Integrative and Comparative Biology
Integrative and Comparative Biology, volume 62, number 3, pp. 641–651
https://doi.org/10.1093/icb/icac114
Society for Integrative and Comparative Biology

SYMPOSIUM INTRODUCTION

# Ecomechanics and the Rules of Life: A Critical Conduit between the Physical and Natural Sciences

Lara A. Ferry [*,1] and Timothy E. Higham [†]

[*]School of Mathematical and Natural Sciences, New College of Interdisciplinary Arts and Sciences, Arizona State University, 4701 W Thunderbird Rd, Glendale, AZ 85036, USA; [†]Department of Evolution, Ecology, and Organismal Biology, University of California Riverside, 900 University Ave, Riverside, CA 92521, USA

From the symposium “Integrating ecology and biomechanics to investigate patterns of phenotypic diversity: Evolution, development, and functional traits” presented at the annual meeting of the Society for Integrative and Comparative Biology virtual annual meeting, January 3–February 28, 2022.

[1]E-mail: Lara.Ferry@asu.edu

**Synopsis** Nature provides the parameters, or boundaries, within which organisms must cope in order to survive. Therefore, ecological conditions have an unequivocal influence on the ability of organisms to perform the necessary functions for survival. Biomechanics brings together physics and biology to understand how an organism will function under a suite of conditions. Despite a relatively rich recent history linking physiology and morphology with ecology, less attention has been paid to the linkage between biomechanics and ecology. This linkage, however, could provide key insights into patterns and processes of evolution. Ecomechanics, also known as ecological biomechanics or mechanical ecology, is not necessarily new, but has received far less attention than ecophysiology or ecomorphology. Here, we briefly review the history of ecomechanics, and then identify what we believe are grand challenges for the discipline and how they can inform some of the most pressing questions in science today, such as how organisms will cope with global change.

## Introduction

Ecology and function are inextricably linked due to the need to perform activities essential for survival, which inevitably require exerting or resisting forces in nature (Fig. 1). Whether it is a mangrove tree experiencing hurricane-force winds (e.g., Yanasigawa et al. 2010), macroalgae in a wave-swept intertidal zone (e.g, Koehl and Wainwright 1977; Martone 2007), a gecko running on a rough surface (e.g, Klittich et al. 2017; Higham et al. 2019), or a bumblebee trying to fly in the wind (e.g, Ravi et al. 2013; Crall et al. 2017), the mechanics of these processes are tightly linked to surrounding environment. For plants, the main ecological factors that influence mechanics are water-induced drag for aquatic species (see reviews in Denny 1988; Janot et al. 2022 ), wind-induced drag for terrestrial species (Higham et al. 2022, and gravitational forces for terrestrial species (reviewed by Niklas 1992). Among animals, predator–prey interactions, searching for mates, dispersal, and competition for resources are among the ecologically based behaviors that require the precise timing and magnitude of biomechanical motions for their execution (e.g, Harley 2013; Higham et al. 2015; Higham et al. 2017. Ecological conditions have profound influences on the successful, or unsuccessful, execution of these mechanically based activities.

Despite the significant impacts of ecology on the mechanical demands of organisms, there is little cross talk between the ecological and biomechanical communities. Doing so will likely provide novel insight into evolutionary patterns and processes (e.g, Wainwright and Reilly 1994; Koehl 1996; Podos and Hendry 2006; Higham et al. 2016; Domenici and Seebacher 2020; Higham et al. 2021). That said, there have been notable efforts to more strongly and wholistically link ecology with morphology (i.e, Wainwright and Reilly 1994;

