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`funrar`: An R package to characterize functional rarity

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Abstract

Emphasis has been put in recent ecological research on investigating phylogenetic, functional and taxonomic facets of biological diversity. While a flourishing number of indices have been proposed for assessing functional diversity, surprisingly few options are available to characterize functional rarity. Functional rarity can play a key role in community and ecosystem dynamics. We introduce here the `funrar` R package to quantify functional rarity based on species trait differences and species frequencies at local and regional scales. Because of the increasing availability of big datasets in macroecology and biogeography, we optimized funrar to work with large datasets of thousands of species and sites. We illustrate the use of the package to investigate the functional rarity of North and Central American mammals.

KEYWORDS
biodiversity, biodiversity indices, functional biogeography, functional trait, R package, rarity

1 | A TOOLKIT FOR THE DEFINITION AND QUANTIFICATION OF FUNCTIONAL RARITY

Biodiversity is multifaceted (Cardoso, Rigal, Borges, & Carvalho, 2014; Safi et al., 2011), and many indices have been proposed to summarize the taxonomic, phylogenetic and functional composition of ecological assemblages (Jarzyna & Jetz, 2016; Mazel et al., 2014). Such indices are used to investigate the influence of ecological, biogeographical and evolutionary processes at local and regional scales (McGill, Enquist, Weiher, & Westoby, 2006; Violle, Reich, Pacala, Enquist, & Kattge, 2014; Weiher et al., 2011). Many indices, such as community-weighted moments, emphasize the contribution of abundant taxa because they are expected to make significant contributions to community and ecosystem functioning (Grime, 1998; Enquist et al. 2015), while the role of rare taxa is less addressed.

