



SYMPOSIUM INTRODUCTION

The Future is Bright for Evolutionary Morphology and Biomechanics in the Era of Big Data

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Synopsis In recent years, the fields of evolutionary biomechanics and morphology have developed into a deeply quantitative and integrative science, resulting in a much richer understanding of how structural relationships shape macroevolutionary patterns. This issue highlights new research at the conceptual and experimental cutting edge, with a special focus on applying big data approaches to classic questions in form–function evolution. As this issue illustrates, new technologies and analytical tools are facilitating the integration of biomechanics, functional morphology, and phylogenetic comparative methods to catalyze a new, more integrative discipline. Although we are at the cusp of the big data generation of organismal biology, the field is nonetheless still data-limited. This data bottleneck is primarily due to the rate-limiting steps of digitizing specimens, recording and tracking organismal movements, and extracting patterns from massive datasets. Automation and machine-learning approaches hold great promise to help data generation keep pace with ideas. As a final and important note, almost all the research presented in this issue relied on specimens—totaling the tens of thousands—provided by museum collections. Without collection, curation, and conservation of museum specimens, the future of the field is much less bright.

“For the harmony of the world is made manifest in Form and Number, and the heart and soul and all the poetry of Natural Philosophy are embodied in the concept of mathematical beauty.”
—D’Arcy Wentworth Thompson, *On Growth and Form* (1917)

All biological motion is dependent on the laws of physics. Imagine taking an afternoon stroll on a nearby trail. All around you, an intimate partnership between physics and biology is underway. Sensing your footfalls, a springtail uses a special spring on its abdomen to store energy and rapidly launch itself away. In the sky, swifts and Cooper’s hawks search for food, their wings differently shaped to leverage the laws of aerodynamics for speed or maneuvering. Falling maple seed pods create air vortices to stay aloft during dispersal, and fungi slowly accumulate water to ballistically launch their spores far away. Movement of any kind, in air, on the ground, and through the water involves contending with distinct physical forces, such as gravity, friction, and torque.

Evolutionary fitness is shaped by these physical forces, as they determine, among other things, how organisms escape from predators, feed, and reproduce. The connection between functional diversity and physical laws has a rich conceptual history that has sometimes bordered on poetic. For example, D’Arcy Wentworth Thompson described a “beautiful” mathematics that underlies organismal structures (Thompson 1917). According to our count, the term “beauty” or “beautiful” is used to describe the natural world 100 times in *On Growth and Form*. Adolf Seilacher (1970) contended that the *bautechnischer* (or “architecture”) and evolutionary history of organisms were deeply intertwined, such that one could not properly be interpreted without the other. To Stephen Jay Gould, an integration of organismal structure and phylogeny was necessary to disentangle adaptationist “spandrels” from the products of natural selection (Gould and Lewontin 1979, Gould 2002). From such fertile conceptual ground

the fields of functional morphology and evolutionary biomechanics grew and blossomed into a highly integrative science (e.g., Liem 1973, Lauder 1981, Arnold 1983, Wake 1992) with the advent of the comparative method (Felsenstein, 1985). Note that whether or not “evolutionary biomechanics” and “functional morphology” should be considered equivalent or distinct disciplines is subject to disagreement (Wake 1982).

A comprehensive understanding of form–function evolution across temporal, spatial, and phylogenetic scales is still elusive, as access to functional trait data and robust phylogenies has been limited. However, recent technological advances are overcoming these challenges, and the field of evolutionary biomechanics is rapidly developing into a deeply quantitative and comparative science. New and improved imaging methods (e.g., Yopak et al. 2018) and computing infrastructure allow the generation, storage, and analysis of vast quantities of photographs, three-dimensional (3D) scans and videos (e.g., Goswami et al. 2019; Santana et al. 2019). Technological developments, including machine learning techniques (e.g., Macleod 2017) and crowd-sourcing platforms (e.g., Chang and Alfaro 2016, Cooney et al. 2017), are facilitating the collection and analysis of massive morphological datasets (e.g., Alfaro et al., 2019, Goswami et al., 2019). Concomitantly, evolutionary analysis of the data, which requires building large time-calibrated phylogenies, is facilitated by Next Generation Sequencing and rapid advances in comparative phylogenetic methods. The goal of our symposium “*Comparative Evolutionary Morphology and Biomechanics in the Era of Big Data*” was to highlight new research at the conceptual, methodological, and analytical vanguard, with a strong focus on cutting-edge work by junior scientists. The manuscripts in this issue demonstrate that comparative evolutionary biomechanics is now a tractable research arena, with the potential to provide important insights into the patterns and processes of form–function evolution.

Several major themes emerged from the symposium: (1) museum collections are critical for the future of big data in integrative biology, (2) new methodologies are catalyzing the collection and analysis of massive datasets but, (3) the collection of phenotypic data is still the rate limiting step and thus represents an ongoing challenge for the field. In combination, the research illustrates how new technologies are facilitating the integration of the fields of biomechanics, functional morphology, and phylogenetic comparative methods to build the emerging discipline(s) of macroevolutionary functional morphology and biomechanics.