Advance Access publication July 25, 2022

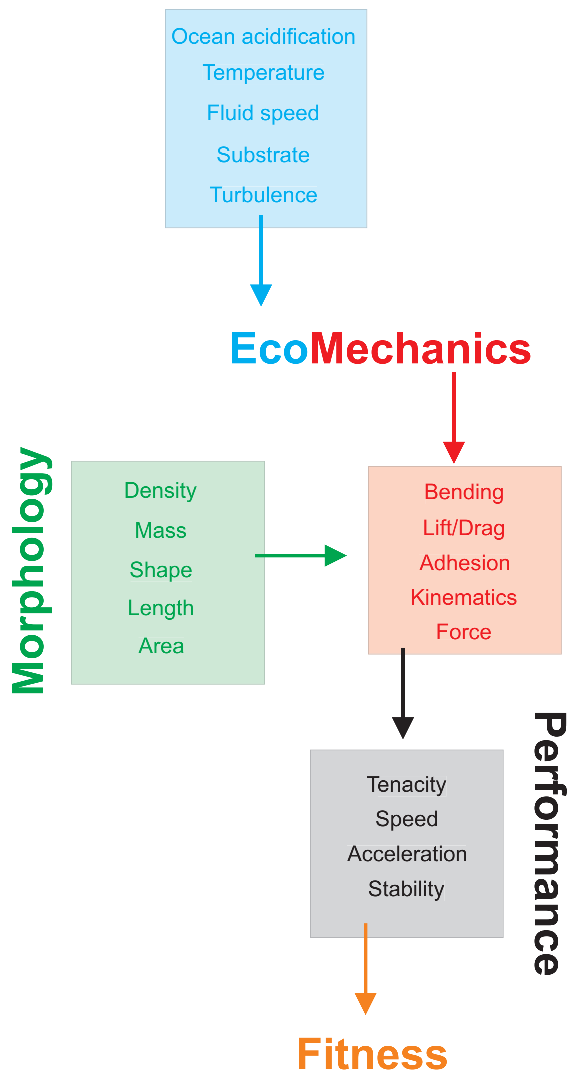


**Fig. 1** General schematic indicating the possible ways in which fitness is shaped.

Bauer et al. 2020) and physiology (e.g, Chown et al. 2004). As aptly summarized by Bauer and Poppinga (2022), the development of smaller and more powerful portable devices for measurement and acquisition, facilitated by recent technological advances, are likely leading to push the field forward faster and faster.

Whether it is termed ecological biomechanics (Koehl 2022), mechanical ecology (Bauer et al. 2020), or ecomechanics (Denny 2016; Higham et al. 2021), the general goal is to utilize biomechanical tools to address ecological questions (Denny and Gaylord 2010; Denny 2016). Ecomechanics, the term we shall use throughout the current paper, is inherently integrative. Any researcher conducting ecomechanical research must understand both the mechanics of the organism of interest, but must also understand the ecological conditions that are experienced. Our aim is to first discuss ecomechanics from a historical perspective, but then identify ways in which an ecologist can incorporate biomechanics, as well as ways that biomechanists can adopt an ecological perspective. The benefits and costs of conducing laboratory-based studies and field studies are also addressed.

## History of ecomechanics

In order to understand where ecomechanics needs to go, as a field, we need to understand where we have been. One of the first mentions of ecomechanics was by Wainwright et al. (1976). In this contribution, they made the rather obvious, but important, point that plants and animals evolved in nature, not laboratories. Thus, one must study organisms in the harsh environments in which they live. The challenges in nature are often physical, whether, it is a wave pounding the intertidal, hurricane winds bashing trees, or simply tree trunks that must be climbed. They go on to state that "no ecologist would claim that gravity, wind, and water flow are unimportant, but as yet no general account of their implications for organisms exist." This has advanced considerably in the intervening 45 years. It is only by knowing the physical bases of phenomena that one can apply general principles to predict how an organism will respond to environmental perturbations. As is quite clear to all biologists, we live in a world with rapidly changing environmental perturbations, making this early work incredibly important today.

Ecomechanics started in the intertidal zone, the region where the ocean meets the land and which is affected in a very obvious way by some of nature's most extreme forces. There has long been fascination with wave-swept shores given the paradox of diversity in the midst of apparent physical adversity (Denny 1988). It is predominantly comprised of sessile organisms that are relatively accessible, and the substrate lends itself to having equipment implanted. Some of the earliest research focused on cnidarians with comparisons between sea anemones that occupy areas exposed to extreme wave action and those that are subtidal and experience tidal currents (Koehl and Wainwright 1977). By combining morphological measurements, flow regimes in the localities where the species occur, and flow force measurements on the anemones themselves (using a force plate), Koehl (1977) found that the shape, size, flexibility, texture, and behavior can all influence the forces experienced in nature.

