RH: dispRity package.

# dispRity: a modular R package for measuring disparity.

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Abstract

1. Biological data is multivariate in essence: many traits in organisms co-vary with each other in space and time. This causes biologists to either reduce these variables in a manageable number of variables or, increasingly, to use multivariate toolkits. One such toolkit is based on creating a multidimensional space where the variables are the axis of this space. It is then possible to use a summary metrics for measuring some properties of this space for some group of species and compare them. For example, if studying morphology, one can create a morphospace for two groups of species, measure some aspect of these groups (such as their spread in the space - often termed disparity) and then test whether they have a different disparity.

- 2. There are as many definition of these multidimensional spaces, metrics and tests as there are questions that can be tackled with such methods. Many of these methods are implemented in specific software or R packages. However, the definition of the space, metric and test is often dependent on the software/package's author's point of view or specific question. This can unfortunately hamper researchers to apply different methods that suits best their specific questions.
- 3. Here I present the dispRity package, a flexible R package for running multidimensional analysis. This package allows users to define each step of the analysis (whether it is the space, the metric or the test) through a highly modular architecture where each definition can be passed as a function. It also provides a tidy interface through the dispRity object, allowing to easily run

- reproducible multivariate analysis.
- 4. The dispRity package also comes with an extend manual regularly updated 25 following users questions or suggestions. Furthermore, the package contains some simulation tools (e.g to simulate complex multidimensional space or morphological data). Finally it also contains a suit of utilities to work with dispRity objects aimed at helping users to develop their own 29 multidimensional metrics and/or tests.
- (Keywords: disparity, ordination, multidimensionality, disparity-through-time,
- palaeobiology, ecology)

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#### Introduction

Biological data are complex. To understand the ecology and evolution of species 34 we must use multiple variables that inevitably covary with each other through time and space. One solution to this problem is to analyse these data in a multivariate framework (e.g. Price et al., 2015; Díaz et al., 2016). Such analyses aim to capture the complex multidimensionality of biological data, while still providing outputs that are interpretable in our physical world restricted to three dimensions. These multivariate analyses can be used to investigate changes in morphological diversity through time (Close et al., 2015), competitive replacement scenarios (Brusatte et al., 2008), relationships among form and function (Díaz et al., 2016) and even to describe the entirety of possible shapes for a group of organisms (Raup, 1966). The biological variables in such analyses are equally diverse, including morphological traits (discrete traits like the presence or absence of a character, e.g. Brusatte et al. 2012; and continuous traits such as lengths, e.g. Price et al. 2015), life history traits (e.g. Díaz et al., 2016), or even ecosystem properties (e.g. Donohue et al., 2013). In all these analysis, each set of multivariate traits forms a multidimensional 48 space, usually represented as matrices where the columns are the dimensions (or some transformation thereof) and rows are the elements (often species or individuals) within 50 this space. These multidimensional spaces can be defined in many ways, for example as 51 a pairwise distance matrix (Close et al., 2015), or as outputs from a principal coordinates analysis (PCO; Brusatte et al., 2008), a principal components analysis (PCA;

Zelditch et al., 2012), or a multidimensional scaling (MDS; Donohue et al., 2013), among others. The name we give to the multidimensional space tends to vary with the kinds of traits used to construct it. For example, when using morphological traits the multivariate space will be a morphospace, when using ecological traits it may be referred to as an ecospace or trait space. Once the multidimensional space is defined it is then possible to measure a specific aspect of it. This specific measurement (hereafter referred to as a "disparity metric") can in turn be defined in many different ways depending on the specific question being investigated (e.g. Wills, 2001; Ciampaglio et al., 2001; Foth et al., 2012; Donohue et al., 2013; Hughes et al., 2013; Finlay and Cooper, 2015; Close et al., 2015, or combinations thereof). Finally, all these different 63 multidimensional spaces and their associated disparity metrics can be used in an equal 64 variety of statistical tests such as non-parametric multivariate analyses of variance (e.g. Brusatte et al., 2008), multidimensional permutation tests (e.g. Díaz et al., 2016) or even 66 simply by looking at the confidence interval overlaps between disparity measurements 67 (e.g. Halliday and Goswami, 2016). In summary, there are many different ways to perform each step of a multidimensional analysis, making analyses of complexity ever 69 more complex. 70

