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## APPLICATION

# Bioregionalization analyses with the bioregion R package

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Email: [maxime.lenormand@inrae.fr](mailto:maxime.lenormand@inrae.fr)**Handling Editor:** Gavin Simpson**Abstract**

1. Bioregionalization consists in the identification of spatial units with similar species composition and is a classical approach in the fields of biogeography and macroecology. The recent emergence of global databases, improvements in computational power and the development of clustering algorithms coming from the network theory have led to several major updates of the bioregionalizations of many taxa.
2. A typical bioregionalization workflow involves five different steps: formatting the input data, computing a (dis)similarity matrix, selecting a bioregionalization algorithm, evaluating the resulting bioregionalization and mapping and interpreting the bioregions. For most of these steps, there are many options available in the methods and R packages.
3. Here, we present bioregion, a package that includes all the steps of a bioregionalization workflow under a single architecture, with an exhaustive list of the bioregionalization algorithms used in biogeography and macroecology. These algorithms include (non-)hierarchical algorithms as well as community detection algorithms coming from the network theory. Some key methods from the literature, such as the network community detection algorithm Infomap or OSLOM (Order Statistics Local Optimization Method) that were not available in the R language are included in bioregion.
4. By combining different methods coming from different fields to communicate easily, bioregion will allow a reproducible and complete comparison of the different bioregionalization methods, which is still missing in the literature.

**KEYWORDS**

biodiversity, biogeography, bioregionalization, bioregions, R package, species distribution

## 1 | INTRODUCTION

Classifying biodiversity into groups sharing similar species composition, that is bioregionalization, is an essential aspect of biogeography that allows ecologists to understand how biodiversity assembles at large scales and under what drivers (Lomolino

et al., 2017). While bioregionalizations trace back to the early work of Sclater, Darwin and Wallace (Briggs, 2009; Sclater, 1858; Wallace, 1894), the increasing availability of distributional data, the development of new clustering algorithms and improvements in computational power have led to an upsurge in bioregionalization works for many taxa, realms and geographical areas, such as,

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to name a few, for continental mammals (Holt et al., 2013; Kreft & Jetz, 2010), birds (Holt et al., 2013; Procheş & Ramdhani, 2012; Rueda et al., 2013), angiosperms (Liu et al., 2023), trees (Droissart et al., 2018), freshwater fish (Leroy et al., 2019), reptiles (Procheş & Ramdhani, 2012), eukaryotic plankton (Sommeria-Klein et al., 2021), deep-sea benthic taxa (Ramiro-Sánchez et al., 2023), marine taxa (Costello et al., 2017), ophiuroids (Victorero et al., 2023). However, there is a large diversity in the methods and approaches used in bioregionalization, especially with recent developments on network-based clustering (Vilhena & Antonelli, 2015), and there is no unifying framework to perform all the steps of a bioregionalization. Here, we present the bioregion R package which aims at providing a unique and complete toolbox to perform all the necessary steps of bioregionalization.

A typical bioregionalization analysis consists of four main steps summarized in Figure 1: (1) the formatting of the input data, (2) (facultative) computing (dis-)similarity metric(s) between sites, (3) applying a bioregionalization algorithm and (4) evaluating, ecologically interpreting and mapping the bioregions. At step 1, the formatting of the input data involves switching between matrix and network formats depending on algorithm requirements. Step 2 involves computing distance metrics, using up-to-date advances

in beta-diversity metrics (Baselga, 2010, 2017) and preferably choosing metrics recommended for bioregionalization (Leprieur & Oikonomou, 2014). Step 3 consists in producing one or several bioregionalizations. A bioregionalization is defined here as the classification of sites (and sometimes species) into bioregions - a bioregionalization is equivalent to a partition in the clustering literature. We divided bioregionalization algorithms into three categories: hierarchical, non-hierarchical or network-based algorithms. Ecologists have traditionally relied on hierarchical clustering techniques (Kreft & Jetz, 2010), because they produce a dendrogram of bioregions, that supposedly mimics the nested structure of biodiversity (Escalante, 2009; Takhtadzhān & Crovello, 1986). Non-hierarchical algorithms, such as the commonly used K-means algorithm (Hartigan & Wong, 1979) or the Partitioning Around Medoids (PAM; Kaufman & Rousseeuw, 2009), are widely used in other fields and can also be used to generate a predefined set of bioregions. Both hierarchical and non-hierarchical clustering algorithms are based on dissimilarity (or distance) matrices (Figure 1), with few exceptions. More recently, network theory and community detection algorithms have been incorporated into the bioregionalization toolbox (Briega et al., 2023; Denelle et al., 2020; Edler et al., 2017; Lenormand et al., 2019; Leroy et al., 2019;

