
Morphological Disparity

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Abstract

Morphological disparity, the measure of morphological variation among species and higher taxa, has been at the core of an important research program in paleobiology over the last 25 years. Its quantification is based on the construction and exploration of morphospaces, multidimensional spaces spanned by a set of morphological descriptors, and benefits from a well-established analytical protocol. Two main classes of indices are routinely used to describe the distribution of taxa in morphospace in terms of their spread and spacing. This unique focus on the morphological component of clade dynamics has promoted disparity as a distinct measure of biodiversity complementing traditional taxonomic proxies. Disparity studies have led to improved understanding of the evolutionary history of major clades and fostered new research on adaptive radiations, rates of evolution, and morphological innovation. Currently, active areas of methodological development focus on characterizing the geometric properties of morphospaces, devising indices that describe the structure of disparity, and incorporating phylogenetic information. There have also been increasing efforts to identify the determinants of disparity, from developmental to functional and ecological considerations, leading to conceptual extensions such as allometric disparity. The importance of trends, extinction, and chance as factors in the evolution of disparity remains relatively underexplored and needs more attention.

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Contents

Introduction	2
Measuring Disparity	3
Morphological Descriptors	3
Disparity Indices	4
Visualizing Morphospaces	5
Current Issues in Methods	6
Explaining the Evolution of Disparity	7
Developmental Morphospaces and Allometric Disparity	8
Functional Morphospace and Functional Disparity	8
Spatial, Environmental, and Temporal Structure of Morphospace	9
Extinction and Extinction Space	9
Chance and Historical Contingency	9
Concluding Remarks	10
Cross-References	11
References	11

Introduction

Many macroevolutionary patterns in deep time can and have been discussed in purely taxonomic terms. Significant episodes of radiation and extinction, for instance, can be detected from the documentation of changes in the number of species through time. However, even though our ability to distinguish species usually implies the existence of morphological differences between them, change in the number of species alone does not convey the magnitude of these morphological differences.

This is one of the reasons for the rejuvenation of morphological disparity analyses as an important research agenda in paleobiology and macroevolution since the 1990s. Morphological disparity is a macroevolutionary measure of morphological variation. Although it has been used historically in reference to the level of morphological variation observed among body plans, its current and most widespread use is as a description of the degree of morphological distinctness within a set of taxa at and above the species level (morphological diversity within species being intraspecific variation).

Estimates of morphological disparity have been employed primarily to document the evolutionary history of particular clades. Fossil data has been of primary importance for such studies. The fossil record contains examples of extinct morphologies that may not be inferable from modern morphological diversity and provides a direct record of temporal occurrence of different morphologies. Notable patterns include the tendency for disparity to peak early in the evolutionary history of

a clade (Hughes et al. 2013), and the frequent discordances between changes in taxonomic diversity and morphological disparity over the evolutionary history of a clade (Foote 1993a). Important reviews that also describe some of the impact that disparity studies have had on evolutionary biology, particularly in the area of adaptive radiations and rates of evolution, include Foote (1997), Wills (2001), Erwin (2007), and Wagner (2010). In this chapter, we will briefly review common methods for measuring disparity and then focus on the methodological and conceptual developments that occurred over the past decade.

Measuring Disparity

In empirical studies, the quantitative assessment of morphological disparity starts with the definition of an adequate set of morphological descriptors from which can be obtained a measure of dissimilarity between morphologies. In so doing, one establishes a morphospace, the multidimensional state space spanned by these morphological descriptors. The positioning of taxa relative to one another in the morphospace reflects their degree of morphological similarity: the closer, the more morphologically similar.

Morphological Descriptors

Different families of morphological descriptors exist:

1. Traditional morphometric descriptors. These are continuous data measured on a ratio scale. They may include length or perimeter measurements, angles between two linear features, estimates of area, or ratios between such measurements. These descriptors often require some sort of transformation to make them comparable in terms of scale or units.
2. Geometric morphometric descriptors. These are sets of two- or three-dimensional coordinate points whose configuration captures the geometry of the morphological feature of interest. Each point is associated with an intersection, junction or extreme (fixed landmarks), or with a curve (semi-landmarks and outlines).
3. Discrete character descriptors. These are categorical observations, such as the absence or presence of a trait, or qualitative descriptions of different states of expression of a trait that is present. They can have two or more states which may be ordered or not. In order to estimate disparity from discrete character data, the character-taxon matrix is converted to a pairwise distance matrix, or dissimilarity matrix (see Lloyd 2016 for review). Most recent disparity studies based on discrete character descriptors have co-opted character matrices that were originally constructed for phylogenetic purposes, and thus typically do not include autapomorphies. Whether this is a problem remains an open issue: there is currently no consensus on whether autapomorphies should be included in

character matrices intended for disparity analyses (e.g., Gould 1991; Ruta and Wills 2016).

4. Model-based descriptors. These are parameters that describe different shapes or morphological features under a specified model, such as one describing growth. A classic example is Raup's 1966 model for shell coiling, which was based on the geometry of the logarithmic spiral (Gerber 2016).

The use of traditional and geometric morphometric descriptors requires that all taxa express the traits being measured. Because discrete character data sets can also include information about the presence/absence of traits, a broader range of morphologies can be accommodated in the analysis compared to morphometric data. However, this is typically at the expense of a "cruder" description of morphologies. In general, different types of descriptors capture and emphasize different aspects of morphology, different levels of trait correlation and redundancy, and different scales of change. Disparity patterns may or may not be consistent across different types of descriptors even for the same set of sampled taxa; empirical studies to date are summarized in Hopkins (2017).

All of these descriptors are conducive to morphospaces as defined above. The term "morphospace" is thus a very broad designation that includes a great variety of mathematical spaces. Those can have quite distinct properties and geometries (e.g., Gerber 2016), and they may differ in their renditions of given evolutionary patterns. The investigator should therefore have an understanding of the properties of the morphospace employed in order to tease apart the biological signal from potential artifacts associated with a particular methodological approach.

Disparity Indices

Because morphological descriptors define a space, morphological disparity can also be defined as the quantitative characterization of the spread and spacing of taxa in this space, that is, the pattern of morphospace *occupation*. There are two components to morphospace occupation, the amount and structure of disparity, but most studies so far have exclusively focused on the former. The most commonly used disparity indices are based on the standard measures of statistical dispersion and describe the amount of disparity regardless of its structure.

1. Sum of (univariate) ranges, or total range. This metric represents the spread of the distribution in morphospace. The sum of ranges is sensitive to sample size and is thus frequently subjected to rarefaction analysis when comparisons are being made between groups or samples of different numbers of taxa. The sum of ranges is also dependent on orientation. This may have a nontrivial impact on comparison of subgroups ordinated in the same morphospace, since the major axis of variation of the entire group may differ from those of subgroups.
2. Sum of (univariate) variances, or total variance. Computed as the trace of the covariance matrix, or equivalently, the sum of its eigenvalues, it describes the

spacing of taxa in morphospace and is relatively insensitive to sample size. It is not redundant with the previous index. For a given total range, different values of total variance indicate a more or less densely occupied region of morphospace within stable boundaries. Subgroups may contribute differentially to the total variance; the contribution of the subgroup, or the partial disparity, is computed from the sum of the squared distances of each member of the subgroup to the overall centroid (Foote 1993b).

Wills (2001) described these and other indices in extensive detail, and Ciampaglio et al. (2001) ran a series of simulations to study their behavior for various types of morphospace patterns typically encountered in empirical case studies. However, many morphospaces may exhibit an affine rather than a Euclidean geometry. For such spaces, ratios of generalized variances (determinant of the covariance matrix, or equivalently the product of the eigenvalues) have been recommended as affine-invariant measures of disparity (Huttenegger and Mitteroecker 2011). In the case of discrete character space, an alternative to total variance is the average pairwise dissimilarity. One benefit of this index is that it is estimated directly from the dissimilarity matrix and so does not require the use of ordination methods (see below).

Visualizing Morphospaces

Unless one is concerned with very simple description of morphologies, the high dimensionality of most morphospaces prevents the visualization of all their dimensions at once. Getting a visual assessment of the extent and structuring of variation thus requires the use of multivariate ordination methods such as principal component analysis, principal coordinates analysis, or nonmetric multidimensional scaling, which can extract the most relevant and salient features of the variation documented with fewer dimensions.

Importantly, such a representation is a *projection* of the morphospace and not the morphospace itself. This is often an informative and useful depiction but high-dimensional spaces cannot be displayed as bivariate or trivariate plots without loss of information, and thus these projections can be misleading. Fortunately, estimating disparity does not rely on such projections and can be assessed from the entire dataset (the true morphospace). The disparity indices mentioned above extend to any number of dimensions, and there is therefore no need to resort to dimension reduction techniques to measure disparity (e.g., keeping only the set of ordination components that describe 95% of the original variance), even when low-variance components contribute very little to the overall disparity.

It has been customary in the morphospace literature to distinguish empirical from theoretical morphospaces. The latter, constructed from model-based descriptors, are generally singled out as independent from the empirical sample of specimens studied and capable of producing nonexistent morphologies, thus revealing areas of morphospace that have not been occupied through evolution. These features,

however, do not pertain to theoretical morphospaces only but typify many of the so-called empirical morphospaces as well. The use of the empirical/theoretical distinction generally reflects a confusion between the morphospace and its ordination (e.g., projection on principal components). The addition of new taxa may alter the ordination but will not alter the relative distances between the previously measured taxa.

Current Issues in Methods

Recent methodological developments have focused primarily on improving the description of morphospace patterns and incorporating phylogenetic information in their exploration.

Fairly distinct patterns of morphospace occupation have been documented and common disparity indices can sometimes overlook their differences. For example, equally disparate clades can show drastically different structuring of the amount of morphological variation they display. Additional indices of morphospace occupation have been suggested to characterize these distinct patterns, particularly with respect to the dimensionality and the discontinuity of the distribution of taxa in morphospace (e.g., clustering, Wills et al. 2012). Efforts to describe morphospace structure have been complicated by two issues. First, tests for clustering lose statistical power as dimensionality increases. Second, clustering can occur for artifactual reasons, as well as biological reasons (see section “[Explaining the Evolution of Disparity](#)” below). For example, regions of morphospace that cannot be occupied may exist due to the use of character data which includes logically impossible character combinations.

Recent disparity analyses have tended to focus on clades for which phylogenetic hypotheses at the level of the OTUs described can be obtained. It is then possible to map the hypothesized tree onto the morphospace, producing what has come to be referred to as a phylomorphospace. Such a representation can help determine if phylogeny is a strong contributor of the structuring of morphological variation in a clade. Phylogenetic hypotheses have also been suggested as a means to account for the incomplete fossil record of clades. Models of character evolution such as parsimony can be used to assign character states to the internal nodes of the tree (“hypothetical ancestors”), fill in missing data, and correct for ghost-ranges. These approaches still need careful assessments of their statistical properties and heuristic values. They do alter the raw disparity signal in ways (e.g., asymmetric adjustment of stratigraphic range, superimposed model of character evolution) that might obscure the true nature of the processes underlying the clade dynamics.

Finally, there has also been considerable recent interest in inferring past clade disparity from the distribution of morphology among extant members of the clade, usually with the aid of a phylogenetic hypothesis of how clade members are related to one another evolutionarily. However, the robustness of such inferences has rarely been tested against the fossil record. One recent attempt found that the morphological disparity index was the most reliable for inferring an early burst of disparity in

birds, but still failed to recapitulate disparity patterns in the bird fossil record (Mitchell 2015). The inability to estimate extinct morphologies from extant taxa alone is the major obstacle facing this sort of approach, especially when the structure of morphospace occupation has changed, or when large or peripheral regions of morphospace are no longer occupied.

Explaining the Evolution of Disparity

Over the last 25 years, disparity curves have been constructed for many groups – although unevenly among vertebrate, invertebrate, and plant clades – following the methodological framework outlined above. Together with diversity curves, these disparity patterns have proved extremely useful in offering an expanded description of the evolutionary history of biodiversity by combining its taxonomic and morphological components. Comparative surveys and reviews of these studies have focused on the important task of documenting evolutionary histories patterns and assessing their relative frequencies. These include for instance the various modes of morphological diversification (with or without concordance with taxonomic diversification) and the selectivity versus randomness of extinction with respect to morphology.

The recognition of different patterns of disparity across different clades has also led to interest in determining the processes that underlie the evolution of disparity and the often heterogeneous patterning of morphospace. Historically, hypotheses about the determinants of morphospace occupation have fallen into three categories: extrinsic factors, biotic and abiotic; intrinsic factors related to development or growth; and chance. On the theoretical side, a few stochastic and analytical models have been implemented to explore the expected behavior of disparity in face of changing mode of morphological transitions, taxonomic turnover rates, and size of morphospace (e.g., Pie and Weitz 2005; Gerber et al. 2011 and references herein). These studies have highlighted the difficulties in distinguishing the drivers of disparity and isolating their signature from sampling error and stochastic variation. More work is needed in this area to define null models and characterize the expected signature of the various contributors of disparity.

In parallel, empirical efforts to understand the “mechanistic” bases of the dynamics of disparity have concentrated on functional and developmental aspects of morphological variation. These approaches have in common the (sometimes implicit) recognition of morphological phenotypes as being made up of quasi-independent units of evolutionary transformation, a phenomenon referred to as evolutionary modularity. Internally, these units are developmentally and functionally integrated and can be under distinct selective regimes and evolutionary constraints. Hence, while the disparity signal built from the entire set of morphological descriptors (characterizing the overall body) is relevant for documenting the evolutionary history of a particular clade (global pattern), this more comprehensive description of morphologies conflates the (quasi-independent) histories of its constitutive parts. Relevant subsets of the global library of descriptors can be used to build disparity signals attached to specific body parts corresponding to plausible modules, and may

in fact be more informative in identifying the underlying processes driving the evolution of disparity at the global level.

Accordingly, some authors have used character partitions to derive disparity curves reflecting differential functional and developmental contributions, such as external functional biology vs. internal anatomy, or ecological vs. nonecological characters (e.g., Ciampaglio 2002). More recent works have developed approaches directly targeting traits of specific functional and developmental relevance to phenotypic variation. We review them briefly below.

Developmental Morphospaces and Allometric Disparity

Morphological disparity analyses have traditionally focused on adult variation, but changes in adult phenotypes are mediated by development, and development therefore influences morphospace occupation and disparity dynamics (Gerber 2014). Fortunately, the morphological data retrievable from the fossil record are by no means restricted to the adult stage and disparity can be measured at any developmental stage. If the same set of descriptors is used to describe these different stages, then juvenile and adult morphologies can be displayed within the same morphospace. Earlier studies incorporating multiple developmental stages focused on changes in disparity through ontogeny (e.g., Zelditch et al. 2003; Eble 2003). More recent studies have focused on characterizing and analyzing the developmental trajectories themselves.

For example, Gerber et al. (2008) used coefficients describing allometric growth patterns in fossil ammonoids as descriptors for defining a multidimensional space in which each point represents an ontogenetic trajectory (allometric space). The distribution of points in this space, that is, the allometric disparity, can be quantified with the same indices as in standard disparity analysis. Allometric disparity can be compared to morphological disparity and their relative behaviors make it possible to distinguish different types of change in allometric trajectories, thus linking changes in adult disparity to specific modes of developmental evolution.

Functional Morphospace and Functional Disparity

Likewise, it is possible to focus on morphological descriptors that are tied to particular functions in the organisms under study. Commonly used characters relate to feeding ecology or biomechanics; there have also been developments in the use of models to derive functionally relevant descriptors (Anderson et al. 2011). Although functional properties of organisms are related to their morphology, functions that depend on multiple traits can potentially be met by many different morphologies (Wainwright 2007). As a result, the functional disparity and morphological disparity of a particular structure may only be weakly related in some systems. In general, the variation described by anatomical and functional datasets for the same taxa are likely

to be correlated to some degree but not coincident (e.g., Anderson and Friedman 2012).

Spatial, Environmental, and Temporal Structure of Morphospace

Morphologies may be linked with environmental or ecological parameters in other ways when specific morphology-to-function associations are not known. For example, mapping group affiliations – where the group is defined by some ecological relatedness or habitat affinity – onto taxa in morphospace may reveal clustering associated with geographic occurrence or niche occupation, as well as the temporal changes in those associations (e.g., Hopkins 2014).

As should be obvious from any disparity curve (e.g., Foote 1993a), both disparity and morphospace structure are strongly associated with time as clades evolve into new areas of morphospace. Although morphological diversification is often conceptualized as a diffusive process of volume-filling, increases in disparity may be highly structured and uneven due to underlying trends (which are often due to developmental or functional constraints). Indeed, some trends may not increase disparity at all, if areas of morphospace are abandoned as the clade mean shifts (Hopkins 2016). Most of the literature on trends has been concerned with their documentation and categorization for univariate traits, such as body size. Categorical schemes are intended to be indicative of some underlying processes, such as species selection and constraints in the form of upper or lower bounds, but in general, the relationship between trends and the evolution of disparity is largely unexplored.

Extinction and Extinction Space

Areas of morphospace can only be abandoned through extinction. As such, extinction, particularly selective extinction, necessarily alters morphospace occupation and structure and therefore impacts disparity. For example, extinction selectivity has been associated with morphological specialization in some (but not all) clades. Korn et al. (2013) used indices which describe changes in morphospace occupation to define a multidimensional space for distinguishing between different selectivity modes during mass extinction events. One advantage of their approach was that it is not necessarily context-dependent. Because the indices summarize change in morphospace without recourse to the descriptors defining that morphospace, results based on disparate morphospaces can be compared to one another.

Chance and Historical Contingency

The importance of historical contingency in shaping patterns of disparity can be grasped most readily in the context of extinction, where the random culling of taxa can substantially alter the dynamics of disparity and put the evolutionary history of a

clade on new tracks. Contingency pervades at all scales however, and extends beyond the case of random patterns of survivorship. The effect of particular contingent historical events on disparity is nevertheless difficult to apprehend, because they can be context-dependent and affect only one or a few lineages within a clade, or be restricted to specific areas of the clade's geographic distribution. Their effects can still be significant at the global scale, however, and induce temporal shifts in disparity. Contingent explanations can only emerge from detailed studies and "dissections" of disparity signals (e.g., geographic partitions and subclade components of global signals) and should not be confounded with general properties and common "laws" that might underlie all clades' histories. The difficult task of disentangling these classes of explanation invites a better characterization of the expected behavior of disparity, abstracted from the volatility of taxonomic rates, and the proposal of adequate models of diffusion in morphospace accounting for the properties of the mechanisms underlying evolutionary change in morphology.

Concluding Remarks

Since Gould's advocacy for the study of morphological disparity as an important macroevolutionary quantity (Gould 1991), paleontologists have successfully unearthed the history of many groups in terms of changes in diversity and changes in disparity. In so doing, they also have highlighted the frequent decoupling of these two facets of biodiversity. Over the years, methodological approaches to the study of disparity have been standardized in some ways, primarily through the maturation of morphometric techniques and the increasingly popular use of just a few informative indices of morphospace occupation.

These established analytical routines are powerful and will undoubtedly continue to be used to document disparity patterns for many clades. It is also clear, however, that many questions and issues, including some raised in the early years of the disparity research program, are still unresolved and/or lack appropriate conceptual and methodological frameworks for their analyses.

For example, recent research into the properties of different kinds of morphospaces has revealed situations in which classic measures of morphological distance (and thus disparity) might not be mathematically or evolutionary meaningful. Some features of morphospace occupation can also occur for both biological and artifactual reasons. All of these can affect measures of disparity and mislead our descriptions of evolutionary patterns.

Indices that measure the structure of disparity have been neglected compared to those that measure the amount of disparity, and we therefore know much less about the evolution of morphospace structuring (e.g., discreteness and dimensionality) as clades wax and wane, and from a technical viewpoint, the impact of sample size, taxonomic error, and morphospace dimensionality on such indices.

In terms of data, while cladistic matrices are increasingly used as discrete character spaces in disparity analyses and offer the possibility to combine morphospace and phylogenetic approaches, little is known with regard to the validity

of their use as morphospaces (in particular with respect to their usually large amount of missing data, but see Lloyd 2016 for a start).

In parallel to continued empirical research and methodological development, there is a growing need for mathematical models of disparity and of diffusion in morphospace. Explicit incorporation of stochastic effects is a major component in the study of trait evolution within lineages (e.g., “fossil time series”) or across trees; in fact, in this area, there has been a recent shift away from the use of a stochastic model as a null hypothesis towards model selection approaches that use some criterion to select from among a set of models, of which one may represent stochasticity. Similarly, disparity studies may benefit from a shift towards statistical inference, with models that include potential determinants such as growth patterns, modular anatomical organization, functional constraints, selection, extinction, contingency, and chance, and away from post hoc explanations of descriptive patterns.

Cross-References

- [Evolution of Complexity](#)
- [Macroevolution](#)
- [Mass Extinctions](#)
- [Methods and Practices in Palaeo-Evo-Devo](#)
- [Morphometrics and Evo-Devo](#)

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