Since these early studies, many other intertidal animals and plants have been examined, including mussels, macrophytes, and others. Several edited volumes have been dedicated to related topics, including Ecological Morphology by Wainwright and Reilly 1994), and Ecology and Biomechanics, edited by Herrell et al. (2006). These are important studies of how things work in the natural world, but they do not (yet) use biomechanical inference to *advance our understanding of ecological systems*. Indeed, this could be described as a Grand Challenge for Biomechanics, as a field; to become truly integrative. Meaning, to use biomechanical tools and approaches to dive deeper into, and answer, *major ecological questions*. Denny and Helmuth (2009) issued this very challenge, now over a decade ago.

The turning point for the field, in which this Grand Challenge is more fully developed, is Mark Denny's more recent book (2016), Ecological Mechanics. Denny (2016) challenges us to understand the relationship between environmental variation and the mechanical functioning of animals. Denny was able to provide this perspective because much of the work within this discipline has/had largely been limited to intertidal marine habitats (e.g., Carrington 2002), and the research has been undertaken primarily by self-described biomechanists (e.g., Denny and Helmuth 2009; Denny and Gaylord 2010). As Carrington (2002) notes, intertidal (and subtidal) biomechanists and ecologists were largely not considered "physiological ecologists" at the time. Thus, researchers working at the high-energy interface between land and water, asking questions about organismal survival and how it is accomplished, found themselves in an interstitial space, not unlike those spaces used by many of the smaller organisms that they studied. It was a space to not only survive, but to thrive, as these researchers were able to effectively work at the interface of two disciplines; indeed, they had to work at this disciplinary interface in order to address and answer questions about life in this truly brutal ecological zone. As these questions were developed, it became clear that the ecomechanical approach to the study of ecological systems and evolutionary solutions was not a novelty, uniquely applicable to the intertidal system. Instead, the ecomechanical approach defines a way of thinking about and studying all systems, and addressing the "why" questions underlying evolutionary change, the assembly of ecological communities, and organism response to varying environments. Ecomechanics offers a framework for exploring interactions between organisms and their environment(s), and how this fuels evolutionary change (Higham et al. 2016), bounded by the laws of physics (Denny and Gaylord 2010).

A series of more recent symposia and published proceedings further highlights the tremendous value of this integration. A recent, two-day tribute to the late R. McNeill Alexander invited speakers to focus on biomechanical research in natural systems (8th World Congress of Biomechanics; 8–12 July 2018; Dublin, Ireland). While the contributions generally did not investigate the ecological and biomechanical interface, per se, they do very effectively demonstrate the sorts of questions which can be answered with (the addition of) an ecomechanical approach. A more applied example is summarized by Domenici and Seebacher (2020), which focused on the ecological issue of global warming, and how the true integration of biomechanics allows researchers to more realistically predict how species will cope, and ultimately survive. The recent timing of these contributions serves only to underscore the timeliness of a modern ecomechanical approaches to the study of life.

Expanding on this ecomechanical framework, Higham et al. (2021) develop a new modeling framework that specifically defines ecomechanical models. These are an expansion of biomechanical models in that they use mechanical traits coupled with time-varying ecological traits. Their primary example is that of wind-induced drag on trees. The ability of a tree to resist these bending moments depends upon the diameter of the tree stem, the area of the crown, and the height of the tree. Using an ecomechanical model allows researchers to determine how trees will likely respond to very strong winds (e.g, hurricanes), even if they have not experienced them yet. In a changing world, with many extreme weather events increasing, this forward-thinking modeling approach will be instrumental in determining the survival of species. This framework need not apply only to trees; many organisms face external forces that may change as the world goes through a rapid series of changes.