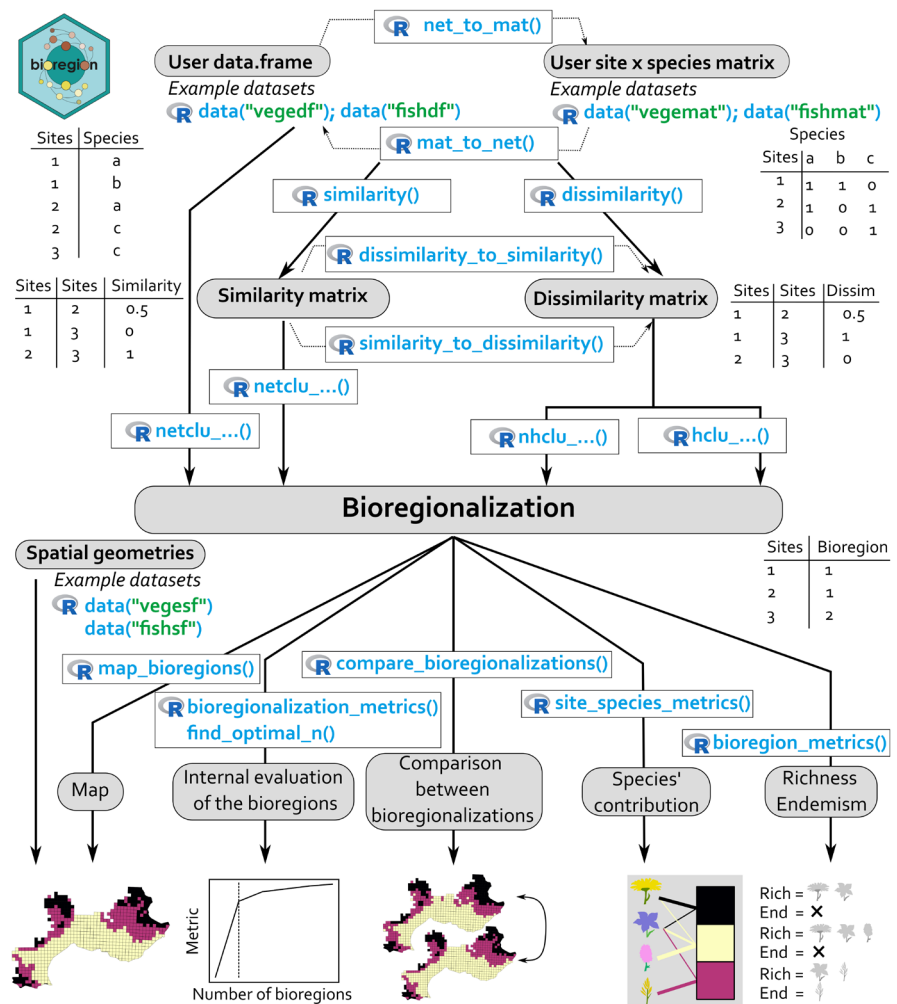


FIGURE 1 Workflow of the bioregion R package. See example code in Box 1.

Vilhena & Antonelli, 2015; Yusefi et al., 2019), but remain out of existing bioregionalization packages such as phyloregion (Daru et al., 2020). In some study cases, such algorithms have been shown to produce more relevant results than classical hierarchical clustering (Bloomfield et al., 2018; Vilhena & Antonelli, 2015). Algorithms derived from network theory are mostly similarity-based, but can also work directly on the bipartite network of species occurrences, or abundances, in sites (Beckett, 2016; Figure 1). Step 4 aims at calculating different evaluation metrics to determine the optimal number of bioregions, as well as interpreting and mapping the obtained bioregions.

In the following, we detail the logic of each step of the workflow. For more in-depth use of the package, we have created a dedicated website (<https://bioregio.github.io/bioregion/>), with detailed tutorials to guide users through the bioregionalization workflow (Box 1). The package is available for direct installation via R from the Comprehensive R Archive Network (CRAN; <https://CRAN.R-proje>

### BOX 1 A minimalistic representation of the R code for implementing the bioregionalization workflow.

```
# 1. Input data -----# install.
packages("bioregion")
library("bioregion")
data("vegdf"); data("vegemat")
# 2. (dis)Similarity -----
d <- dissimilarity(vegemat)
s <- similarity(vegemat)
# 3. Bioregionalization -----
bio1 <- nhclu_kmeans(d, n_clust=3)
bio2 <- hclu_hierarclust(d, n_clust=3)
bio3 <- netclu_walktrap(s)
# 4.1. Evaluation -----
bio2_opt <- hclu_hierarclust(d, n_clust=2:100)
eval_tree <-
bioregionalization_metrics(bio2_opt, d)
find_optimal_n(eval_tree)
# 4.2. Mapping -----
data("vegessf")
map_bioregions(bio1, geometry = vegessf)
# 4.3. Comparison -----
comp <- merge(bio1$clusters, bio2$clusters,
by = "ID")
colnames(comp) <- c("ID", "hclu", "nhclu")
comp_part <-
compare_bioregionalizations(comp[, c(2, 3)])
# 4.4. Summary statistics -----
sp_rho <- site_species_metrics(bio1, vegemat,
indices = "rho")
bioregion_stat <- bioregion_metrics(bio1,
vegemat, vegemap)
```

[ct.org/package=bioregion](https://github.com/bioregion/bioregion)). The development version is hosted on GitHub (<https://github.com/bioregion/bioregion>).

## 2 | INPUT DATA

The common use of bioregionalization is to cluster sites based on their species composition, but bioregionalization can span multiple dimensions. Spatially, bioregionalizations range from micro-scale (e.g. gutters of Paris; Hervé et al., 2018) and small-scale studies (e.g. how plots assemble into communities; Denelle et al., 2020) to regional and global scales (e.g. ecoregions, biogeographic regions). They can also be applied above (McDonald-Spicer et al., 2019) and below the species level (DiBattista et al., 2017). Furthermore, bioregionalization procedures can be based on either presence-absence or on quantitative measures such as abundance, biomass, area covered or relative abundance, which has implications for the calculation of pairwise dissimilarities between sites and the choice of the clustering algorithms. For presence-absence data, most dissimilarity indices and clustering methods assume absences are reliably recorded.

Second, there are two possible formats for input data. Ecologists are generally accustomed to a site-species matrix—called *matrix format* (Figure 1). This site-species matrix can also be encoded in a 'long-format' data frame, where each species-site occurrence or abundance represents one row of the data frame. This long format can be defined as a *network format* (Figure 1), as it is usually required for network clustering algorithms (Figure 1). More specifically, it is here a bipartite network, because it consists of two types of nodes (species and sites) connected by links representing the occurrence or abundance of species in sites. Site-site and species-species links are not allowed in this type of network. *bioregion* provides the functions `mat_to_net()` and `net_to_mat()` (Table 1) to quickly switch between these two formats.

## 3 | (DIS)SIMILARITY METRICS

Most bioregionalization algorithms require the computation of either similarity or dissimilarity metrics (also called  $\beta$ -diversity). It is important to note that hierarchical and non-hierarchical clustering algorithms mostly work with dissimilarity metrics, whereas network algorithms work with similarity metrics, so the package ships functions to conveniently switch from similarity to dissimilarity (`similarity_to_dissimilarity()` and `dissimilarity_to_similarity()`; Table 1). It is also essential to bear in mind that most network algorithms can take a bipartite species-site network directly as input.

There is a plethora of (dis)similarity metrics available in the ecological literature (Koleff et al., 2003), which span occurrence and abundance-based data. We implemented metrics recommended in the bioregionalization literature such as the turnover metrics (Kreft & Jetz, 2010), but also allow users to define their own turnover formula. Turnover metrics measure the proportion

TABLE 1 Overview of the 40 functions available in the bioregion R package.

