poorly protected across California by existing reserves and other high-priority sites (Figure 3f).

# conservation prioritization
init <- terra::rast("data/protection.tif")
cost <- terra::rast("data/popdens.tif")
con <- ps\_prioritize(d, init = init, cost = cost)</pre>

# 3 | CONCLUSIONS

The phylospatial library represents an important addition to existing tools for spatial PD analysis (Table 1). By enabling analysis with probability data, this package addresses a critical methodological gap that has required researchers to artificially threshold species distribution model outputs or occupancy model predictions. Leveraging probabilities not only preserves the intrinsic uncertainty in predicted species distributions but also provides a more statistically sound foundation for conservation prioritization and biodiversity pattern analysis, particularly in regions with imperfect sampling or rapidly changing environmental conditions. The new package also extends the set of capabilities for PD analyses using abundance data, including providing access to a suite of null model algorithms for statistical testing, as well as spatially focused features like endemism metrics and geospatial data handling.

Beyond supporting new types of analysis, the phylospatial framework provides an integrated, flexible, and streamlined toolset that simplifies the process of data integration and analysis. This makes the library useful even for traditional binary data and for non-phylogenetic biodiversity analysis. It combines functionality that has previously been split across multiple packages, helping make computational workflows more efficient and consistent. And as an open source package built around a core spatial phylogenetic data structure, the library can be easily adapted and extended in the future to add support for additional methods and data types.

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### CONFLICT OF INTEREST STATEMENT

No conflict of interest is declared.

### PEER REVIEW

The peer review history for this article is available at https://www. webofscience.com/api/gateway/wos/peer-review/10.1111/2041-210X.70056.

### DATA AVAILABILITY STATEMENT

R package phylospatial is available via CRAN (Kling, 2025b). Code for empirical examples is available via https://doi.org/10.5281/zenodo.15311538 (Kling, 2025a). Data underlying empirical examples is available via Thornhill et al. (2017) and Kling et al. (2019).

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