To wit, expanding on this truly integrative approach to understanding life and the world around us was identified by the National Science Foundation as one of the "Ten Big Ideas for Future NSF Investments." NSF uses the term *convergence* to describe research programs or platforms that truly integrate the tools, even the way of thinking, of different disciplines. Such research, they claim, is perhaps the only way for addressing the most wickedly complex questions. Convergence research is characterized by two elements: (1) addressing a specific and deep challenge or pressing need, and (2) integrating knowledge, theory, data, methods, communities, and language of multiple disciplines such that novel frameworks or new paradigms emerge (National Science Foundation, Growing Convergence Research current program solicitation; https://www.nsf.gov/pubs/2019/nsf19551/nsf19551.htm). We suggest that ecomechanics, as an integrated "field of fields," meets both of these two criteria. Ecomechanics, we argue, is poised to become one of the *most* important fields of study in the present and into the future. **Below we propose several grand challenges in the field of ecomechanics**:

## Using ecomechanics to determine how life will respond to a changing world

Some of the changes we face are related to global climate change, as noted by Domenici and Seebacher (2020). We face more and more frequent "100-year" storms, marine heat waves, record drought, fire, and other environmental extremes relative to life on Earth as we humans know it. How will organisms withstand these extremes? Can organisms evolve rapidly enough to withstand these extremes? What will the landscape look like on our planet 20 years from now? As summarized by Higham et al. (2021), an ecomechanical modeling framework will help us predict the responses of plants and animals to these dramatic changes by using models that include both ecological variables and functional traits of organisms. This approach has been adopted by ecologists and physiologists in an attempt to determine if abiotic factors, such as temperature, will impact the distribution and success/survival of organisms in the future (e.g, Crowell et al. 2022).

Understanding how organisms will respond requires an understanding of what factors might change, but also other influences of these changes on the organism (see, for example, Newcomb et al. 2022). This means understanding both the chemical and physical environments. With human-induced global change, ocean acidification a primary concern. Acidification-induced degradation of defensive structures, for example, such as shells, spines, and adhesive tissue, is documented for marine species (i.e, O'Donnell et al. 2013); though the degree of degradation is highly variable among species, ranging from only very slight changes to fairly radical changes in the size, shape, and strength of such structures (Gaylord et al. 2019). Work by Janot et al. (2022), focuses on the relationship between the chemical ecology and the biomechanics of coralline algae. Coralline algae are physically hardened on their external surfaces, presumably to resist damage. The formation of these protective tissues is reliant upon the process of calcification, which, the authors have discovered, is remarkably similar among evolutionary lineages and morphologies (Janot et al., 2022). This suggests that potentially *all* species of coralline algae are vulnerable to environmental changes that impact the calcification process, such as ocean acidification and warming.

As temperature and acidity affect the rates of chemical processes and reactions, this threat extends to all sorts of life in the oceans. Di Santo (2022) proposes a theoretical framework for studying such impacts on locomotion, a well-studied "model system" in organismal biology. Locomotor performance is similarly affected by temperature and acidity as these abiotic parameters affect oxygen delivery to the muscles, muscle contraction, and nervous system function, among other physiological processes (Nudds et al. 2020). These types of impacts have consequences for organism survival (Carrington et al. 2015), population sizes (Gaylord et al. 2019), community structure (Harley 2013), and community-level interactions like predation (Frey and Gagnon 2015). The overarching and cascading effects on community structure may potentially have dire consequences for the entire ecosystem (Domenici and Seebacher 2020).

Finally, terrestrial environments are subject to changes that might influence the biomechanics of organisms. Anderson and Kawano (2022) describe a mechanism for considering the mechanical performance curve and, in particular, the rates at which forces are experienced in the lab and in the field. Strain rate, for example, can be dynamic. And, how a bone is loaded affects its performance (Anderson and Kawano 2022). If one then extends this concept to a changing physical landscape, this means that how bones perform to move an organism from one place to the next also may change. Selvitella and Foster (2022) provide interesting insight into behavioral plasticity, and how organisms like *Anolis* lizards can cope with a changing physical landscape as they try to move within and through it. Interestingly, *Anolis* shows tremendous flexibility in the behaviors it employs as well as the ability to successfully navigate even subtle changes.