Category	Functions	Description	Source package function
Utils	install_binaries()	Download, unzip, check permission and test the bioregion's binary files	
	mat_to_net() net_to_mat()	Create a data.frame from a site x species matrix and reverse	
	site_species_subset()	Extract a subset of nodes (sites or species) from a bioregionalization	
Pairwise similarity and distance metrics	similarity()	Compute similarity metrics between sites based on species composition	
	dissimilarity()	Compute dissimilarity metrics (beta-diversity) between sites based on species composition	
	similarity_to_dissimilarity()	Convert similarity indices to dissimilarity metrics	
	dissimilarity_to_similarity()	Convert dissimilarity indices to similarity indices	
	betapart_to_bioregion()	Convert betapart dissimilarity to bioregion dissimilarity	
Hierarchical clustering	hclu_hierarclust()	Hierarchical clustering based on dissimilarity or beta-diversity	fastcluster::hclust()
	hclu_diana()	Hierarchical clustering based on dissimilarity or beta-diversity	cluster::diana()
	cut_tree()	Cut a hierarchical tree	
	hclu_optics ()	OPTICS hierarchical clustering algorithm	dbscan::optics()
Non-hierarchical clustering	nhclu_dbscan()	dbscan clustering	dbscan::dbscan()
	nhclu_kmeans()	Non-hierarchical clustering: k-means analysis	stats::kmeans()
	nhclu_pam()	Non-hierarchical clustering: partitioning around medoids	cluster::pam()
	nhclu_clara()	Non-hierarchical clustering: partitioning around medoids	fastkmedoids::fastclara()
	nhclu_clarans()	Non-hierarchical clustering: partitioning around medoids	fastkmedoids::fastclarans()
	nhclu_affprop()	Affinity propagation	apcluster::apcluster()
Network clustering	netclu_beckett()	Community structure detection in weighted bipartite network via modularity optimization	bipartite::computeModules()
	netclu_infomap()	Infomap community finding	Code compiled from <a href="http://www.mapequation.org/infomap/">www.mapequation.org/infomap/</a>
	netclu_greedy()	Community structure detection via greedy optimization of modularity	igraph::cluster_fast_greedy()
	netclu_labelprop()	Finding communities based on propagating labels	igraph::cluster_label_prop()
	netclu_leadingeigen()	Finding communities based on leading Eigen vector of the community matrix	igraph::cluster_leading_eigen()
	netclu_louvain()	Louvain community finding	igraph::cluster_louvain() or code compiled from <a href="https://sourceforge.net/projects/louvain/">https://sourceforge.net/projects/louvain/</a>
	netclu_oslom()	OSLOM community finding	Code compiled from <a href="https://sourceforge.net/projects/louvain/">https://sourceforge.net/projects/louvain/</a>
	netclu_walktrap()	Community structure detection via short random walks	netclu_walktrap()
	netclu_leiden()	Finding communities using the Leiden algorithm	netclu_leiden()

(Continues)

TABLE 1 (Continued)

Category	Functions	Description	Source package function
Clustering analysis	bioregionalization_metrics()	Calculate comparative metrics for entire bioregionalizations	
	find_optimal_n()	Search for an optimal number of bioregions in a list of bioregionalizations	
	compare_bioregionalizations()	Compare sites and species memberships across multiple bioregionalizations	
	site_species_metrics()	Evaluate the contribution of sites and species to bioregions	
	bioregion_metrics()	Summary statistics for each bioregion	
Visualization	map_bioregions()	Map the bioregions	
Datasets	vegdf()	Spatial distribution of Mediterranean vegetation (data.frame; co-occurrence matrix and spatial grid)	
	vegemat()		
	vegese()		
	fishdf()	Spatial distribution of fish in Europe (data.frame; co-occurrence matrix and spatial grid)	
	fishmat()		
	fishsf()		

of unique species between pairs of sites (Baselga, 2010). Among turnover metrics, we recommend to use metrics that are not biased by differences in species richness, such as the Simpson dissimilarity index ( $\beta_{sim}$ ; Leprieur & Oikonomou, 2014). All these metrics are implemented in bioregion.

## 4 | CLUSTERING INTO BIOREGIONS

bioregion includes 18 clustering algorithms that can be classified as hierarchical, non-hierarchical or derived from the network theory (Table 2). To help users understand the different categories of algorithms, we name our function using a prefix, hclu\_, nhclu\_ or netclu\_ for hierarchical, non-hierarchical and network-based algorithms, respectively, followed by the name of the algorithm. Non-hierarchical and hierarchical clustering require dissimilarity matrices, with the exception of the affinity propagation, while network clustering works with either similarity matrices or bipartite networks. The bioregionalization algorithms available in bioregion come from existing R packages, such as bipartite (Dormann et al., 2022), cluster (Maechler et al., 2023), fastcluster (Müllner & Google Inc., 2021) or igraph (Csárdi et al., 2023), as well as external software such as the network algorithms Infomap (Rosvall & Bergstrom, 2008) and the Order Statistics Local Optimization Method (OSLOM; Lancichinetti et al., 2011). All parameters of the original algorithms remain accessible.

### 4.1 | Non-hierarchical distance-based clustering

Classic non-hierarchical clustering algorithms are either centroid-based or density-based. Centroid-based algorithms group sites into the same bioregion if they are close enough to a cluster centre. The centre of the cluster is determined by optimizing a function that

measures the distance between the centre and the members of the cluster. We included the two classical algorithms, K-means (Hartigan & Wong, 1979) and PAM (Kaufman & Rousseeuw, 2009) and two algorithms that are less common in biogeography: CLustering LARge Applications (CLARA) and CLARA based on RANdomized Search (CLARANS; Kaufman & Rousseeuw, 2009), both of which are extensions of PAM. We also included one density-based algorithm, the Density-based Spatial Clustering of Applications with Noise (DBSCAN) algorithm (Ester et al., 1996), which identifies areas of high density in the dissimilarity matrix and group them into similar bioregions. Density-based algorithms are rarely utilized in biogeography, with one instance being used to identify endemic plant bioregions in Crete (Kougioumoutzis et al., 2020).

A major methodological aspect of dissimilarity-based non-hierarchical algorithms is their dependence on user-defined number of bioregions. This number is typically found by evaluating multiple bioregionalizations (see Section 5), but they can also be defined a priori by users based on their expert knowledge or expectations. A final non-hierarchical algorithm sometimes used in biogeography (e.g. Marchese et al., 2022; Rueda et al., 2013) is the affinity cluster propagation (Frey & Dueck, 2007), which uses the similarity between pairs of sites and searches for clusters in an iterative process. This algorithm does not require an a priori number of bioregions.