In theory, this multitude of ways to generate and define multidimensional spaces, measure disparity within and analyse these metrics is not an issue, in fact, it allows researchers to choose both the most appropriate method for their question or data, or even to test their question using multiple methods (such as Matzke, 2013, for

biogeography). In practice, however, this is hampered by existing software implementations. Although many software packages exist for multidimensional analysis (e.g. Bouxin, 2005; De Caceres et al., 2007; Oksanen et al., 2007; Adams and Otárola-Castillo, 2013; Lloyd, 2015; Adams et al., 2017), package maintainers/software developers choose their preferred definition of multidimensional space and disparity metric and then enforce this on users by allowing little to no flexibility. For example, in the excellent and widely used geomorph package, morphological disparity analysis uses 81 the morphol.disparity function that defines the multidimensional space as the ordination of the Procrustes transform of morphometric data, the disparity metric as the Procrustes variance, and uses a permutation tests to test hypotheses (Zelditch et al., 84 2012; Adams and Otárola-Castillo, 2013; Adams et al., 2017). This is ideal in some cases, but in others may not be the most appropriate analysis. This can lead to inappropriate analyses by users confined by the existing software implementations. 87

The aim of the dispRity package is to solve such problems by providing a

completely flexible framework for studying multidimensional data. This package is

based on a highly modular architecture where each crucial decision in

multidimensional analysis (which data, which metric and which test) can be provided

by the user. It implements many commonly used metrics and definitions of disparity, as

well as providing a simple interface for users to implement their own disparity

functions. The package is described here for the use of discrete morphological data

diversity analysis but can be generalised to any type of multidimensional data (see the

96 package vignette for more examples).

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#### DESCRIPTION

In brief, the package takes a matrix object (the multidimensional space), calculates
some aspect of it (the disparity metric) and allows users to analyse the resulting
dispRity object (see Manuals and Vignettes below). Some additional functions modify
the multidimensional space, for example by dividing it by groups or through time
and/or bootstrapping it (see Fig. 1 and Table 1).

# Measuring disparity

The dispRity function measures disparity of any multidimensional space (of class
matrix or data.frame) where the columns correspond to the dimensions and the rows
correspond to the elements present in the space. The disparity metric (i.e. the aspect of
interest of the space) is passed through the metric argument and is defined by the user
as any function or combination of functions that can either transform the matrix into:

- Another matrix (a dimension-level 3 function e.g. a variance-covariance matrix;
   stats::cor)
- A vector (a dimension-level 2 function e.g. the variance of each dimension;

  dispRity::variances see below)
- A single value (a dimension-level 1 function e.g. the overall standard deviation;

  stats::sd)

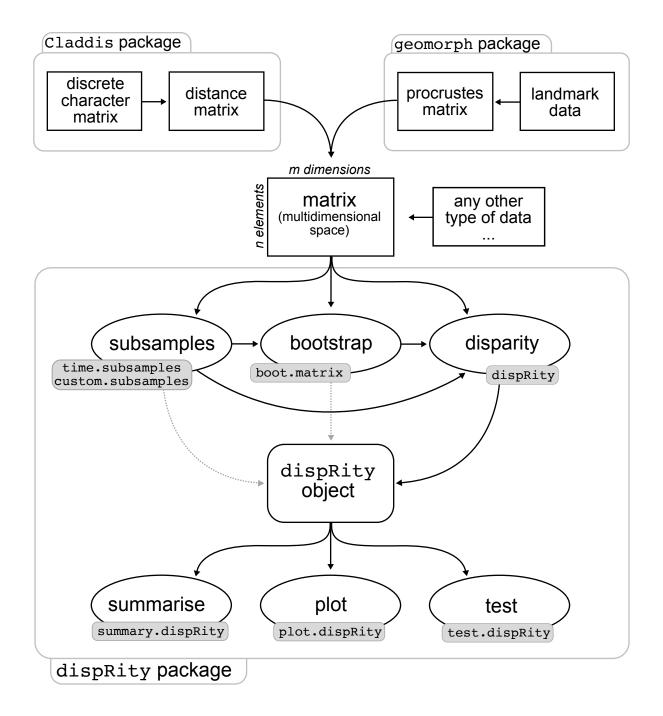


Figure 1: dispRity package workflow: rectangles represent matrices; ellipses represent functions; plain black arrows indicate input/output; dashed grey arrows indicate output (though the summary, plot, and test function cannot be applied if no disparity has been calculated).

| Function              | Description   |  |  |  |
|-----------------------|---|--|--|--|
| geomorph.ordination   | Imports data from the geomorph package.                   |  |  |  |
| Claddis.ordination    | Imports data from the Claddis package.                    |  |  |  |
| custom.subsamples     | Separates data into custom subsamples.                    |  |  |  |
| time.subsamples       | Separates data into time subsamples.                      |  |  |  |
| boot.matrix           | Bootstraps and rarefies a matrix or a dispRity object.    |  |  |  |
| dispRity              | Calculates disparity from an matrix or a dispRity object. |  |  |  |
| summary.dispRity      | Summarises a dispRity object.                             |  |  |  |
| plot.dispRity         | Plots a dispRity object.                                  |  |  |  |
| test.dispRity         | Applies statistical tests to a dispRity object.           |  |  |  |
| dispRity.per.group    | Pipeline for disparity within groups analysis.            |  |  |  |
| dispRity.through.time | Pipeline for disparity-through-time analysis.             |  |  |  |

Table 1: Main functions in the dispRity package.

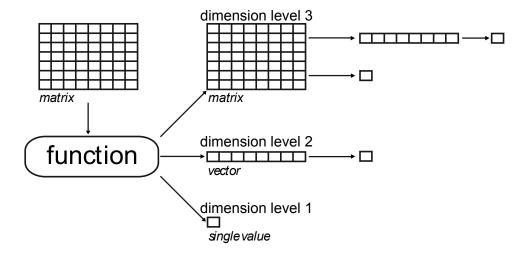


Figure 2: Illustration of the different metric dimension-levels in the dispRity package. In this example, each cell correspond to a single value (e.g. a  $8 \times 7$  matrix or a vector of eight elements).

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The disparity metrics can be functions from other packages, defined by the user or from the dispRity package (see Table 2 for the currently implemented metrics).

When multiple functions are passed to the metric argument, the functions are sorted by dimension-level and applied in decreasing order to the data. For example, if the metric is defined as metric = c(mean, range), the range function (dimension-level 2) is first applied to the data and the function mean is then applied to the result (e.g. mean(range(data))). There is no limitation on the metric dimensions only that at least one dimension-level 2 or 1 function must be present in the metric definition (i.e. disparity can only be defined as distribution or a single value).

Splitting the multidimensional space into subsets

| name                | description                            | dimen | - definition   | source                |
|---------------------|--|-------|--|-----------------------|
|                     |  | sion  |  |                       |
|                     |  | level |  |                       |
| ellipse.            | The volume of the ellip-               | 1     | $\left  \frac{\pi^{k/2}}{\Gamma(\frac{k}{2}+1)} \prod_{i=1}^{k} (\lambda_i^{0.5}) \right $ | Donohue et al. (2013) |
| $\mathtt{volume}^1$ | soid                                   |       | <i>i</i> -1  |                       |
| convhull.           | The surface of the convex              | 1     | NA   | geometry::convhulln   |
| surface             | hull                                   |       |  |                       |
| convhull.           | The volume of the convex               | 1     | NA   | geometry::convhulln   |
| volume              | hull                                   |       |  |                       |
| diagonal            | The greatest Euclidean                 | 1     | $\sqrt{\sum_{i=1}^{k}  max(k_i) - min(k_i) }$  | dispRity::diagonal    |
|                     | distance                               |       |  |                       |
| mode.val            | The modal value                        | 1     | NA   | dispRity::mode.val    |
| ranges              | The absolute ranges of                 | 2     | $ max(k_i) - min(k_i) $  | dispRity::ranges      |
|                     | each dimension                         |       |  |                       |
| variances           | The variance of each di-               | 2     | $\sigma^2 k_i$   | dispRity::variances   |
|                     | mension                                |       |  |                       |
| centroids           | The distance between each              | 2     | $\sqrt{\sum_{i=1}^{n} (k_n - Centroid_k)^2}$   | dispRity::centroids   |
|                     | element and a fixed point <sup>2</sup> |       |  |                       |
|                     | of the space                           |       |  |                       |

Table 2: Where k is the number of dimensions, n the number of elements,  $\lambda_i$  is the eigenvalue of each dimensions,  $\sigma^2$  is their variance and  $Centroid_k$  is their mean. <sup>1</sup> this function uses a fast estimation of the eigenvalue that only works in an ordinated space based on MDS or PCO/PCoA (not PCA); <sup>2</sup> by default that point is the centroid of the elements.

Prior to calculating disparity, the multidimensional space can be subdivided into subsamples, typically to be compared to each other. For example, one may be interested in seeing how the disparity of a specific subsample of the space compares to another (e.g. difference among groups) or, how different subsamples change sequentially (e.g. through time). In essence, the original space corresponds to the overall space (e.g. a morphospace contains all the possible observed morphologies).

Conversely, subsamples correspond to parts of the space with pooled characteristics (i.e. only a subset of the total morphospace).

This splitting can be done using the custom.subsamples or time.subsamples 133 functions. The first takes as argument the matrix defining the multidimensional space 134 and a list of elements to group into different subsamples. The second also takes a 135 matrix and arguments giving the age of the taxa (a phylogeny and/or a table 136 containing the first and last occurrence data for all/some elements - this allows species 137 with a longer timespan to be present in multiple time subsamples for example) and 138 which subsamples to create: (1) discrete time subsamples (or time-binning) or (2) 139 continuous time subsamples (or time-slicing). 140

The time-binning method groups elements by specific age range. The
time-slicing method works by using a phylogeny and looking at which taxa are present
at any specific point in time. This method thus requires the nodes to be part of the
multidimensional space, a dated phylogeny (chronogram) and which model to use
when slicing through branches rather than tips and nodes. When a slice occurs not on a

- tip or a node, four methods are available to select either the descendent or the ancestor's node/tip as an element for this time slice:
- "acctran" (accelerated transformation) where the data chosen along the branch is always the one of the descendant
  - "deltran" (delayed transformation) where the data chosen along the branch is always the one of the ancestor
  - "punctuated" where the data chosen along the branch is randomly chosen between the descendant or the ancestor

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• "gradual" where the data chosen along the branch is either the descendant or the ancestor depending on branch length

# Bootstrapping and rarefying

Disparity measurement can be influenced by sampling (Butler et al., 2012). To take this source of bias into account, it is common practice to bootstrap the multidimensional space (to minimise the effect of outliers) or/and to rarefy the data (to minimise the effect of different sample sizes in different subsamples). Additionally, if disparity is defined as a dimension-level 1 metric, it can be useful to measure it on bootstrapped data to obtain a distribution on which to perform statistical analyses.

Bootstrapping can be achieved by using the boot.matrix function which
pseudo-replicates the multidimensional space following two algorithms (1) the "full"

algorithm where the bootstrapping is entirely stochastic (*n* elements are replaced by any *m* elements drawn from the data) and (2) the "single" algorithm where only one random element is replaced for each pseudo-replicate (somewhat akin to jackknife resampling).

Similarly, rarefaction can be achieved through the same boot.matrix function.

Rarefaction can be useful when looking at the effect of reducing the number of
elements on the results of an analysis or for allowing the comparisons of subsamples
with the same number of elements in each. In practice, rarefaction limits the number of
elements to be drawn for each bootstrap replication: only n - x elements are selected at
each bootstrap replicate (where x is the number of non-sampled elements).

# Interpreting results

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The functions above all generate a dispRity object that can be summarised or plotted using the S3 method functions summary.dispRity and plot.dispRity (provided disparity was calculated). These results can then be analysed using the test.dispRity function for comparing subsamples or testing hypotheses.

Summarising and plotting.— The summary.dispRity and plot.dispRity functions allow users to set which central tendency and which quantiles should be represented.

Additionally, the plot.dispRity function graphically represents the summarised results using different representations: (1) "continuous" for displaying continuous disparity curves (in the case of disparity-through-time analysis for example) and (2)

"box", "lines", or "polygons" to display them using boxplots, confidence interval lines

or polygons respectively. Additional arguments specific to dispRity objects can also be

used such as observed to display the observed disparity (i.e. non-bootstrapped) or

rarefaction to only plot the disparity for a certain number of elements (i.e. the

rarefaction level). The function can also take any additional graphic arguments (main,

xlab, col, etc...) from base R.

Testing hypotheses.— The test.dispRity function allows users to test hypotheses on the disparity data (e.g. by comparing the different subsamples to each other). Similarly to the dispRity function described above, this function can take any test defined by the 193 user or from other R packages. The comparison arguments indicates in which order (if any) the tests should be applied to the subsamples: (1) "pairwise" for pairwise 195 comparisons; (2)"referential" for comparing the first subsample to all the others; (3) 196 "sequential" for comparing subsamples sequentially (e.g. first against second, second 197 against third, etc.); (4) 'all" for comparing all the subsamples simultaneously (i.e. 198 disparity  $\sim$  subsamples - this can be used for lm or glm) or (5) any list of pairs (or 199 more) of subsamples to compare. 200

Some tests are implemented within the package such as the Bhattacharrya

Coefficient (bhatt.coeff; Bhattacharyya, 1943; Guillerme and Cooper, 2016) or a

permutation test based on null hypothesised multidimensional space following Díaz

et al. (2016) (null.test). Additionally, this function also allows additional arguments

such as rarefaction (as described above) or correction to adjust p-values when using

206 multiple parametric tests.

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# Examples

Multivariate analysis can be really useful for looking multiple aspects of organisms
diversity together. For example, one classic univariate trait used in ecology and
evolution can be the sheer number of species present in a ecosystem or/and through
time. This trait can be useful to test whether some ecosystems or/and time periods
have more species diversity than others. In this case one can then test some hypothesis
such as: environments with bigger altitudes gradients contain more species.

Conversely, in the case of species diversity, one can also look at another independent multivariate trait: the diversity of morphologies (or disparity; Ruta et al., 2013). Using disparity, it is then also possible to assess whether one ecosystem or/and time period display more morphological variation. Following the previous example, if disparity is also higher with bigger altitudes gradients, one could argue that the species richness is caused by an increased number of morphologies adapted to more ecological niches (or something akin).

The following example is based on a classical palaeobiology morphological disparity analysis. Note that more examples are available in the package manual (https:

//rawgit.com/TGuillerme/dispRity/master/inst/gitbook/\_book/index.html).

dispRity data.— The package contains a dataset that is a subset from Beck and Lee

#### 226 (2014) and includes:

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- BeckLee\_mat50: an ordinated matrix for 50 mammals based on the distance between discrete morphological characters.
- BeckLee\_mat99: the same matrix BeckLee\_mat50 but also containing the
   reconstruction of their 49 ancestors.
- BeckLee\_tree: a chronogram with the 50 mammal species present in

  BeckLee\_mat50 and BeckLee\_mat99.
- BeckLee\_ages: the first and last occurrence data for 14 of the mammal species present in BeckLee\_mat50 and BeckLee\_mat99.
  - disparity: a pre-made dispRity object based on the data above.

In this example, the multidimensional space is defined as a morphospace: the ordination of the distances among discrete morphological characters for 50 mammal species (from Beck and Lee, 2014). Additionally, we can define disparity as the sum of the variances on each dimension (Wills et al., 1994) that will represent an aspect of the the volume of the morphospace (i.e. a large sum of variances approximates a large morphospace and vice versa).

## Typical disparity among groups analysis

One typical question with such analysis would be to test whether two groups of species have a different disparity. For example, using the data described above, we can test

whether the crown mammals (the living mammals and their descendants) are more diverse in term of morphology than the stem mammals (the fossil mammals with no living descendants). In other words, whether the approximation of the volume within the morphospace (the disparity as defined above) is different in crown or stem mammals. These two groups can be defined as follows (where the integers are the row number of the species in the matrix): 251 > mammal\_groups < list('crown' = c(16, 19:41, 45:50), 'stem' = c(1:15, 252 17:18, 42:44)) 253 It is then possible to measure the disparity between the two groups as follows: > disparity <- dispRity.per.group(data = BeckLee\_mat50, group =</pre> 255 mammal\_groups, metric = c(sum, variances)) 256 Note that this function is a wrapper function that is the equivalent to: 257 > subsamples <- custom.subsamples(data = BeckLee\_mat50, group = 258 mammal\_groups) 259 > bootstraps <- boot.matrix(subsamples)</pre> 260 > disparity <- dispRity(bootstraps, metric = c(sum, variances))</pre> 261 Which allows a finer tuning of the optional arguments in each function. The three arguments here are defined as follows: data = BeckLee\_mat50 is our definition of the 263 multidimensional space, group = mammal\_groups indicates which mammals belong to which group and metric = c(sum, variances) is our definition of disparity.

This function returns a dispRity object that summarises the disparity analysis:

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As indicated, the dispRity object contains two customised subsamples (called "crown" and "stem") from a morphospace made of 50 elements for 48 dimensions. The dispRity object also displays information on the number and method of the bootstrap replicates as well as the definition of disparity. To visualise the actual disparity values, one can use the summary or/and plot options (Table 3 and Fig. 3):

<sub>278</sub> > summary(disparity)

|   | subsamples | n  | obs  | bs.median | 2.5% | 25%  | 75%  | 97.5% |
|---|------------|----|------|-----------|------|------|------|-------|
| 1 | crown      | 30 | 2.00 | 1.93      | 1.87 | 1.92 | 1.95 | 1.98  |
| 2 | stem       | 20 | 1.72 | 1.63      | 1.53 | 1.60 | 1.66 | 1.69  |

Table 3: Summarising a dispRity object (disparity per groups). *n* is the number of elements per subsamples, *obs* the observed disparity (not bootstrapped), *bs.median* is the median bootstrapped disparity (here the median of the sum of ranges) and the 2.5, 25, 75 and 95% are the confidence intervals.

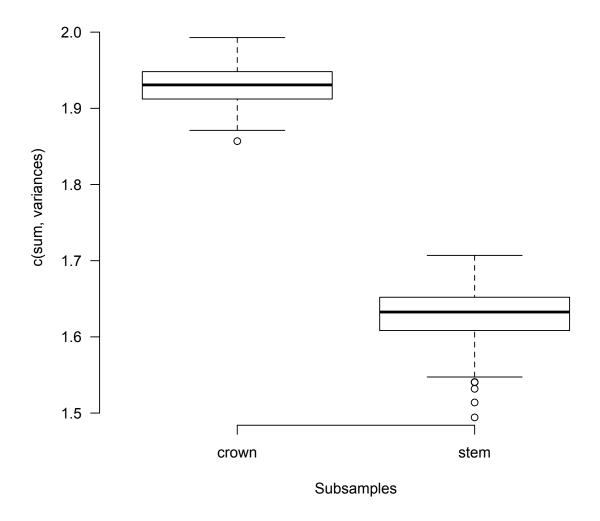


Figure 3: dispRity plot of disparity differences between groups.

As we can see from the summary table (Table 3) and the plot (3), there seems to
be a significant difference in morphospace volume occupied between the two groups. It
is possible to test this hypothesis by using, for example, a non-parametric Wilcoxon test

```
(stats::wilcox.test):
   > test.dispRity(disparity, test = wilcox.test)
   [[1]]
285
    statistic
286
   crown:
             stem 10000
287
   [[2]]
288
    p.value
289
             stem 2.562144e-34
   crown:
290
```

As indicated by the p value, there is a significant difference in disparity between the groups. Relating back to our question: yes, crown mammals display a higher 292 diversity in morphologies than their stem counterparts (in this example and dataset!). *Typical disparity-through-time analysis.*— A following up question to this observation 294 could be to test whether this difference is due to an overall change in disparity through 295 time or not. In other words, did disparity increased through time in mammals globally 296 or is it only between stem and crown mammals. Using the same definition of the multidimensional space and disparity as in the previous example, we can measure, for example, changes in disparity through time between the Late Cretaceous (100.5 to 66.0 million years ago - Mya), the Paleocene (66.0 to 56.0 Mya) and the Eocene (56.0 to 33.9 Mya). 301  $> time_bins <- c(100.5, 66, 56, 33.9)$ 

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It is then possible to measure disparity-through-time using the following

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function:
   > disparity <- dispRity.through.time(data = BeckLee_mat50, tree =
   BeckLee_tree, time = time_bins, metric = c(sum, variances))
   Note that this function is a wrapper function that is the equivalent to:
   > subsamples <- time.subsamples(data = BeckLee_mat50, tree = BeckLee_tree,
308
   time = time_bins, method = 'discrete')
   > bootstraps <- boot.matrix(subsamples)</pre>
310
   > disparity <- dispRity(bootstraps, metric = c(sum, variances))</pre>
311
   The arguments data = BeckLee_mat50 and metric = c(sum, variances) are the same
312
   as in the example above. However, in this type of analysis, we also need to have
313
   additional arguments: the time = time_bins indicates the boundaries of the different
314
   time bins, the tree = BeckLee_tree argument provides information on the age of each
315
   element and method = 'discrete' indicates that the data is time-binned.
316
          Again, the resulting dispRity object can be summarised and plotted (Table 4 and
317
   Fig. 4):
318
   > summary(disparity)
319
   > plot(disparity, type = 'continuous')
320
   Note that many plot options specific to dispRity objects are available such as plotting
   disparity in a "continuous" fashion (inferring disparity between the time bins).
322
          From the plot and the summary, disparity seems to change (increase) through
   time from the Cretaceous to the Eocene. Similarly to the example above, it is also
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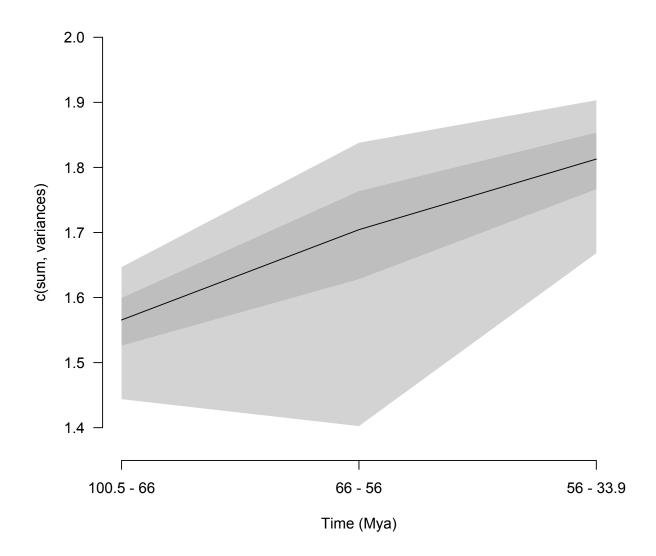


Figure 4: dispRity plot of disparity-through-time. The black line represents the median disparity (median sum of variances), the dark grey and light surfaces represent respectively the 50% an 95% confidence intervals.

|   | subsamples | n  | obs  | bs.median | 2.5% | 25%  | 75%  | 97.5% |
|---|------------|----|------|-----------|------|------|------|-------|
| 1 | 100.5 - 66 | 15 | 1.67 | 1.55      | 1.40 | 1.51 | 1.58 | 1.65  |
| 2 | 66 - 56    | 9  | 1.88 | 1.69      | 1.43 | 1.63 | 1.77 | 1.83  |
| 3 | 56 - 33.9  | 13 | 1.96 | 1.83      | 1.62 | 1.77 | 1.86 | 1.90  |

Table 4: Summarising a dispRity object (disparity through time). n is the number of elements per subsamples, obs the observed disparity (not bootstrapped), bs.median is the median bootstrapped disparity (here the median of the sum of ranges) and the 2.5, 25, 75 and 95% are the confidence intervals.

possible to statistically test this hypothesis using, for example, an ANOVA (Table 5):

326 > anova(test.dispRity(disparity, test = lm, comparisons = 'all'))

|            | Df  | Sum Sq | Mean Sq | F value | Pr(>F) |
|------------|-----|--------|---------|---------|--------|
| subsamples | 2   | 3.14   | 1.57    | 177.84  | 0.0000 |
| Residuals  | 297 | 2.62   | 0.01    |         |        |

Table 5: ANOVA performed on a dispRity object.

To answer our specific question above: yes there is an effect of time on morphological disparity (an increase) in this dataset.

### Additional information

### Manuals and vignette

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Supplementary information about the package is available on the project page

(https://TGuillerme/dispRity). Information concerning each function can be found

in R in the individual function manuals and a package manual with more detailed

information is available online (https:

//rawgit.com/TGuillerme/dispRity/master/inst/gitbook/\_book/index.html). This

manual contains substantially more information and detailed examples including a

tutorial for a "classic" disparity analysis in palaeobiology as well as an introduction to

the use of this package in ecology or other disciplines.

#### Data simulations

This package also contains functions for simulating random discrete morphological
matrices (sim.morpho) or random multidimensional spaces (space.maker). These
functions are based on a similar modular architecture as that used by the dispRity
functions, allowing users to provide their own distribution parameters for the
simulations. For example, stats::rnorm can be provided as an argument for drawing
normal characters rates with sim.morpho or normally distributed multidimensional
space with space.maker. The discrete morphological data simulations are based on
protocols from Guillerme and Cooper (2016), O'Reilly et al. (2016) and Puttick et al.
(2017). The multidimensional space simulations are based on the methods from Díaz
et al. (2016). Both functionalities are described in more details in the package manual.

### Conclusion

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The dispRity package is based on a highly modular architecture allowing researchers to simply define both their multidimensional space and their disparity metric to efficiently analyse multivariate data. The dispRity object allows users to easily pipeline disparity analysis from the data input (the matrix) to publication standard results (tables, plots, hypothesis testing). With the help of this package, researchers will be able to run multivariate analysis in an easy way while still allowing the flexibility necessary to such analyses.

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- 369 References
- Adams, D., M. Collyer, A. Kaliontzopoulou, and E. Sherratt. 2017. Geometric morphometric analyses of 2d/3d landmark data .
- Adams, D. C. and E. Otárola-Castillo. 2013. geomorph: an r package for the collection and analysis of geometric morphometric shape data. Methods in Ecology and
  Evolution 4:393–399.
- Beck, R. M. and M. S. Lee. 2014. Ancient dates or accelerated rates? Morphological clocks and the antiquity of placental mammals. Proceedings of the Royal Society B:

  Biological Sciences 281:1–10.
- Bhattacharyya, A. 1943. On a measure of divergence between two statistical populations
  defined by their probability distributions. Bulletin of the Calcutta Mathematical
  Society 35:99–109.
- Bouxin, G. 2005. Ginkgo, a multivariate analysis package. Journal of Vegetation Science
  16:355–359.
- Brusatte, S., R. J. Butler, A. Prieto-Márquez, and M. A. Norell. 2012. Dinosaur morphological diversity and the end-Cretaceous extinction. Nature Communications 3:804–804.

- Brusatte, S. L., M. J. Benton, M. Ruta, and G. T. Lloyd. 2008. Superiority, competition,
- and opportunism in the evolutionary radiation of dinosaurs. Science 321:1485–1488.
- Butler, R. J., S. L. Brusatte, B. Andres, and R. B. J. Benson. 2012. How do geological
- sampling biases affect studies of morphological evolution in deep time? a case study
- of pterosaur (Reptilia: Archosauria) disparity. Evolution 66:147–162.
- Ciampaglio, C. N., M. Kemp, and D. W. McShea. 2001. Detecting changes in
- morphospace occupation patterns in the fossil record: characterization and analysis
- of measures of disparity. Paleobiology 71:695–715.
- <sup>394</sup> Close, R., M. Friedman, G. Lloyd, and R. Benson. 2015. Evidence for a mid-Jurassic
- adaptive radiation in mammals. Current Biology.
- De Caceres, M., F. Oliva, X. Font, and S. Vives. 2007. Ginkgo, a program for
- non-standard multivariate fuzzy analysis. Advances in Fuzzy Sets and Systems
- 398 **2:41–56.**
- Díaz, S., J. Kattge, J. H. Cornelissen, I. J. Wright, S. Lavorel, S. Dray, B. Reu, M. Kleyer,
- 400 C. Wirth, I. C. Prentice, et al. 2016. The global spectrum of plant form and function.
- 401 Nature 529:167.
- 402 Donohue, I., O. L. Petchey, J. M. Montoya, A. L. Jackson, L. McNally, M. Viana,
- K. Healy, M. Lurgi, N. E. O'Connor, and M. C. Emmerson. 2013. On the
- dimensionality of ecological stability. Ecology Letters 16:421–429.

- Finlay, S. and N. Cooper. 2015. Morphological diversity in tenrecs (Afrosoricida,
- Tenrecidae): comparing tenrec skull diversity to their closest relatives. PeerJ 3:e927.
- Foth, C., S. Brusatte, and R. Butler. 2012. Do different disparity proxies converge on a
- common signal? insights from the cranial morphometrics and evolutionary history of
- Pterosauria (Diapsida: Archosauria). Journal of evolutionary biology 25:904–915.
- Guillerme, T. and N. Cooper. 2016. Effects of missing data on topological inference
- using a Total Evidence approach. Molecular Phylogenetics and Evolution 94, Part
- 412 A:146-158.
- Halliday, T. J. D. and A. Goswami. 2016. Eutherian morphological disparity across the
- end-cretaceous mass extinction. Biological Journal of the Linnean Society
- 415 118:152–168.
- Hughes, M., S. Gerber, and M. A. Wills. 2013. Clades reach highest morphological
- disparity early in their evolution. Proceedings of the National Academy of Sciences
- 418 **110:13875–13879.**
- 419 Lloyd, G. T. 2015. Claddis: Measuring Morphological Diversity and Evolutionary
- Tempo. R package version 0.1.
- 421 Matzke, N. J. 2013. Biogeobears: Biogeography with bayesian (and likelihood)
- evolutionary analysis in r scripts. R package, version 0.2 1:2013.
- Oksanen, J., R. Kindt, P. Legendre, B. OHara, M. H. H. Stevens, M. J. Oksanen, and
- M. Suggests. 2007. The vegan package. Community ecology package 10:631–637.

- O'Reilly, J. E., M. N. Puttick, L. Parry, A. R. Tanner, J. E. Tarver, J. Fleming, D. Pisani,
- and P. C. J. Donoghue. 2016. Bayesian methods outperform parsimony but at the
- expense of precision in the estimation of phylogeny from discrete morphological
- data. Biology Letters 12.
- Price, S., S. Friedman, and P. Wainwright. 2015. How predation shaped fish: the impact
- of fin spines on body form evolution across teleosts. Page 20151428 in Proc. R. Soc. B
- vol. 282 The Royal Society.
- Puttick, M. N., J. E. O'Reilly, A. R. Tanner, J. F. Fleming, J. Clark, L. Holloway,
- J. Lozano-Fernandez, L. A. Parry, J. E. Tarver, D. Pisani, et al. 2017. Uncertain-tree:
- discriminating among competing approaches to the phylogenetic analysis of
- phenotype data. Proceedings of the Royal Society B 284:20162290.
- Raup, D. M. 1966. Geometric analysis of shell coiling: general problems. Journal of
- Paleontology Pages 1178–1190.
- Ruta, M., K. D. Angielczyk, J. Fröbisch, and M. J. Benton. 2013. Decoupling of
- 439 morphological disparity and taxic diversity during the adaptive radiation of
- anomodont therapsids. Proceedings of the Royal Society of London B: Biological
- 441 Sciences 280.
- Wills, M. 2001. Morphological disparity: A primer. Pages 55–144 in Fossils, Phylogeny,
- and Form (J. M. Adrain, G. D. Edgecombe, and B. S. Lieberman, eds.) vol. 19 of *Topics*
- in Geobiology. Springer US.

- Wills, M. A., D. E. G. Briggs, and R. A. Fortey. 1994. Disparity as an evolutionary index:
- A comparison of Cambrian and recent arthropods. Paleobiology 20:93–130.
- <sup>447</sup> Zelditch, M. L., D. L. Swiderski, and H. D. Sheets. 2012. Geometric morphometrics for
- biologists: a primer. Academic Press: Waltham.