## How has ecomechanics influenced the evolution of life?

Being able to survive in an environment will depend upon the challenges that organisms face. Therefore, it is expected that the phenotype, whether it is morphological or functional, will reflect those demands. This idea has emerged in many areas of biology, including the concept of ecomorphology, where morphology is thought to be related to both behavior and ecology. A prime example is the feeding morphology of fish. Wainwright (1991) examined the link between jaw morphology, ability to crush hard prey, and diet in labrid fish. Morphology accurately predicted crushing ability, and this was related to a transition from soft-bodied prey to hard-shelled prey. Another classic example of ecomorphology is among *Anolis* lizards, where species with similar morphological traits were also similar in performance, ecology, and behavior (Losos 1990). The former example demonstrates how ecological pressures can drive evolutionary convergence in functional traits.

Less understood is the link between ecology and biomechanics. Morphology is often used as a proxy for function, but there are several cases in which morphology and function do not exhibit a clear relationship (Koehl 1996). Thus, there is a need for direct connections between ecology and function, something that is harder to do given the logistics. However, we are at a point in time where higher-level phenotypes, including biomechanical traits, can be quantified in large numbers (see "How can modern tools/technology be incorporated into the study of ecomechanics?" for more information). Given that animals must perform, using biomechanics, ecologically relevant tasks in order to survive, it is clear that ecomechanics is directly related to evolution. In fact, biomechanics likely plays a key role in ecological speciation (Podos and Hendry 2006; Higham et al. 2016). Given a scenario where two populations are separated and diverging, due to differing selective pressures, in allopatry, one might expect that reproductive isolation might emerge (Higham et al. 2016). This might, in turn, result in hybrid inviability, due to inferior biomechanics, if the two populations were to come together at some point in the future. This could potentially lead to speciation. Although this is theoretically possible, data are needed to support such a conclusion. This, over the coming years, is a grand challenge in ecomechanics.

## Ecomechanics and the rules of life

### *Rigid versus flexible: how do sessile organisms deal with fluid forces?*

Environmental forces include such things as gravity, pressure, surface tension, and fluid flow. Fluid flow is a ubiquitous force for terrestrial, aquatic, and aerial organisms. When considering adaptations to the velocity of fluid flow, strength, and rigidity are the main variables of concern (Wainwright 1976). Yet, our knowledge is currently limited to select groups of animals and plants/macrophytes. Rigid coral and compliant seaweeds are one example of a more well-studied system, and offer a study in contrasts when considering the ways in which they deal with flow. Corals, presumably, are trying to resist bending, and therefore depend on rigidity (e.g., Tunnicliffe 1982; Ferrario et al. 2014; Rogers et al. 2016). Alternatively, seaweeds can reduce drag by being flexible and bending with the flow (e.g, Koehl 1996, 1999; Martone 2007; Gaylord et al. 2008; Vettori and Nikora 2019. Compliance, in this case, is critical. Both have advantages and disadvantages; but, how these strategies have shaped the diversity of life is only beginning to be understood. For example, Dugauquier et al. (2021) were able to demonstrate that branching corals were less stiff than whip-like corals, and that this difference in morphology, and flexibility, related directly to where, and potentially how successfully, different species can feed even when inhabiting the same flow regime. Corals and seaweeds both must cope with a range of ecological conditions with very little ability to modify their location in the environment. Thus, mechanical and material properties of largely sessile organisms will be a primary driver of survival (or death) in dynamic habitats (*sensu* Koehl 1999). These rules of life are dictated by ecomechanics. It is important to note that marine ecosystems have received almost all of the attention when it comes to organism–flow interactions. Nikora (2010) emphasizes that our understanding of plant–flow interactions is much more extensive for terrestrial and marine systems compared to freshwater systems.

Trees are not unlike corals in their tendency to be more rigid in response to flow (excluding saplings), in this case air flow. Trees are among the world's largest organisms and can grow extremely tall. Wood, which defines trees, is a composite material made up of microfibrils composed of crystalline cellulose embedded in a matrix of lignins and hemicelluloses (Barnett and Bonham 2004). The mechanical stiffness and strength of wood is highest in a direction parallel to the stem axis (Fournier et al. 2006), which is typically where loading is greatest. Although wood density is typically a strong predictor of other functional traits in the stem of trees (Niklas and Spatz 2010; Higham et al. this issue), the angle of the cellulose microfibrils contributes significantly to wood stiffness, after accounting for density. Juvenile trees will typically have a higher microfibril angle, leading to a reduction in stiffness (Barnett and Bonham 2004). This allows these trees to bend and reduce form drag. Older and taller trees require greater stiffness, which means having lower microfibril angles. Thus, ecomechanics plays a role during the development of trees, and is likely a major contributor to the overall phenotypic diversity we see among trees.

When it comes to the ecomechanics of trees, wind is the dominant mechanical factor that constrains size, shape, and an upright growth form (Ennos 1997; Rowe and Speck 2005). Trees have the ability to respond to physical perturbations, such as wind, through thigmomorphogenetic reactions. These responses often involve morphological changes, but the signaling and transduction pathways are not fully understood. The actual changes in response to mechanical perturbations can also be difficult to uncover under experimental and field conditions, although recent studies suggest that the responses (stimulus threshold) differ among species (Coutand et al 2010; Martone 2010).

Higham et al. (this issue) examined the evolution of mechanical properties in conifers and angiosperms, and they found that multiple groups (pine trees, genus *Shorea*, and elm trees) exhibit elevated rates of trait evolution. These elevated rates appear correlated with increases in mechanical properties, such as stiffness, density, and strength. Ecological scenarios for these increases are discussed by Higham et al. (this issue), but much more work is needed to tease apart how mechanical properties are related to environmental conditions. Although angiosperms and conifers appear to differ in their functional traits (stiffness, density, strength, etc.), these differences seem to go away after accounting for phylogenetic relationships (Higham et al. this issue). Thus, any future comparative ecomechanical analyses should include phylogenetic information (see Garland et al. 2005).

### *Moving in a turbulent world: how do mobile organisms deal with fluid forces?*

Although the majority of ecomechanical studies have focused on sessile plants and animals, mobile animals must also deal with fluid forces as well. Higham et al. (2015) discuss the ecomechanics of predator–prey interactions among fish, with key ecological variables being turbulence, turbidity, and temperature. These factors can not only influence the sensory and motor systems of the predator, but they can also influence the ability of the prey to escape. Turbulence is an issue for foraging animals at all scales, ranging from small zooplankton (e.g., Costello et al. 1990; Hwang et al. 2014; Ticocci et al. 2022), invertebrates such as crabs (Finelli 2000), seabirds (Lieber et al. 2021), and marine mammals (Mendes et al. 2002; Fandel et al. 2020). External perturbations increase when an organism is in turbulent flow (Webb 2002; Weihs 2002), A fish, for example, will need to stabilize the swimming trajectory in this case, using hydrostatic or hydrodynamic damping and correcting forces (Webb 2002; Johansen et al. 2020). Fish can use their pectoral and median fins to correct for these disturbing forces, but very little information relates fin function to realistic ecological conditions (Higham et al. 2015). This will be a key area of research moving forward.

Aerial animals experience similar pressures in their environment. Given their relatively small size, insects are arguably most influenced by fluid flows, though this is a factor affecting birds (Safi et al. 2013; Nourani et al. 2021), bats (Cryan et al. 2014; Marshall et al. 2015), and other gliding animals (Bahlman et al. 2013; Krishnan et al. 2014). Wind is ubiquitous and can influence behaviors such as take-off, foraging, flying/gliding, and landing (Pennycuick 1972). When faced with turbulent flow, wild orchid bees, for example, extend their hindlegs ventrally, improving roll stability but incurring greater energetic costs (Combes and Dudley 2009). More recently, bumblebees were subjected to unsteady flows that caused either lateral or vertical disturbances (Ravi et al. 2013). Compared to smooth flow, the bees were able to deal with the disturbances, but still experienced translational and rotational fluctuations. These unsteady flow conditions also reduce flight speed, suggesting increased energy expenditure. Insects not only need to fly in windy conditions, but they also need to take off and land. When bumblebees face strong winds, they employ a different tactic when landing on flowers (Chang et al. 2016). Specifically, they maintain a high flight speed (compared to still air) and experience higher peak decelerations upon impact. These studies highlight the need to incorporate ecologically relevant situations when studying the mechanics of organisms in flight.