### 4.2 | Hierarchical clustering

Hierarchical clustering generally refers to a method of grouping sites in a hierarchical tree (also called dendrogram) on the basis of their dissimilarity. This hierarchical tree can then be cut at different heights to identify bioregions. The hierarchical tree can be constructed in an agglomerative manner (i.e. all sites are initially assigned to their own bioregion and they are progressively grouped together) or in a divisive manner (i.e. all sites belong to the same unique bioregion and they are

**TABLE 2** Overview of the different algorithms available in bioregion. Algorithms can be categorized as hierarchical clustering, non-hierarchical clustering or network clustering.

Category	Algorithm	Hierarchical	Dissimilarity or similarity based
Hierarchical clustering (bioregions nested in a dendrogram)	Agglomerative clustering with method Ward.D, Ward.D2, single, complete, UPGMA, WPGMA, WPGMC, UPGMC	Yes	Dissimilarity
	Divisive clustering (DIANA)	Yes	Dissimilarity
	Ordering Points To Identify the Clustering Structure (OPTICS) (Ankerst et al., 1999)	Yes	Dissimilarity
Non-hierarchical clustering (unique non-nested partition of bioregions)	Density-based Spatial Clustering of Applications with Noise (DBSCAN) (Ester et al., 1996)	No	Dissimilarity
	K-means (Hartigan-Wong, Lloyd, Forgy and MacQueen) (Hartigan & Wong, 1979)	No	Dissimilarity
	Partitioning Around Medoids (PAM) (Kaufman & Rousseeuw, 2009)	No	Dissimilarity
	Clustering Large Applications (CLARA) (Kaufman & Rousseeuw, 2009)	No	Dissimilarity
	Clustering Large Applications based on RANdomized Search (CLARANS) (Kaufman & Rousseeuw, 2009)	No	Dissimilarity
	Affinity Propagation (Frey & Dueck, 2007)	No	Similarity
Network clustering (unique non-nested partition of bioregions)	Newman modularity measure optimized by Beckett (2016)	No	Bipartite network
	INFOMAP, also known as the Map Equation (Rosvall et al., 2009)	No and yes	Similarity or bipartite network
	Fast greedy modularity optimization (Clauset et al., 2004)	No	Similarity
	Propagating labels (Raghavan et al., 2007)	No	Similarity
	Leading eigenvector (Newman, 2006)	No	Similarity
	Louvain community detection (Blondel et al., 2008)	No	Similarity
	Order Statistics Local Optimization Method (OSLOM, Lancichinetti et al., 2011)	No and yes	Similarity
	Random walks (Pons & Latapy, 2005)	No	Similarity
	Leiden algorithm (Traag et al., 2019)	No	Similarity

progressively divided into different bioregions). For divisive hierarchical clustering, we included the Divisive ANALysis clustering (DIANA; Kaufman & Rousseeuw, 2009). In agglomerative clustering, a linkage function is used to determine whether two sites should belong to the same bioregion. There are several linkage functions, including the Ward's method, unweighted pair-group method with Arithmetic mean (UPGMA or between-group average), unweighted pair-group method using centroids (UPGMC), weighted pair-group method using arithmetic averages (WPGMA), weighted pair-group method using centroids (WPGMC), Ward's method, single (SL) and complete linkage (CL). All of these methods are available in the `hclu_hierarclust()` function.

Importantly, the order of sites in the distance matrix can influence the topology of the hierarchical tree, or dendrogram. Indeed, one of the conclusions of Dapporto et al. (2013) was to show that, when tied dissimilarity occurs between pairs of sites during the construction of an agglomerative tree, there is an arbitrary choice of one of the many different trees generated. This arbitrary selection can greatly bias the bioregionalization by producing dendrograms with a low cophenetic correlation coefficient. This coefficient represents the correlation between distances in the distance matrix and the cophenetic distance (i.e. the height of nodes in the hierarchical

tree), that is how much of the original information is retained in the dendrogram (Sneath & Sokal, 1973).

This major issue is still ignored in most published bioregionalizations based on agglomerative clustering. To tackle this issue, Dapporto et al. (2015) developed a robust method to overcome row-order bias and identify a consensus clustering for a given number of regions (the `recluster.region` algorithm implemented in the `recluster` package (Dapporto et al., 2013)). However, their method did not provide a tree topology, which is generally one of the objectives of hierarchical clustering as it allows understanding the relationships between regions. We address this issue by extending the algorithm of Dapporto et al. (2015) to produce a consensus tree topology. This new algorithm, called Iterative Hierarchical Consensus Tree (IHCT), reconstructs the tree from top to bottom by iteratively identifying the majority-decision binary split among many randomizations. We implemented this algorithm as an argument to `hclu_hierarclust()`, and also included options to select the tree with the highest cophenetic correlation coefficient or to determine a consensus tree (Dapporto et al., 2013). We recommend users to scrutinize the changes in tree topology across randomization trials and understand how well does their final tree represent the distance matrix with the cophenetic correlation coefficient.

We also included the semi-hierarchical clustering approach called Ordering Points To Identify the Clustering Structure (OPTICS; Ankerst et al., 1999). In the OPTICS method, sites are ordered so that the closest sites are neighbours. From this, a 'reachability' distance is calculated between each site. Bioregions are then extracted from this reachability distance in a hierarchical fashion. However, the hierarchical nature of the clusters is not directly provided by the algorithm in a tree-like output, but follows the structure of the 'reachability plot' (Hahsler et al., 2019).

#### 4.3 | Network clustering

Network clustering relies on community detection algorithms, where a community is defined as a cluster of nodes within a larger network—i.e. community in network theory does not convey the same definition as community in ecology. Community detection algorithms aim to identify nodes in a network that are more densely connected to each other than the other parts of the network or than expected by chance (Blondel et al., 2008; Newman, 2006; Traag et al., 2019). To identify such parts of a network, algorithms can maximize a statistic such as modularity—which compares the ratio of within- and between-cluster links (e.g. Blondel et al. (2008), or rely on other principles such as random walks in the network (Pons & Latapy, 2005; Rosvall & Bergstrom, 2008)).

In biogeography, network clustering can be performed using two different approaches, (i) clustering on pairwise site-site similarity matrices, in the form of a weighted unipartite network (e.g. Lenormand et al., 2019), (ii) clustering on bipartite species-site networks, without calculation of similarity metrics (e.g. Leroy et al., 2019; Vilhena & Antonelli, 2015). Bipartite species-site networks can be unweighted (i.e. occurrence of species in sites) or weighted (e.g. abundance, density or biomass of species in sites).

We implemented the most common community detection algorithms in bioregion in functions with the prefix `netclu_` followed by the name of the algorithm, for example `netclu_infomap`. Among these algorithms, most work with both unipartite (argument `bipartite = FALSE`) and bipartite approaches (argument `bipartite = TRUE`). Such algorithms include Infomap (Rosvall et al., 2009), walktrap (Pons & Latapy, 2005), fastgreedy (Clauset et al., 2004), label propagation (Raghavan et al., 2007), leading eigenvector (Newman, 2006); OSLOM (Lancichinetti et al., 2011), Leiden (Traag et al., 2019) and the Louvain algorithm (Blondel et al., 2008). We also included two algorithms that only work on weighted bipartite networks: Label Propagation Algorithm based on weighted bipartite modularity optimization (LPAwb+) for large networks and its thorough search extension DIRTLPAwb+ for small networks, Beckett (2016).

Two important algorithms, OSLOM (Lancichinetti et al., 2011) and Infomap (Rosvall et al., 2009), were not available in the R language so far. We compiled and implemented them in bioregion. To use them, the function `install_binaries()` has to be run first. It will install the binary files needed to run both algorithms.

## 5 | EVALUATION OF THE BIOREGIONS

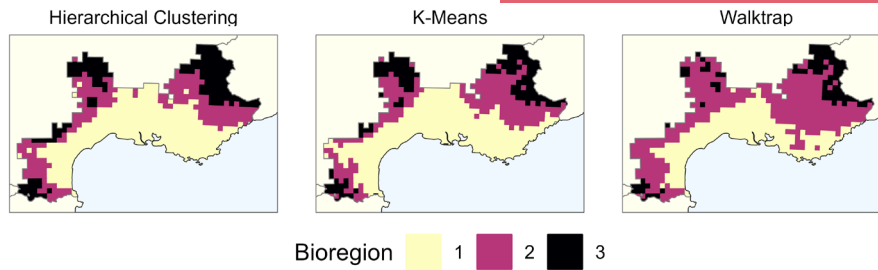
Clustering evaluation is the process of evaluating the quality of bioregions in terms of how well the algorithm has grouped similar sites and species together and separated dissimilar ones. Clustering evaluation has multiple dimensions: (1) evaluating the clustering structure with bioregionalization metrics (referred to as 'internal evaluation' in the clustering literature), (2) visual inspection of bioregion results and, when applicable, hierarchical relationships among bioregions, (3) comparing similarity among bioregionalizations or against an external validation bioregionalization (referred to as 'external evaluation' in the clustering literature) and (4) assessing the contribution of sites and species to bioregions. The package comes with functions for all four dimensions of clustering evaluation (Table 1).

### 5.1 | Evaluating the bioregionalization structure and choosing an adequate number of bioregions

Evaluation metrics are statistics that summarize the quality of the bioregionalization. Generally, they are used for those algorithms that require a predefined number of bioregions, to help users identify an adequate number. However, they can also be used to make quantitative comparisons between different algorithms. Many evaluation metrics exist, but not all metrics make sense to evaluate bioregionalization results. We have included four metrics used or recommended in biogeography, all of which can be computed with the `bioregionalization_metrics()` function:

- The percentage of dissimilarity explained by bioregions, which is the sum of within-cluster  $\beta$ -diversity divided by the total  $\beta$ -diversity of the distance matrix (Holt et al., 2013).
- The ANalysis Of SIMilarity (anosim) statistic (Clarke, 1993), which compares the between-cluster dissimilarities to the within-cluster dissimilarities.
- The average endemism among bioregions (Kreft & Jetz, 2010).
- The total endemism across all bioregions (Kreft & Jetz, 2010).

For algorithms requiring a user-defined number of bioregions, we provide guidelines based on standard practices in biogeography in the online help on how to identify an appropriate number of clusters with the `find_optimal_n()` function, which involves calculating metrics for a range of possible numbers of bioregions, and inspecting evaluation plots (evaluation metric plotted against the number of bioregions). Unlike existing bioregionalization packages (Daru et al., 2020), `find_optimal_n()` provides the user with several methods to determine an optimal number of bioregions. However, we recommend biogeographers to question the assumption that there is only one optimal number of clusters, which may be an oversimplification of the biological reality when a hierarchy of bioregions is expected. For example, Ficetola et al. (2017) investigated shallow, intermediate and deep bioregions, using different levels of dissimilarity, which



**FIGURE 2** Spatial mapping of three different bioregionalizations obtained using the hierarchical clustering with McQuitty linkage, K-means (Hartigan & Wong, 1979) and network walktrap approaches (Pons & Latapy, 2005), applied to the vegetation dataset provided in bioregion. The `hclu_hierarclust()`, `nhclu_kmeans()` and `netclu_walktrap()` functions from the package were used to generate this figure. The R code needed to reproduce this figure is available in the Appendix S1.

provides a more complete description of the hierarchy of natural regions.

## 5.2 | Mapping bioregions for visual inspection

Mapping the bioregions obtained in a bioregionalization analysis is important to assess the quality of bioregions (e.g. spatial distribution, cohesiveness of regions; Bloomfield et al., 2018; Victorero et al., 2023) and to understand and test the environmental drivers of a bioregionalization (Daru et al., 2020; Ficetola et al., 2017; Lomolino et al., 2017). If sites, or the spatial unit used, come with a ready to use shapefile, we can then link the obtained bioregions with its spatial component and map the bioregions with the function `map_bioregions()`, which relies on the `sf` package (Pebesma et al., 2023; Figure 2).

## 5.3 | Comparing different bioregionalizations

Comparing different bioregionalizations is useful for (i) comparing the results with an external validation, (ii) identifying which algorithms produced similar results, (iii) assessing the uncertainty of stochastic algorithms such as Infomap, where bioregionalization results can be highly variable between runs (e.g. Brown et al., 2023). `compare_bioregionalizations()` allows to do so using two metrics based on the confusion matrix between pairs of bioregionalizations, the Rand index (Rand, 1971) and the Jaccard index.

## 5.4 | Summary statistics

Computing individual summary statistics per site, species and bioregion is a necessary step to understand the composition and nature of bioregions. For sites and species, we have implemented the function `site_species_metrics()`, which computes metrics that quantify the contribution of species or sites to each bioregion. The metrics include the participation coefficient  $C$  and the relative intra-module degree  $z$  described in Guimera and Nunes Amaral (2005), the

contribution metric  $\rho$  used in Lenormand et al. (2019) as well as the fidelity and affinity metrics used in Bernardo-Madrid et al. (2019). For bioregion-level metrics, we implemented the `bioregion_metrics()`, which provides measures of richness, endemism and spatial coherence of bioregions, as defined in Divíšek et al. (2016).

## 6 | CONCLUSION

Because of biogeographical connections, environmental gradients and biological processes such as speciation and biotic dispersal, bioregions are usually considered to be hierarchically ordered (Kreft & Jetz, 2010; McLaughlin, 1992). Consequently, hierarchical clustering algorithms have become widely used in bioregionalization studies. The emergence of community detection algorithms coming from the network theory led to important studies with updated maps of natural bioregions (Edler et al., 2017; Leroy et al., 2019; Rojas et al., 2017; Vilhena & Antonelli, 2015) or the recent exploration of Anthropocene bioregions (Bernardo-Madrid et al., 2019; Brown et al., 2023; Capinha et al., 2015; Leroy et al., 2023). However, with a few exceptions (Bloomfield et al., 2018; Hill et al., 2020), no large-scale study has yet compared the different methods. By putting all the different steps of the bioregionalization workflow in a common place with the same architecture, bioregion provides the perfect background to realize such a study.

### AUTHOR CONTRIBUTIONS

Pierre Denelle, Boris Leroy and Maxime Lenormand developed the bioregion R package and the associated website. Pierre Denelle led the writing of the manuscript. All authors wrote the tutorials on the associated website, contributed critically to the drafts and gave final approval for publication.

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## CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

## 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.14496>.

## DATA AVAILABILITY STATEMENT

The bioregion R package is available for download from CRAN at <https://CRAN.R-project.org/package=bioregion>. The development version of the package is available at <https://github.com/bioRgeo/bioregion>. An associated website with tutorials is available at <https://bioregion.github.io/bioregion/>. Updates to the package are submitted to the CRAN repository and archived on the Zenodo repository, with each new release having its own DOI (version 1.2.0 of the package is archived at <https://doi.org/10.5281/zenodo.14781826>; Denelle et al., 2024).

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## REFERENCES

- Ankerst, M., Breunig, M. M., Kriegel, H.-P., & Sander, J. (1999). OPTICS: Ordering points to identify the clustering structure. *ACM SIGMOD Record*, 28(2), 49–60. <https://doi.org/10.1145/304181.304187>
- Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, 19(1), 134–143.
- Baselga, A. (2017). Partitioning abundance-based multiple-site dissimilarity into components: Balanced variation in abundance and abundance gradients. *Methods in Ecology and Evolution*, 8(7), 799–808. <https://doi.org/10.1111/2041-210X.12693>
- Beckett, S. J. (2016). Improved community detection in weighted bipartite networks. *Royal Society Open Science*, 3(1), 140536. <https://doi.org/10.1098/rsos.140536>
- Bernardo-Madrid, R., Calatayud, J., González-Suárez, M., Rosvall, M., Lucas, P. M., Rueda, M., Antonelli, A., & Revilla, E. (2019). Human activity is altering the world's zoogeographical regions. *Ecology Letters*, 22(8), 1297–1305. <https://doi.org/10.1111/ele.13321>
- Blondel, V. D., Guillaume, J.-L., Lambiotte, R., & Lefebvre, E. (2008). Fast unfolding of communities in large networks. *Journal of Statistical Mechanics: Theory and Experiment*, 2008(10), P10008.
- Bloomfield, N. J., Knerr, N., & Encinas-Viso, F. (2018). A comparison of network and clustering methods to detect biogeographical regions. *Ecography*, 41(1), 1–10.
- Briega, A., Rodriguez, M. A., Siebert, H., & Varela, S. (2023). Bioregionalization: From Wallace and Humboldt to deep-time paleoregion dynamics. *bioRxiv* 2023–03. <https://doi.org/10.1101/2023.03.28.534545>
- Briggs, J. C. (2009). Darwin's biogeography. *Journal of Biogeography*, 36(6), 1011–1017.
- Brown, M. J. M., Walker, B. E., Budden, A. P., & Nic Lughadha, E. (2023). Re-evaluating the importance of threatened species in maintaining global phytoregions. *New Phytologist*, 240(4), 1673–1686. <https://doi.org/10.1111/nph.19295>
- Capinha, C., Essl, F., Seebens, H., Moser, D., & Pereira, H. M. (2015). The dispersal of alien species redefines biogeography in the Anthropocene. *Science*, 348(6240), 1248–1251. <https://doi.org/10.1126/science.aaa8913>
- Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, 18(1), 117–143. <https://doi.org/10.1111/j.1442-9993.1993.tb00438.x>
- Clauset, A., Newman, M. E. J., & Moore, C. (2004). Finding community structure in very large networks. *Physical Review E*, 70(6), 066111. <https://doi.org/10.1103/PhysRevE.70.066111>
- Costello, M. J., Tsai, P., Wong, P. S., Cheung, A. K. L., Basher, Z., & Chaudhary, C. (2017). Marine biogeographic realms and species endemicity. *Nature Communications*, 8(1), 1057. <https://doi.org/10.1038/s41467-017-01121-2>
- Csárdi, G., Nepusz, T., Traag, V., Horvát, S., Zanini, F., Noom, D., Müller, K., Salmon, M., Antonov, M., & Chan Zuckerberg Initiative. (2023). igraph: Network analysis and visualization (version 1.5.1) [computer software]. <https://cran.r-project.org/web/packages/igraph/index.html>
- Dapporto, L., Ciolli, G., Dennis, R. L. H., Fox, R., & Shreeve, T. G. (2015). A new procedure for extrapolating turnover regionalization at mid-small spatial scales, tested on British butterflies. *Methods in Ecology and Evolution*, 6(11), 1287–1297. <https://doi.org/10.1111/2041-210X.12415>
- Dapporto, L., Ramazzotti, M., Fattorini, S., Talavera, G., Vila, R., & Dennis, R. L. H. (2013). recluster: An unbiased clustering procedure for beta-diversity turnover. *Ecography*, 36(10), 1070–1075. <https://doi.org/10.1111/j.1600-0587.2013.00444.x>
- Daru, B. H., Karunaratne, P., & Schliep, K. (2020). phyloregion: R package for biogeographical regionalization and macroecology. *Methods in Ecology and Evolution*, 11(11), 1483–1491. <https://doi.org/10.1111/2041-210X.13478>
- Denelle, P., Lenormand, M., & Leroy, B. (2024). bioregion: Bioregionalisation methods in R (version v1.2.1) [computer software]. *Zenodo*. <https://doi.org/10.5281/zenodo.14781826>
- Denelle, P., Violle, C., Consortium, D., & Munoz, F. (2020). Generalist plants are more competitive and more functionally similar to each other than specialist plants: Insights from network analyses. *Journal of Biogeography*, 47, 1922–1933.
- DiBattista, J. D., Travers, M. J., Moore, G. I., Evans, R. D., Newman, S. J., Feng, M., Moyle, S. D., Gorton, R. J., Saunders, T., & Berry, O. (2017). Seascape genomics reveals fine-scale patterns of dispersal for a reef fish along the ecologically divergent coast of northwestern Australia. *Molecular Ecology*, 26(22), 6206–6223. <https://doi.org/10.1111/mec.14352>
- Divíšek, J., Storch, D., Zelený, D., & Culek, M. (2016). Towards the spatial coherence of biogeographical regionalizations at subcontinental and landscape scales. *Journal of Biogeography*, 43(12), 2489–2501. <https://doi.org/10.1111/jbi.12832>
- Dormann, C. F., Freund, J., Gruber, B., Beckett, S., Devoto, M., Felix, G. M. F., Iriondo, J. M., Opsahl, T., Pinheiro, R. B. P., Strauss, R., & Vazquez, D. P. (2022). bipartite: Visualising bipartite networks and calculating some (ecological) indices (version 2.18) [computer software]. <https://cran.r-project.org/web/packages/bipartite/index.html>
- Droissart, V., Dauby, G., Hardy, O. J., Deblauwe, V., Harris, D. J., Janssens, S., Mackinder, B. A., Blach-Overgaard, A., Sonké, B., Sosef, M. S. M., Stévant, T., Svenning, J., Wieringa, J. J., & Couvreur, T. L. P. (2018). Beyond trees: Biogeographical regionalization of tropical Africa. *Journal of Biogeography*, 45(5), 1153–1167. <https://doi.org/10.1111/jbi.13190>
- Edler, D., Guedes, T., Zizka, A., Rosvall, M., & Antonelli, A. (2017). Infomap bioregions: Interactive mapping of biogeographical regions from species distributions. *Systematic Biology*, 66(2), 197–204.
- Escalante, T. (2009). Un ensayo sobre regionalización biogeográfica. *Revista Mexicana de Biodiversidad*, 80(2), 551–560.
- Ester, M., Kriegel, H.-P., Sander, J., & Xu, X. (1996). A density-based algorithm for discovering clusters in large spatial databases with noise. *Kdd*, 96(34), 226–231.

- Ficetola, G. F., Mazel, F., & Thuiller, W. (2017). Global determinants of zoogeographical boundaries. *Nature Ecology & Evolution*, 1(4), 0089.
- Frey, B. J., & Dueck, D. (2007). Clustering by passing messages between data points. *Science*, 315(5814), 972–976. <https://doi.org/10.1126/science.1136800>
- Guimera, R., & Nunes Amaral, L. A. (2005). Functional cartography of complex metabolic networks. *Nature*, 433(7028), 895–900. <https://doi.org/10.1038/nature03288>
- Hahsler, M., Piekenbrock, M., & Doran, D. (2019). dbscan: Fast density-based clustering with R. *Journal of Statistical Software*, 91, 1–30.
- Hartigan, J. A., & Wong, M. A. (1979). Algorithm AS 136: A k-means clustering algorithm. *Journal of the Royal Statistical Society: Series C: Applied Statistics*, 28(1), 100–108.
- Hervé, V., Leroy, B., da Silva Pires, A., & Lopez, P. J. (2018). Aquatic urban ecology at the scale of a capital: Community structure and interactions in street gutters. *The ISME Journal*, 12(1), 253–266.
- Hill, N., Woolley, S. N. C., Foster, S., Dunstan, P. K., McKinlay, J., Ovaskainen, O., & Johnson, C. (2020). Determining marine bioregions: A comparison of quantitative approaches. *Methods in Ecology and Evolution*, 11(10), 1258–1272. <https://doi.org/10.1111/2041-210X.13447>
- Holt, B. G., Lessard, J.-P., Borregaard, M. K., Fritz, S. A., Araújo, M. B., Dimitrov, D., Fabre, P.-H., Graham, C. H., Graves, G. R., & Jønsson, K. A. (2013). An update of Wallace's zoogeographic regions of the world. *Science*, 339(6115), 74–78.
- Kaufman, L., & Rousseeuw, P. J. (2009). *Finding groups in data: An introduction to cluster analysis*. John Wiley & Sons.
- Koleff, P., Gaston, K. J., & Lennon, J. J. (2003). Measuring beta diversity for presence-absence data. *Journal of Animal Ecology*, 72(3), 367–382.
- Kougioumoutzis, K., Kokkoris, I. P., Panitsa, M., Trigas, P., Strid, A., & Dimopoulos, P. (2020). Spatial phylogenetics, biogeographical patterns and conservation implications of the endemic flora of Crete (Aegean, Greece) under climate change scenarios. *Biology*, 9(8), 199.
- Kreft, H., & Jetz, W. (2010). A framework for delineating biogeographical regions based on species distributions. *Journal of Biogeography*, 37(11), 2029–2053.
- Lancichinetti, A., Radicchi, F., Ramasco, J. J., & Fortunato, S. (2011). Finding statistically significant communities in networks. *PLoS One*, 6(4), e18961.
- Lenormand, M., Papuga, G., Argagnon, O., Soubeyrand, M., De Barros, G., Alleaume, S., & Luque, S. (2019). Biogeographical network analysis of plant species distribution in the Mediterranean region. *Ecology and Evolution*, 9(1), 237–250.
- Leprieur, F., & Oikonomou, A. (2014). The need for richness-independent measures of turnover when delineating biogeographical regions. *Journal of Biogeography*, 41(2), 417–420. <https://doi.org/10.1111/jbi.12266>
- Leroy, B., Bellard, C., Dias, M. S., Hugueny, B., Jézéquel, C., Leprieur, F., Oberdorff, T., Robuchon, M., & Tedesco, P. A. (2023). Major shifts in biogeographic regions of freshwater fishes as evidence of the Anthropocene epoch. *Science Advances*, 9(46), eadi5502. <https://doi.org/10.1126/sciadv.adi5502>
- Leroy, B., Dias, M. S., Giraud, E., Hugueny, B., Jézéquel, C., Leprieur, F., Oberdorff, T., & Tedesco, P. A. (2019). Global biogeographical regions of freshwater fish species. *Journal of Biogeography*, 46(11), 2407–2419. <https://doi.org/10.1111/jbi.13674>
- Liu, Y., Xu, X., Dimitrov, D., Pellissier, L., Borregaard, M. K., Shrestha, N., Su, X., Luo, A., Zimmermann, N. E., & Rahbek, C. (2023). An updated floristic map of the world. *Nature Communications*, 14(1), 2990.
- Lomolino, M. V., Riddle, B. R., & Whittaker, R. J. (2017). *Biogeography*. Sinauer Associates is an imprint of Oxford University Press.
- Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., Hornik, K., Studer, M., Roudier, P., Gonzalez, J., Kozłowski, K., Schubert, E., & Murphy, K. (2023). cluster: "Finding groups in data": Cluster analysis extended Rousseeuw et al. (version 2.1.6) [computer software]. <https://cran.r-project.org/web/packages/cluster/index.html>
- Marchese, C., Hunt, B. P. V., Giannini, F., Ehrlér, M., & Costa, M. (2022). Bioregionalization of the coastal and open oceans of British Columbia and Southeast Alaska based on sentinel-3A satellite-derived phytoplankton seasonality. *Frontiers in Marine Science*, 9. <https://doi.org/10.3389/fmars.2022.968470>
- McDonald-Spicer, C., Knerr, N. J., Encinas-Viso, F., & Schmidt-Lebuhn, A. N. (2019). Big data for a large clade: Bioregionalization and ancestral range estimation in the daisy family (Asteraceae). *Journal of Biogeography*, 46(2), 255–267.
- McLaughlin, S. P. (1992). Are floristic areas hierarchically arranged? *Journal of Biogeography*, 19, 21–32.
- Müllner, D., & Google Inc. (2021). fastcluster: fast hierarchical clustering routines for R and "Python" (version 1.2.3) [computer software]. <https://cran.r-project.org/web/packages/fastcluster/index.html>
- Newman, M. E. J. (2006). Finding community structure in networks using the eigenvectors of matrices. *Physical Review E*, 74(3), 036104. <https://doi.org/10.1103/PhysRevE.74.036104>
- Pebesma, E., Bivand, R., Racine, E., Sumner, M., Cook, I., Keitt, T., Lovelace, R., Wickham, H., Ooms, J., Müller, K., Pedersen, T. L., Baston, D., & Dunnington, D. (2023). sf: Simple features for R (version 1.0-14) [computer software]. <https://cran.r-project.org/web/packages/sf/index.html>
- Pons, P., & Latapy, M. (2005). Computing communities in large networks using random walks (long version). *arXiv:Physics/0512106*. <http://arxiv.org/abs/physics/0512106>
- Procheş, Ş., & Ramdhani, S. (2012). The world's zoogeographical regions confirmed by cross-taxon analyses. *BioScience*, 62(3), 260–270.
- Raghavan, U. N., Albert, R., & Kumara, S. (2007). Near linear time algorithm to detect community structures in large-scale networks. *Physical Review E*, 76(3), 036106. <https://doi.org/10.1103/PhysRevE.76.036106>
- Ramiro-Sánchez, B., Martin, A., & Leroy, B. (2023). The epitome of data paucity: Deep-sea habitats of the southern Indian Ocean. *Biological Conservation*, 283, 110096.
- Rand, W. M. (1971). Objective criteria for the evaluation of clustering methods. *Journal of the American Statistical Association*, 66(336), 846–850. <https://doi.org/10.1080/01621459.1971.10482356>
- Rojas, A., Patarroyo, P., Mao, L., Bengtson, P., & Kowalewski, M. (2017). Global biogeography of Albian ammonoids: A network-based approach. *Geology*, 45(7), 659–662.
- Rosvall, M., Axelsson, D., & Bergstrom, C. T. (2009). The map equation. *The European Physical Journal Special Topics*, 178(1), 13–23. <https://doi.org/10.1140/epjst/e2010-01179-1>
- Rosvall, M., & Bergstrom, C. T. (2008). Maps of random walks on complex networks reveal community structure. *Proceedings of the National Academy of Sciences of the United States of America*, 105(4), 1118–1123.
- Rueda, M., Rodríguez, M. Á., & Hawkins, B. A. (2013). Identifying global zoogeographical regions: Lessons from Wallace. *Journal of Biogeography*, 40(12), 2215–2225.
- Slater, P. L. (1858). On the general geographical distribution of the members of the class Aves. *Zoological Journal of the Linnean Society*, 2(7), 130–136.
- Sneath, P. H., & Sokal, R. R. (1973). Numerical taxonomy: The principles and practice of numerical classification. <https://www.cabdirect.org/cabdirect/abstract/19730310919>
- Sommeria-Klein, G., Watteaux, R., Ibarbalz, F. M., Pierella Karlusich, J. J., Iudicone, D., Bowler, C., & Morlon, H. (2021). Global drivers of eukaryotic plankton biogeography in the sunlit ocean. *Science*, 374(6567), 594–599.
- Takhtadzhīān, A. L., & Crovello, T. J. (1986). *Floristic regions of the world*. University of California Press.
- Traag, V. A., Waltman, L., & Van Eck, N. J. (2019). From Louvain to Leiden: Guaranteeing well-connected communities. *Scientific Reports*, 9(1), 5233.

- Victorero, L., Samadi, S., O'Hara, T. D., Mouchet, M., Delavenne, J., Leprieur, F., & Leroy, B. (2023). Global benthic biogeographical regions and macroecological drivers for ophiuroids. *Ecography*, 2023(9), e06627. <https://doi.org/10.1111/ecog.06627>
- Vilhena, D. A., & Antonelli, A. (2015). A network approach for identifying and delimiting biogeographical regions. *Nature Communications*, 6, 6848. <https://doi.org/10.1038/ncomms7848>
- Wallace, A. R. (1894). What are zoological regions. *Nature (London)*, 49(1278), 610–613.
- Yusefi, G. H., Safi, K., & Brito, J. C. (2019). Network-and distance-based methods in bioregionalization processes at regional scale: An application to the terrestrial mammals of Iran. *Journal of Biogeography*, 46(11), 2433–2443.

## SUPPORTING INFORMATION

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

### Appendix S1.

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