Museums are the future of big-data integrative biology

Without the millions of specimens from living and extinct species housed in museum collections around the world, most of the research presented in this volume would have been impossible. The museum resources used by these studies range from online photographic databases (Alfaro et al. 2019, Baliga and Mehta 2019) through to simple measurements taken on museum specimens (Price et al. 2019, McHorse et al. 2019) or 2D photographs (Baliga and Mehta 2019) and 3D scans of specimens (Evans et al. 2019; Goswami et al. 2019, Santana et al. 2019; Sherratt et al. 2019). Photographs and scans require further analysis to generate useful phenotypic data. Our authors extracted shape data using 2D and 3D geometric morphometrics (Baliga and Mehta 2019, Evans et al. 2019, Sherratt et al. 2019, Goswami et al. 2019, Santana et al. 2019) and color pattern data by applying machine learning approaches along with newly developed tools to quantify color pattern geometry (Alfaro et al. 2019).

Once quantified, these phenotypes facilitate the investigation of biomechanics and functional morphology at the macroevolutionary scale. For example, by accessing ecological, morphological, and phylogenetic data from hundreds of fishes, Baliga and Mehta (2019) reconstructed the evolution of cleaning behavior (in which one species of fish will “clean” ectoparasites [or other material] from a “client” fish) in five families of ray-finned fishes. Highly specialized, obligate cleaners from different families (wrasses and gobies) converged on elongate body shapes, and the evolution of cleaning behavior was limited to small-sized species (Baliga and Mehta 2019). In contrast, the link between morphology and cleaning behavior was much weaker in facultative cleaners, suggesting that greater ecological specialization is a stronger constraint on form–function evolution.

The spatial and temporal depth afforded by digitized museum records are already extensively leveraged for Geographic Information System (GIS)-based studies, particularly in biogeographic studies of biodiversity and in assessment of global shifts in response to climate change (Page et al. 2015). Specimens similarly span an important spatial breadth and temporal depth, with paleontological specimens providing a much needed deep-time perspective on functional evolution. For example, in this issue, McHorse et al. (2019) leveraged paleontological collections to understand the evolution of digit reduction in horses and litopterns (an artiodactyl

lineage in which monodactyly also evolved). By modeling stress loads on different types of limb bones, [McHorse et al. \(2019\)](#) predicted how digit reduction and loss impacted kinematic performance in throughout the evolutionary history of these lineages.

New methodologies are catalyzing the collection and analysis of data, and contributing to massive open-access data platforms

New methods are helping to save time and extract more data from digital representations of specimens. As with all technologies, deciding on an appropriate technology involves a tradeoff between image/video resolution and time/money invested. For example, micro-computed tomography (CT) and dice-CT both provide 3D access into small anatomical structures; in some cases, the additional precision afforded by high-resolution dice-CT are preferable, whereas in others micro-CT perform just as well ([Santana et al. 2019](#)).

To compare shape differences among scales of organization, transformation approaches through geometric morphometrics have become standard practice. The flexibility of this approach is exemplified in this issue by [Sherratt et al. \(2019\)](#), in which geometric morphometrics neatly illustrated how heterochrony contributed to the evolution of microcephaly in sea snakes. Comparing shape among closely related species, for which homologous landmarks are clear, is often relatively straightforward. However, as phenotypic and phylogenetic diversity of species incorporated into studies increases, so too will the number of ambiguous landmarks for geometric morphometric comparisons. Through a detailed series of simulations, [Goswami et al. \(2019\)](#) demonstrated that the number of landmarks and superimposition approach are key determinants for accurately detecting shape variation. High-density approaches (as opposed to traditional landmark approaches), resulted in a more robust analysis of shape, and allow researchers to detect subtle differences in shape.

Geometric morphometric approaches can also be applied to ecologically relevant motion. For example, [Martinez and Wainwright \(2019\)](#) applied geometric morphometrics to infer jaw mechanics in the cichlid four-bar linkage system. The approach is powerful because it illustrates how shape data can be used to model kinesis, without suffering from several of the pitfalls that have been applied to rotation-based ratios ([Cooper and Westneat 2009](#)). The metric employed by [Martinez and Wainwright \(2019\)](#), termed kinematic asynchrony (KA), describes the

non-linear deformation of a structure's motion. As such, KA can be leveraged to describe and compare form–function relationships among species. When compared to underlying morphological structures, biomechanical metrics like KA can highlight different patterns of form–function evolution (e.g., [Muñoz et al. 2017, 2018](#)).