### *Gravity, prey, and substrates: adaptations to non-fluid forces*

Non-fluid forces are important for both plants and animals. Arguably the most important are gravitational forces, as they influence all organisms, but more significantly terrestrial organisms. Plants, especially large trees, must deal with gravity as they grow large and support their own structures such as branches or bending of the stem (Niklas 1992). Ecological situations, such as competition for light, might drive trees to grow larger, thus strongly influencing the mechanics. For vertebrates, gravity plays a key role when considering locomotion. Body size has a tremendous influence over the mechanical function of the limbs, and has likely shaped the evolution of locomotor posture in many lineages (e.g., Biewener 1989). This could profoundly influence the ecology of an animal, but ecology might also dictate the locomotor biomechanics. The latter point has been examined extensively among animals, where researchers have studied locomotor biomechanics in relation to specific habitat features such as arboreal perch diameter (Losos and Sinervo 1989; Schmitt 1994; Astley and Jayne 2007; Gerald et al. 2008; Foster and Higham 2012) and surface incline (Vilensky et al. 1994; Jayne and Irschick 1999; Zaaf et al. 2001; Higham and Jayne 2004; Herrel et al. 2013; Clemente et al. 2019). With a few exceptions (e.g., Jayne and Ellis 1998; Irschick and Jayne 1999), most of these analyses have been done in a laboratory setting. Given the technological advancements, such as wireless accelerometry and high-speed video in the field, examining the role of habitat structure on field locomotion is a next step. The ecomechanics of terrestrial locomotion is, therefore, a prime area for future research.

External forces need not be limited to locomotion. Santana et al. (2022) describe how the shapes of the jaws of bats have been shaped over the course of evolution in response to forces experienced by the jaws, particularly in the region of the first molar, and sometimes the premolar. The shapes and sizes of molariform teeth, and when they appear in the jaw over the course of development, appear to have similarly shaped in response to forces experienced during food acquisition. The first molar and premolar develop first over ontogeny, and may set the pace for remaining tooth development. As such, the need to withstand the forces generated during feeding, to ensure feeding success, has potentially shaped developmental trajectories to ensure that the tissues that can withstand such forces are in the right places at the right time.

The rate at which forces are experienced has the potential to alter traits. Anderson and Kawano (this issue) review the dynamic properties of structural traits and how these traits change function under different strain rates. Puncture mechanics is an example of a function that depends strongly on the rate at which it occurs. Increasing loading speed increases the performance of fang penetration (up to 2.5 m/s) of gaboon viper fangs (Anderson et al. 2019). Thus, it is clear that both ecology and loading rate have the potential to influence mechanical function, and both should be considered in future research. Changing environmental conditions is likely to influence the trait due to changes in the rate at which forces are applied. This framework will nicely form the basis for future ecomechanical studies.

Not only can this approach help us to understand the diversity of life on the planet today, but we can also examine which forms of life will be successful in hypothetical future environments based upon certain rules of physics which all forms of life must obey (Higham et al. 2021). Physics determines the parameters that evolution can "work with"—variation in the surface features of substrates, like rocks or plants, drives the evolution of gecko adhesion, and, specifically, the microstructures of the toe pads used to cling to these surfaces (Higham et al. 2019), and the degree of "wrinkliness" of the skin/cuticle of animals and plants relates directly to how well the surface resists stress (Surapeneni et al. 2022). This could provide insight into the ways in which stress is tolerated and the evolutionary pathways that lead to surface architecture.

## How can modern tools/technology be incorporated into the study of ecomechanics?

Biomechanics embraces technological advancements in order to better quantify and understand how organisms work. Increasingly sophisticated tools will allow for more precise measurements. Although rapid and extensive phenotyping, especially for biomechanical traits, can be difficult, modern tools are permitting such endeavors. Selvitella and Foster (2022) explore how machine learning, in the context of arboreal locomotion in *Anolis* lizards, can be used to assist with biomechanical questions. As mentioned previously, *Anolis* navigates complex and changing landscapes well. Machine learning allowed Selvitella and Foster 2022) to explore how this ability was affected, or facilitated, by certain morphologies, or not. Lailvoux et al. (2022)also have used machine learning to predict performance from Anolis morphology, and to fill in missing data in large trait datasets, further demonstrating the use of this tool for successfully understanding and predicting patterns of evolution. They found that their predictions were so robust that phylogenetic data did not need to be added to the models; these sorts of data did not improve predictions. Machine learning, being outstanding for classifying things based upon their features, has recently been applied to categorizing cells (Li et al. 2021; Phillip et al. 2021; Lan et al. 2022), including nerves (Williams et al. 2020; Alipanahi et al. 2021), and allowing for reconstruction of structures (Schubert et al. 2019), all based upon very fine scale morphology. These tools further help us to understand the underlying bases for behavior, which similarly has been shaped by evolution. Similarly, Harter et al. (2022) used data mining and models to explore aerobic performance in fish, determined by the diffusive properties of gill tissues, and its relationship with species distributions.

Both Wolf and Lauder (2022), and Lauder (2022), examine the specific application of using robots, as tools, to explore possible evolutionary outcomes. Robots represent a physical ecomorphological model, as opposed to a computer-based or theoretical model. Both physical and computer-based models facilitate experimentation with organisms in a way that working with live animals cannot. The utility of models in this way has long been recognized, and hence the incorporation of modeling as a research tool into many areas of biology including ecology and evolution. Indeed, evolutionary robotics aims to apply the principles of selection, variation, and heredity to the design of robots (Doncieux et al. 2015). There are even myriad plant-inspired robots to examine the movement and light-harvesting properties of plants, as well as structural rigidity (as reviewed in Frazier et al. 2020). With ecomechanical modeling specifically, we gain the ability to manipulate or more physical factors experimentally, and to predict the impact on such ecological factors as distribution and community composition (Higham et al. 2021), providing a more holistic explanation for the diversity of life we see now, and which, existed in the past.

## Conclusions

Given its central role in bridging different facets of physical and natural sciences, we suggest that ecomechanics is the quintessential "discipline of disciplines" that can help us to truly advance on grand challenges, including those posed by a rapidly changing world. Here we have identified four different grand challenges which would be advanced significantly through this interdisciplinary approach. While the cross talk between the ecological and biomechanical communities is still rather limited, the significant impacts of ecology on the mechanical demands of organisms demands that we collaborate across the interfaces of these disciplines to ask the truly relevant questions relating to ecology, evolution, and studies of life in general.

## Funding

We thank the Society for Experimental Biology and the Society for Integrative and Comparative Biology for funding the symposium and its participants.

## Data availability

Data not Available.

## References

Alipanahi B, Hormozdiari F, Behsaz B, Cosentino J, McCaw ZR, Schorsch E, Sculley D, Dorfman EH, Foster PJ, Peng LH, et al. 2021. Large-scale machine-learning-based phenotyping significantly improves genomic discovery for optic nerve head morphology. Am J Hum Genet 108: 1217–30.

Anderson PSL, Crofts SB, Kim J-T, Chamorro LP. 2019. Taking a stab at quantifying the energetics of biological puncture. Integr Comp Biol 59: 1586–96.

Anderson PSL, Kawano SM. 2022. Different Traits at Different Rates: The Effects of Dynamic Strain Rate on Structural Traits in Biology. Integrative and Comparative Biology icac066, https://doi.org/10.1093/icb/icac066.

Astley HC, Jayne BC. 2007. