Version dated: December 11, 2017

RH: disparate views on disparity.

Disparate views on disparity.

Thomas Guillerme[1,*], Natalie Cooper[2], Philip Donoghue[3]

[1]*Imperial College London, Silwood Park Campus, Department of Life Sciences, Buckhurst Road, Ascot SL5 7PY, United Kingdom.*

***Corresponding author.** *guillert@tcd.ie*

Abstract

blablalbalba

(Keywords: disparity)

Introduction

Disparity is an old concept blabalbal coming from the observation that some groups of species are more similar/dissimilar than other.

It can be also applied between groups as a concept of ecological niches: a group occupying many niches will have a stronger disparity than a groups with less niches.

It is decoupled from diversity.

In palaeobiology, morphological disparity (the (dis)similarities between the morphologies of groups of organisms) concept as a tool for macroevolutionary studies stems to several seminal papers from the 90s: Gould (1989, 1991); Briggs et al. (1992); Wills et al. (1994); Foote (1994, 1996); Jernvall et al. (1996); Foote (1997).

This concept was then used in geometric morphometric and expanded to macroevolutionary studies in general (Harmon's dtt).

Prentice et al. (2011) define disparity as: "a term widely (albeit not always consistently) used to describe the range of forms in a group of organisms, or the difference among different body plans".

Disparity is really popular (Fig. 1):

Why do we need disparity

Which macroevolutionary questions are tackled through disparity analysis?

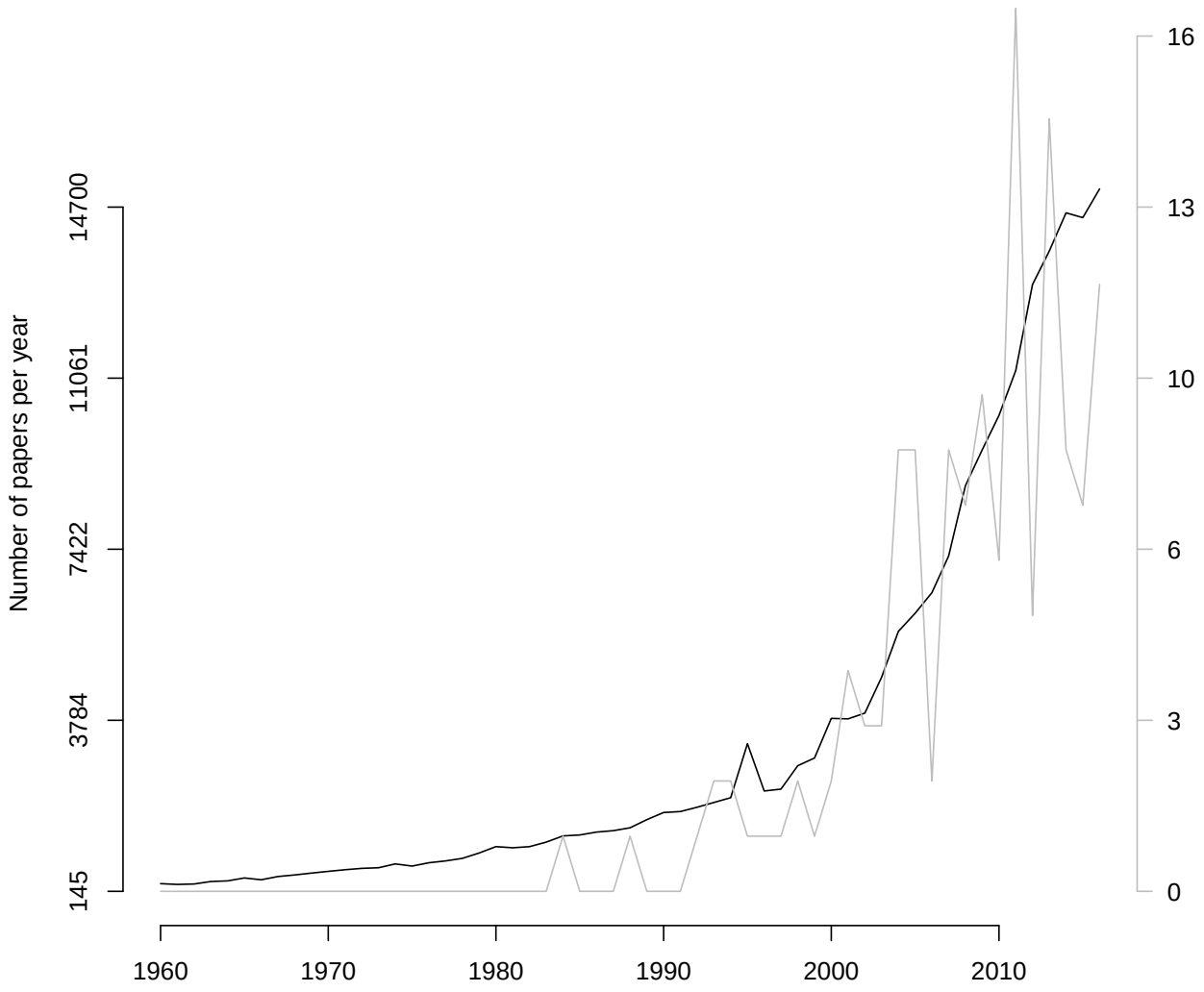

Figure 1: Number of papers on Google Scholar matching the search "morphological disparity" per year. In black, the match is in the paper and in grey, in the title. We collected the number of matches per year from 1960 to 2016 in Google Scholar for the terms "morphological disparity" both in the text (fuzzy matching) or in the title (exact matching). The data was collected on the 1st of November 2017.

What are the fundamental questions we should use to answer disparity questions?

What are the questions we should not answer with disparity?

Disparity can be -From a semantic view: morphospace or aspect of the morphospace? -From a biological view: what does an increase or a decrease in disparity represent?

But in the end, what *is* disparity

But what *is* disparity?

Disparity can describe either the metric (disparity index (Hopkins and Gerber, 2017) or disparity metric (Wills, 2001)) or the whole pipeline (Lloyd, 2015; Zelditch et al., 2012)

Data collection methodology

To assess the usage of disparity in different published studies, we collected methodological data from the 500 first Google Scholar results for the key words "morphological disparity" per order of appearance (accessed on the 1st of November 2017). For the 230 relevant papers among the 500 matches, we collected the following methodological data:

- What was the focal biological group?
- What kind of data was measured (e.g. landmarks, discrete data, etc.)?

- Was data collected on the full organism or not?
- How was the morphospace explicitly defined (e.g. PCA, PCO, MDS, etc.)?
- How was the disparity metric(s) explicitly defined?
- Which statistical test was applied to test the disparity related hypothesis?
- Was phylogeny taken into account or not?

We used only the explicit definition of the morphospace and the disparity metric(s) in this search since a few number of papers had a vague definition of either or both (e.g. a disparity metric was measured but not described anywhere in the paper).

The remaining 270 matches were disparity was mentioned but not measured felt in the following categories: papers out of topic, papers mentioning morphological disparity without measuring it, review papers, papers not accessible (either through a broken link or a paywall) or referenced citation without the paper (as a Google Scholar match).

To reduce the amount of categories for the 230 recorded methods, we concatenated different methods in the following categories:

[DESCRIBE THE CATEGORIES HERE (from `https://github.com/TGuillerme/Disparity_Working_Group/blob/master/Analysis/data_cleaning.Rmd`)]

[ADD Biological group, full organism and phylogeny in the supplementary]

Disparity data

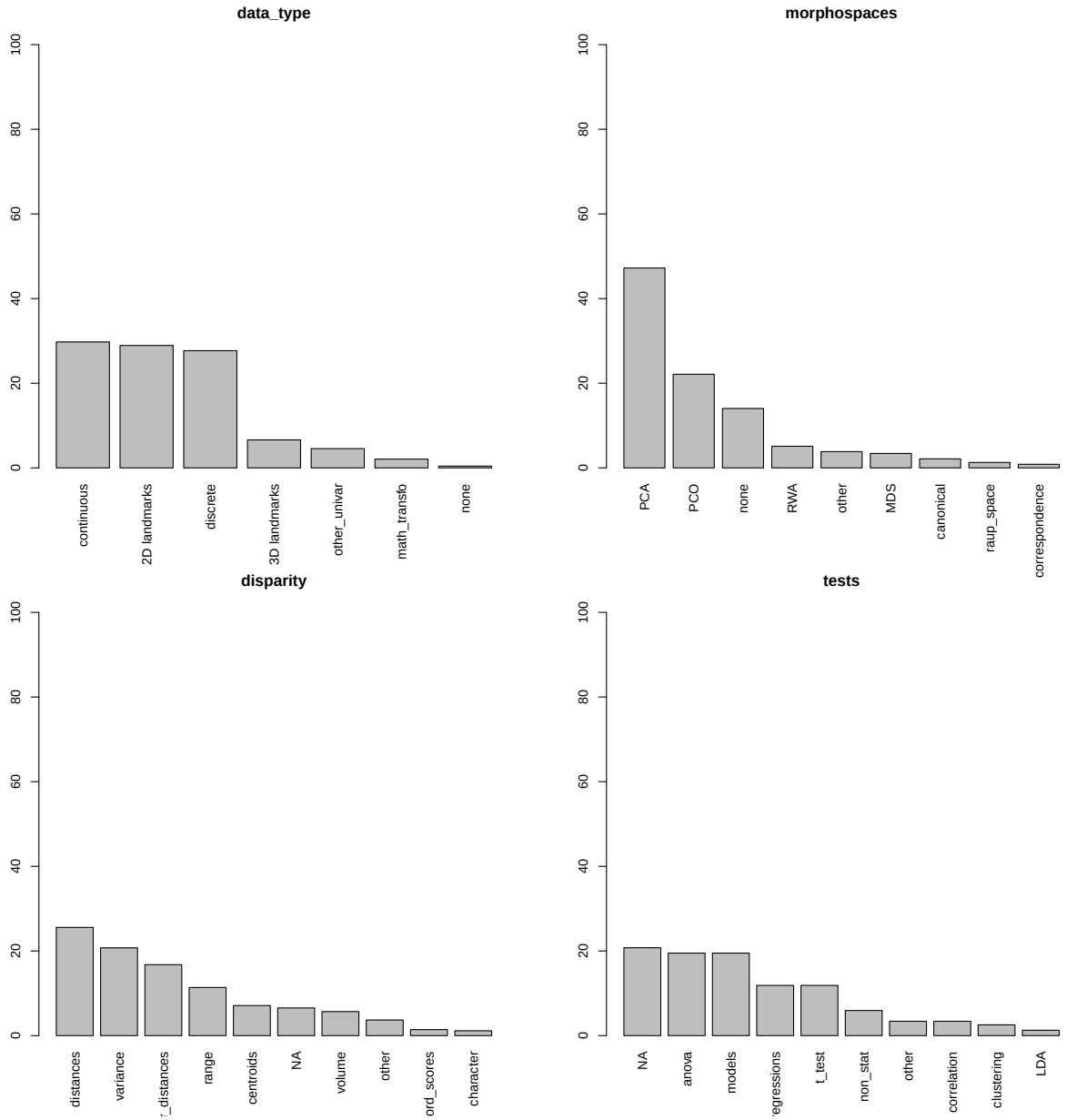

Figure 2: Disparity methods proportional usage: (1) Data type: which input data was used (...); (2) Morphospace: how was the morphospace obtained (...); (3) disparity: what type of disparity metric was calculated (...); (4) test: what type of test was applied (...).

Describing the many data inputs (from collected data to morphospace):

Disparity metrics

Describing the many metrics (what is actually measured):

Disparity hypothesis

Describing the many outputs (what and how is it tested):

The three main disparity analysis

From the collected data, we can highlight the use of three main different disparity analysis with their associated data/morphospace/metric/tests and related to specific methodological implementations.

- **The "`Claddis`" approach:** this group of methods uses discrete morphological data for the full organisms to build a PCO from the organism's pairwise distance as a morphospace. Disparity is then often measured as a variation of the ordinated matrix dimensions' variances or ranges (e.g. the sum of variance or/and the sum of ranges). Hypothesis are often tested using multivariate ANOVAs on the pairwise distance matrix or by simply comparing the confidence intervals overlap of the disparity from different groups.

- **The "`geomorph`" approach:** this group of method is based on landmark data (2D or 3D) on parts of the organism studied usually the skull) and use a Procrustes transformation of the landmarks that are then directly ordinated using a PCA (but sometimes RWA). Disparity is often measured as a distance metric (e.g. the distance between the species and a point in the morphospace such as its centroid). Hypothesis are then tested using ANOVA type tests with usually no phylogenetic correction (although phylogeny is sometimes used to correct the morphospace).

- **The "`dtt`" approach:** continuous data for the full organism, not ordinated, with a pairwise distance based disparity metric and phylogenetic correction.

Of course some studies use a combination of these three methods or none of them at all!

Also, among each category XX% of studies use multiple approaches.

[ADD Biological group, full organism and phylogeny in the supplementary]

What is missing

How to compare disparity between groups?

How to compare disparity between methods?

Hot to compare disparity between disciplines?

It bears strong parallels with β-diversity in ecology (a measure of ecological communities (dis)similarity): one biological observation described by a vast array of metrics (Baselga, 2010; Anderson et al., 2011; Donohue et al., 2016).

Conclusion

A quick guideline for good disparity analysis:

Maybe we need something like in Parham et al 2012 (Best Practices for Justifying Fossil Calibrations): an easy an identifiable description of the pipeline containing: 1) the type of data, 2) the morphospace and 3) the metric?

Acknowledgments

The Royal Society. I acknowledge support from European Research Council under the European Union's Seventh Framework Programme (FP/2007 2013)/ERC Grant Agreement number 311092 awarded to Martin D. Brazeau.

*

References

Anderson, M. J., T. O. Crist, J. M. Chase, M. Vellend, B. D. Inouye, A. L. Freestone, N. J. Sanders, H. V. Cornell, L. S. Comita, K. F. Davies, et al. 2011. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. Ecology letters 14:19–28.

Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity. Global Ecology and Biogeography 19:134–143.

Briggs, D. E., R. A. Fortey, and M. A. Wills. 1992. Morphological disparity in the cambrian. Science 256:1670–1673.

Donohue, I., H. Hillebrand, J. M. Montoya, O. L. Petchey, S. L. Pimm, M. S. Fowler, K. Healy, A. L. Jackson, M. Lurgi, D. McClean, et al. 2016. Navigating the complexity of ecological stability. Ecology letters 19:1172–1185.

Foote, M. 1994. Morphological disparity in Ordovician-Devonian Crinoids and the early saturation of morphological space. Paleobiology 20:320–344.

Foote, M. 1996. Ecological controls on the evolutionary recovery of post-Paleozoic Crinoids. Science 274:1492–1495.

Foote, M. 1997. The evolution of morphological diversity. Annual Review of Ecology and Systematics 28:129–152.

Gould, s. J. 1989. Wonderful Life: The Burgess Shale and the Nature of History. W. W. Norton & Co., New York.

Gould, S. J. 1991. The disparity of the burgess shale arthropod fauna and the limits of cladistic analysis: why we must strive to quantify morphospace. Paleobiology 17:411–423.

Hopkins, M. J. and S. Gerber. 2017. Morphological Disparity Pages 1–12. Springer International Publishing, Cham.

Jernvall, J., J. P. Hunter, M. Fortelius, et al. 1996. Molar tooth diversity, disparity, and ecology in cenozoic ungulate radiations. Science 274:1489–1492.

Lloyd, G. T. 2015. Claddis: Measuring Morphological Diversity and Evolutionary Tempo. R package version 0.1.

Prentice, K. C., P. Ruta, and M. J. Benton. 2011. Evolution of morphological disparity in pterosaurs. Journal of Systematic Palaeontology 9:337–353.

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.

Zelditch, M. L., D. L. Swiderski, and H. D. Sheets. 2012. Geometric morphometrics for biologists: a primer. Academic Press: Waltham.