Rarity relates to biodiversity dynamics at multiple scales of geographical and niche space. Rabinowitz (1981) defined rarity based on the geographical range, habitat specificity and local population size of taxa, yielding seven forms of rarity. More recently, Violle et al. (2017) extended the scope of Rabinowitz's (1981) classification to further incorporate differences in functional traits among taxa, defining a new component—functional rarity. In this perspective, a species (or an individual) can be rare because of the uncommonness of its trait values and/or because of its low abundance at the local scale (Pavoine, Ollier, & Dufour, 2005). Indices of Functional Distinctiveness and Taxon Scarcity were proposed to quantify those two aspects at the local scale, respectively. A species can also be functionally rare at the regional scale because its functional characteristics are unique given the pool of species and/or because it is spatially restricted. Functional Uniqueness and Taxon Restrictedness respectively assess these two aspects at the regional scale. The four indices together provide a framework for characterizing functional rarity (Figures 1 and 2). Because functional rarity is expected to play a major role in ecosystem and biodiversity dynamics, the indices can be used to assess the influences of rare trait values on local and regional dynamics (Ricotta et al., 2016; Violle et al., 2017). We here introduce an R (R
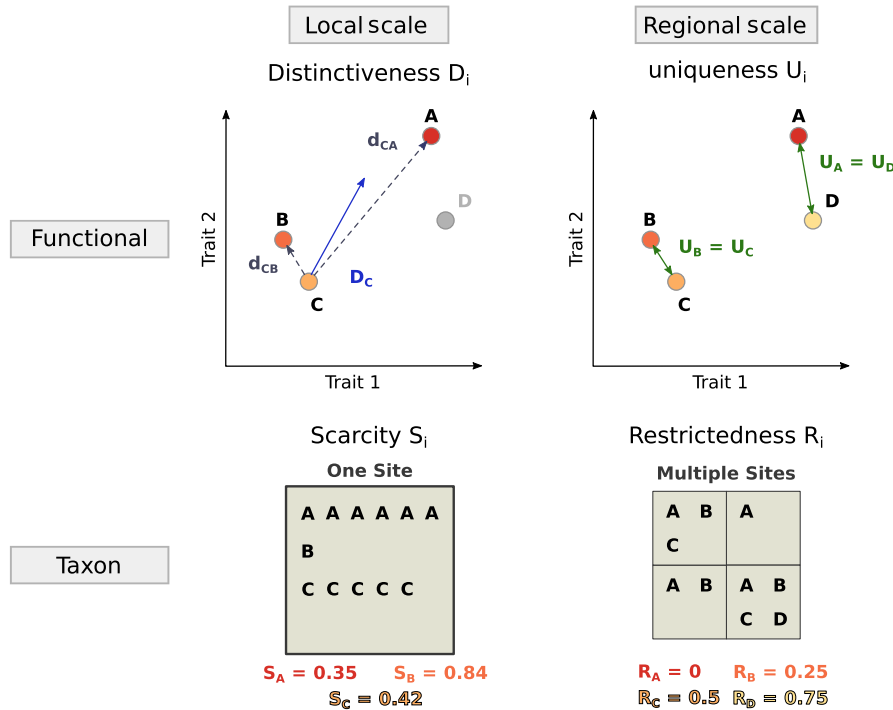
FIGURE 1 Basic patterns of Functional Rarity. Four species *A* to *D* are illustrated. Functional indices are represented in top figures: Functional Distinctiveness (left) is the average functional distance of a species to the other species in the community, species *D* is absent from this community, thus, the Distinctiveness of species *C* D_C is simply the average of distance of species C to species A, d_{CA}, and to species B, d_{CB}; Functional Uniqueness (top right) is the functional distance of a species to its nearest neighbour in a regional species pool (see Equation 3); here, *A* and *D* are nearest neighbours as well as *B* and *C*. Taxon Scarcity (bottom left), where S_i denotes the Scarcity of species *i*, it is inversely proportional to the abundance of species *i* (see Equation 4), because species *D* is absent from the community its scarcity cannot be computed; Taxon Restrictedness (bottom right) is assessed from the occurrences of species across four sites (four tiles) and R_i denotes the Restrictedness of species *i*, it equals one minus the number of times a species across all sites over the total number of sites (see Equation 5), species *A* is present in all four sites, thus its Restrictedness R_A equals zero
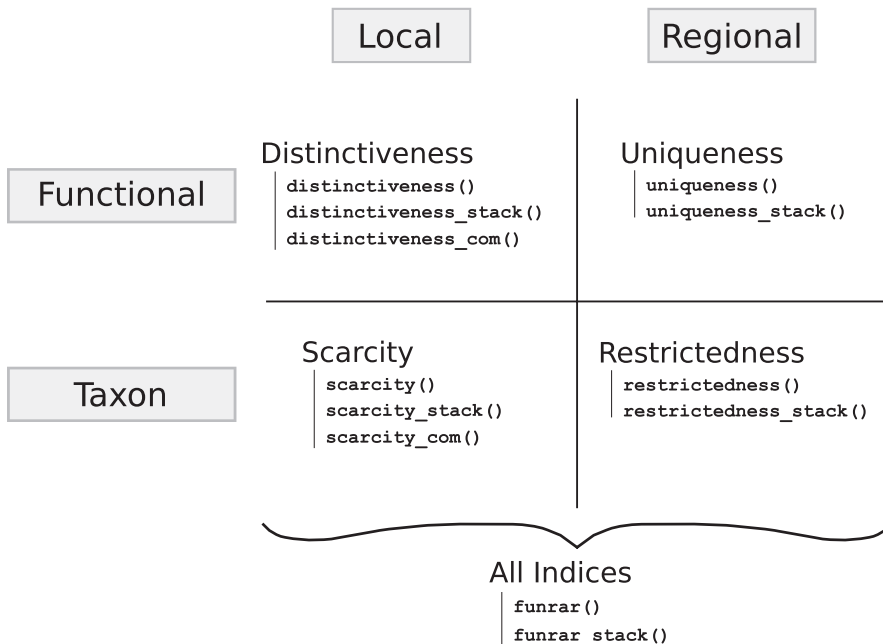

FIGURE 2 Functions available in `funrar` to compute the different facets of functional rarity. Functions handle two formats of site composition, the default one assumes that the input dataset is a site-species matrix, while the `_stack()` versions use "tidy" format; `_com()` functions provided for Functional Distinctiveness and Scarcity take a single community as input. Note that regional-level indices—Restrictedness and Functional Uniqueness—are computed using the complete dataset, giving a single index per species. The site-level indices—Functional Distinctiveness and Scarcity—are computed for each site-species combination, giving one value per site-species combination

Core Team, 2016) package named `funrar`, to quantify **fun**ctional **rar**ity based on abundance or occurrence data and trait data. The `funrar` package, available through the Comprehensive R Archive Network (CRAN), computes Functional Distinctiveness, Functional Uniqueness, Taxon Scarcity and Taxon Restrictedness and is optimized to handle high-dimensional data (large number of sites and/or large number of

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species) using sparse matrix algebra. We illustrate the application of this package for examining functional rarity using data on North and Central American mammals (Lawing, Eronen, Blois, Graham, & Polly, 2016a) (the code to run the analyses is available on Github at https://github.com/Rekyt/mamm_funrar archived on Zenodo https://doi.org/10.5281/zenodo.375605).

2 | QUANTIFYING FUNCTIONAL RARITY USING `funrar` FUNCTIONS

Users must provide a site-by-species matrix of community composition across sites, with either the presence–absence or relative abundances of species. `funrar` functions can handle site-by-species data in any of three formats: site-species matrix (with sites as rows and species as columns, see Figure 1 for available functions); "tidy" format (Wickham, 2014), with each row coding the observation of a single species at a given site (the function has a `_stack` suffix); or as a single community (the function has a `_com` suffix). Abundance or occurrence information can be based on population or community census and possibly account for imperfect detection (Dénes, Silveira, & Beissinger, 2015; Iknayan, Tingley, Furnas, & Beissinger, 2014; Jarzyna & Jetz, 2016).

Functional distances or dissimilarities are used in the calculation of functional rarity indices (Violle et al., 2017). In `funrar`, a functional distance matrix can be calculated from a table of one or several traits measured for each taxa with `compute_dist_matrix()`. Different kinds of traits (continuous, categorical, ordinal) can be scaled or weighted in various ways when combined (Pavoine, Vallet, Dufour, Gachet, & Daniel, 2009). By default `compute_dist_matrix()` computes the unweighted Gower's (1971) distance because it covers classes of trait data and makes them comparable, but the user can also specify `euclidean` or `manhattan` distances. It is possible to scale traits using the `center` and `scale` arguments when traits are continuous.

Functional Distinctiveness and Functional Uniqueness are computed from the functional distance and species composition matrices. Functional Distinctiveness (D_i, `distinctiveness()`) of a species, that is the uncommonness of a species' traits compared to other species' traits in an assemblage (Figure 1 bottom left), weighted or not by species' relative abundances (Violle et al., 2017) is:

$$D_i = \frac{\sum_{j=1, j\neq i}^{N} d_{ij} A_j}{\sum_{j=1, j\neq i}^{N} A_j}, \quad (1)$$

with d_{ij} the functional dissimilarity between species i and species j, N the total number of species in the given assemblage, A_j the relative abundance of species j in the given assemblage. D_i is scaled between zero, if the focal species is identical to all the other species, and one when the focal species is most dissimilar to the other species. If only the presences–absences are provided, $A_j = 1/N$ for all j and D_i simplifies as:

$$D_i = \frac{\sum_{j=1, j\neq 1}^{N} d_{ij}}{N-1}, \quad (2)$$

D_i is the mean dissimilarity of a focal species as defined in Ricotta et al. (2016), that is the mean pairwise functional dissimilarity from a focal species to all the others. Functional Distinctiveness then relates to functional redundancy in an assemblage: the larger the index value, the more distant (less redundant) a species (or an individual) is to the average functional position of the assemblage in the functional space, that is the centroid.

Functional Uniqueness (U_i, `uniqueness()`) is the functional distance of a focal species i to its nearest neighbour in a set of assemblages (Figure 1 bottom right):

$$U_i = \min(d_{ij}), \quad (3)$$

with d_{ij} the functional dissimilarity between species i and species j, for all pairs of species considered across the site-species matrix with $j \neq i$. It quantifies how isolated a species is in the functional space without considering abundances: the higher the index value, the more distant a species is to its closest neighbour in the functional space.

As emphasized by Violle et al. (2017), a species can be functionally distinct (high D_i) in a given community but not functionally unique in an entire region (small U_i). In this regard, Distinctiveness and Uniqueness are used to uncover scale-dependent biodiversity dynamics: by default, `funrar` provides the former at local site level while the latter is computed at regional scale (whole site-species matrix). At local scale, community dynamics involve all coexisting species and their relative abundance is expected to convey the signature of assembly processes. Between-species dissimilarities and Functional Distinctiveness are thus relevant to assess the role of functional originality in community assembly. At regional scale, Functional Uniqueness can represent how taxa depart from a regional pool due to specific biogeographical and evolutionary legacies and should then be estimated based on the whole site-species matrix. Nevertheless, each index can be computed at both scales to grasp the different aspects of functional rarity (examples in the help of `distinctiveness()` and `uniqueness()`).

Because Distinctiveness and Uniqueness are computed using multiple traits, it can be difficult to disentangle if a species exhibits high values because of a single extreme trait value or because it has several rare trait values. The `uniqueness_dimensions()` and `distinctiveness_dimensions()` functions respectively compute Uniqueness and Distinctiveness values from the traits taken one by one as well as altogether. The former outputs a table with the value of Uniqueness for each trait and for all the traits considered together, while the latter outputs a list of site-species matrices of computed Distinctiveness values, one matrix per trait and one for all the traits considered together.

The second set of functions deals with the taxon component of functional rarity. Two indices estimate it: Taxon Scarcity (`scarcity()`) in an assemblage and Taxon Restrictedness (`restrictedness()`) in a set of assemblages. Taxon Scarcity (`scarcity()`) of a species in a given assemblage gets close to one when the species has low abundance in the site and gets close to zero when it dominates the assemblage:

$$S_i = \exp(-N A_i \ln 2), \quad (4)$$

where *N* is the number of species and A_i the relative abundance of species *i* at the focal site. When species are equally abundant in the assemblage, with $1/N$ relative abundances, S_i equals 0.5. Scarcity cannot be computed with only the presence–absence data in the site-by-species matrix.

Taxon Restrictedness is an index between zero and one. It increases when a species is present in less sites of the site-species matrix. Restrictedness nearly equals one when a species is present in a single site (examples on Figure 1):
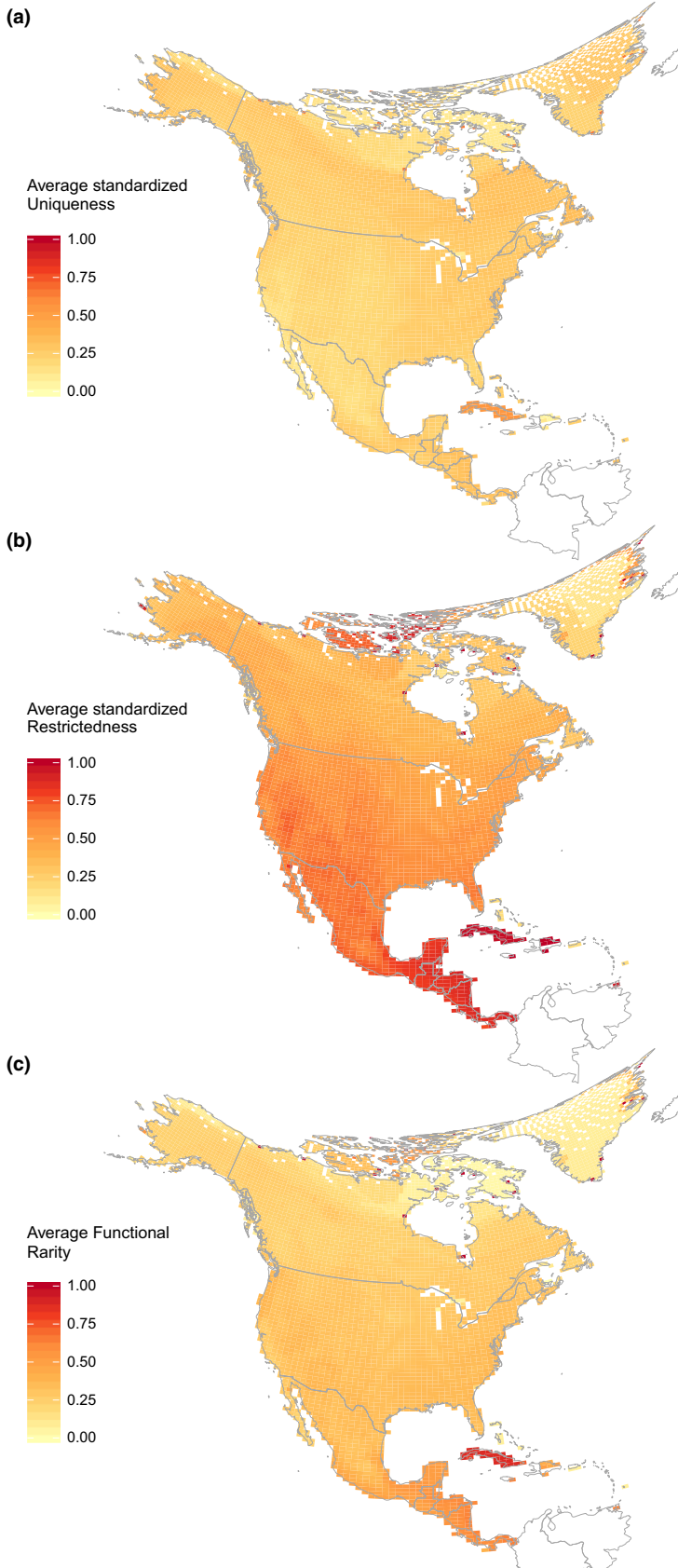
(a)

(b)

(c)

FIGURE 3 Maps of functional rarity indices averaged per site in North and Central America using a subset of the dataset of North and Central American Mammals from Lawing et al. (2016a). All indices have been scaled per site between 0 and 1. (a) Functional Uniqueness; (b) Taxon Restrictedness; (c) Functional Rarity, the average of Functional Uniqueness and Taxon Restrictedness per site. The geographical projection of maps is Albers Equal Area (ESRI:102008)

$$R_i = 1 - \frac{K_i}{K_{\text{tot}}}, \tag{5}$$

where K_i is the number of sites where species i occurs and K_{tot} the total number of sites in the dataset. R_i equals one when the species is completely absent from the dataset. Restrictedness can also be computed for predicted species distributions from ecological models (Guisan & Thuiller, 2005). A threshold of the predicted probabilities of occurrence (Jiménez-Valverde & Lobo, 2007; Liu, Berry, Dawson, & Pearson, 2005) is then used to derive the matrix of species occurrences per pixel.

Because of the increasing availability of large-scale and intensive datasets in ecology (Hampton et al., 2013), a site-species matrix can contain thousands of sites and thousands of species. However, as not all species are everywhere, site-species matrices are usually filled with many zeroes. Sparse matrices allow storing only the position of non-zero cells, saving memory. `funrar` performs sparse matrix calculations using the `Matrix` package for quicker and memory-efficient computations (Bates & Maechler, 2016). For more details, see the vignette included in the package.

3 | FUNCTIONAL RARITY OF NORTH AND CENTRAL AMERICAN MAMMALS

We used `funrar` to analyse a subset of the dataset of North and Central American Mammals from Lawing et al. (2016a), Lawing,

Eronen, Blois, Graham, and Polly (2016b). We selected 265 species out of 558 for which trait information was available. We used six traits relevant to mammal ecology (body mass, litter size, diet breadth, trophic level, habitat breadth and terrestriality, see Jones et al. (2009) for detailed trait explanation). The dataset comprises the presence–absence information for the 265 species across 9699 50 km x 50 km cells. We asked whether there are "hotspots" of Functional Uniqueness in North America and Central America for the six aforementioned traits; whether species that are functionally unique are geographically restricted; what the most functionally distinct and unique mammal species in the dataset are; and whether there are more functionally rare species in temperate, tropical or boreal areas.

For each species, we calculated Functional Uniqueness and Taxon Restrictedness indices and averaged them across species by grid cell. Because those two indices are regional-level indices, each species had a unique value, and the variation in averaged indices among grid cells thus reflects change in species composition. We produced maps of the average values for indices in North and Central America (Figure 3). We also computed functional rarity—the average of Functional Uniqueness and Taxon Restrictedness—where each is scaled between zero and one. The most functionally unique cells were in Cuba (Figure 3a), meaning that they hosted, on average, species that are quite functionally unique compared to the species pool of North and Central America. This pattern may be due to the tropical climate present in Cuba, which is less present
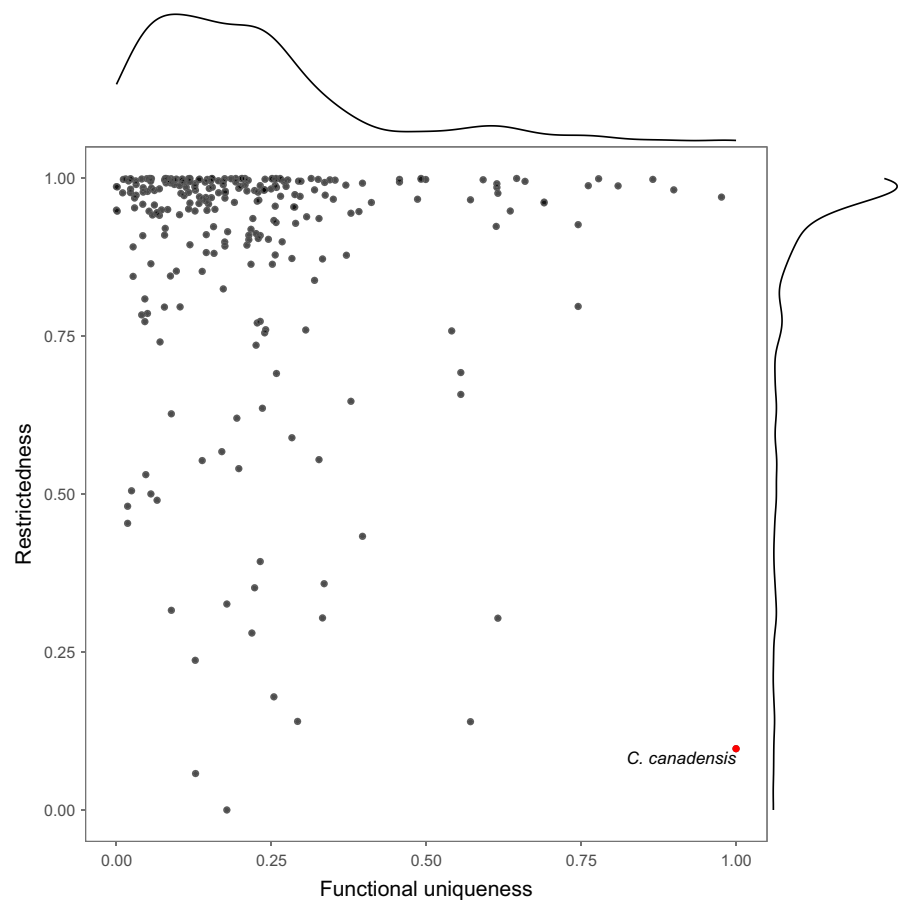

FIGURE 4 Biplot of Functional Uniqueness against Taxon Restrictedness per species across the whole dataset (*N* = 265 species). Note that both Functional Uniqueness and Taxon Restrictedness have been scaled between zero and one for easier comparison (Spearman's rho = −.06, *p* = .323, S = 3290600). The red dot indicates the position of *Castor canadensis*. Marginal distributions are indicated on the sides of the graph

across the rest of the dataset. We also identified a latitudinal gradient in Taxon Restrictedness (Figure 3b): sites at low latitude hosted more restricted species on average than sites in temperate and boreal regions, a pattern that complies with Rapoport's rule (Gaston, Blackburn, & Spicer, 1998; Rapoport, 1982). Altogether, combining the two facets into a single index highlighted Cuba as a hotspot of functional rarity (Figure 3c).

At the species level, Functional Uniqueness and Taxon Restrictedness were not correlated (Spearman's rho = −.06, *p* = .323) (Figure 4). Most species were geographically restricted (with many values around 1, meaning that they were present in a few grid cells only) but functionally redundant, that is with low values of Functional Uniqueness. Conversely, almost no species were both geographically widespread and functionally unique, apart from *Castor canadensis* (red dot in the bottom right corner of Figure 4), which occupies a very specific habitat (fossorial and ground dwelling) and is distributed continent-wide. Functional Distinctiveness and Functional Uniqueness were correlated (Spearman's rho = .37, *p* < .001), indicating that species that were locally functionally distinct tended to be regionally functionally unique. Even though local functional rarity and regional functional rarity were quite correlated, the weak correlation implies that rarity should be estimated both at the local and regional scale because it contrasts different types of rarity.

In summary, North and Central American mammals display a biogeographical gradient of functional rarity, such as species at low latitude show higher Functional Uniqueness and Taxon Restrictedness (Figure 3), even though most mammal species have low Functional Uniqueness and high Taxon Restrictedness (top left corner in Figure 4). The absence of correlation of Functional Uniqueness and Taxon Restrictedness shows that these components of functional rarity provide complementary information. Therefore, both components should be considered when mapping rarity and defining priority targets in conservation programs.

4 | CONCLUSION

Conservation biology has historically focused on the protection of rare species in terms of taxon occurrences and abundances (Prendergast, Quinn, Lawton, Eversham, & Gibbons, 1993). Although it can be decomposed in local, regional and habitat dimensions (Rabinowitz, 1981), this approach has emphasized taxonomic rarity and neglected the originality of functional attributes. Recently though, assessing species originality in terms of phylogenetic rarity (Cadotte & Jonathan Davies, 2010; Isaac, Turvey, Collen, Waterman, & Baillie, 2007; Rosauer, Laffan, Crisp, Donnellan, & Cook, 2009) and functional rarity (Mouillot et al., 2013; Umaña, Zhang, Cao, Lin, & Swenson, 2015; Violle et al., 2017) has gained momentum. It underlines the need to characterize patterns of rarity through the ecological and evolutionary attributes that influence biodiversity dynamics at multiple scales. Uncorrelated Functional Uniqueness and Restrictedness in North and Central American Mammals suggest that the functional component of rarity should be considered for a more

comprehensive assessment of biodiversity dynamics and a better design of conservation strategies. Such integrated view on rarity echoes Winter, Devictor, and Schweiger (2013) suggestion to "[include] other facets of diversity" for conservation. The `funrar` package contributes to the growing toolbox available for researchers to study and quantify the various dimensions of biodiversity and rarity. Adding the functional rarity string would strengthen the bow of diversity and rarity facets.

DATA ACCESSIBILITY

`funrar` stable version is available on CRAN (via `install.package("funrar")` or https://cran.r-project.org/package=funrar) and the development version is on Github at https://github.com/Rekyt/funrar. The code necessary to reproduce the analyses is on Github at https://github.com/Rekyt/mamm_funrar, an archived version is accessible on Zenodo https://doi.org/10.5281/zenodo.375605

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BIOSKETCH

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Author contributions: M.G. and P.D. designed the package; C.T. reviewed it; M.G. wrote the first draft of the manuscript; and all the authors edited and commented it.