Collecting vast phenotypic datasets is an ongoing challenge, but the future is open-access

Big-data projects in integrative biology are confronted from the outset with a major time challenge. Despite new methods speeding up the extraction of data from digital representations of specimens, accessing the original specimens and measuring, photographing, or scanning them still is the rate limiting step, even more so when specimens need to be alive to generate kinematic data. Extraordinary time investment, often in the tens of thousands of hours, is required to create digital repositories of specimens. Thus, while museum collections are readily available sources of biological data, extracting biologically relevant data at the scales necessary to inform large-scale evolutionary analyses presents several challenges. By harnessing the power of large teams and sophisticated pipelines for digitization and analysis, our authors ([Alfaro et al. 2019](#), [Evans et al. 2019](#), [Goswami et al. 2019](#) and [Price et al. 2019](#)) and others like them (e.g., [Rabosky et al. 2013](#), [Cooney et al. 2017](#), [Navalón et al. 2019](#)) are incorporating biological data from hundreds, thousands, and even tens of thousands of specimens into evolutionary morphology studies. Whilst the taxonomic scope of these studies (e.g., Aves or Teleostei) is impressive, they still represent small branches of the tree of life. Automated phenotyping methods, inspired by those being developed for large-scale genomic studies and ecological monitoring, which use machine learning and sometimes robots to extract behavioral (e.g., [Weissbrod et al. 2013](#)), morphological and physiological data (e.g., [Virlet et al. 2017](#)), have the potential to speed up future data collection efforts.

Numerous open-access efforts are leading the charge on democratizing scientific data, such as oVert (short for openVertebrate), an NSF-funded initiative to make 3D vertebrate scans from >20,000 specimens freely available through Morphosource (www.morphosource.org). The work presented by [Evans et al. \(2019\)](#) in this issue contributes to this massive, open access effort. Moreover, continued support for multiple open

access initiatives that promote the digitization of museum collections (e.g., www.idigbio.org), the collation and sharing of biological images (e.g., www.morphbank.com, www.morphobank.org), and kinematic data (e.g., www.zmaportal.org), as well as ontologies that link phenotypes across vast taxonomic scales (e.g., www.phenoscape.org), will facilitate future macroevolutionary studies of functional morphology and biomechanics at even greater phylogenetic breadth.

Towards and integrative framework for form–function macroevolution

Ultimately, the goal of amassing large mechanical, morphological, and phylogenetic datasets is to discover how diversity evolves and how it is distributed among traits, lineages, and geographic regions (Muñoz 2019). The articles in this issue illustrate how these types of questions can be rigorously addressed through an integrative approach. For example, many-to-one mapping of form-to-function is an emergent property of many mechanical systems in nature (Wainwright et al. 2005). In this issue, Muñoz (2019) compares patterns of evolution in mechanically simple (one-to-one mapping) and complex (many-to-one mapping) systems. Overall, mechanical complexity can decouple morphological and performance evolution. For example, the degree of parallel evolution becomes weaker as the number of morphological pathways to adaptation increase, indicating multiple potential “solutions” to a common ecological “problem.” Nonetheless, even in mechanically complex systems, morphological evolution can often be biased to a few traits of high mechanical effect. This indicates that multiple pathways to functional adaptation are not tantamount to equal freedom of evolution. As a general rule, the tempo and mode of morphological evolution become more predictable when form–function relationships are stronger, even in mechanically redundant systems (Muñoz 2019).

Structural relationships are not the only features that contribute to macroevolutionary patterns. In many cases, the habitats that organisms occupy can be important drivers of morphological evolution. Coral reefs, for example, exhibit exceptional patterns of diversity. The complexity of coral reef habitats is generally considered a motor for diversity in the feeding apparatus of reef fish. In this issue, Evans et al. (2019) explicitly tested this hypothesis by comparing rates of pharyngeal jaw evolution in 134 species of reef and non-reef wrasses (Labridae). High-resolution micro-CT scans were generated, allowing the researchers to quantify fine-scale shape

differences in the pharyngeal apparatus, which correspond to major tropic differences (Wainwright et al. 2012). Surprisingly, reef-dwelling was not a key predictor of morphological diversity or rates of evolution, except in parrotfishes and tubelips, indicating that the mechanisms underlying prolific morphological diversity are more complex than simply occupying reef environments.

By performing dense sampling across major clades, patterns of form–function evolution can be directly compared among lineages. In this issue, Price et al. (2019) describe the potential of the largest macroevolutionary database of vertebrate morphology to date, which includes measurements on over 16,000 specimens from approximately 6100 species of teleost fish, about a fifth of extant diversity. Their initial analyses of the dataset identified elongation and a contrast between head and tail size as key axes of body shape variation. Price et al. (2019) also revealed interesting patterns of evolutionary heterogeneity across the fish tree. For example, fast rates of morphological evolution characterize elephantfish (Mormyridae), crocodile icefish (Channichthyidae), eelpouts (Zoarcidae), guanards (Triglidae), and snailfishes (Liparidae). Future studies may examine whether the processes shaping rapid evolution are shared or different among these lineages.

An overarching theme of these studies is that morphological and functional diversity is unequally distributed across the tree of life. Structural relationships, biogeography, and evolutionary history all impart macroevolutionary footprints on phenotypic diversity. Our hope is that the emerging trends from these (and other) studies erect conceptual frameworks and working hypotheses that can be rigorously tested, and contribute to a broader understanding of form–function evolution.

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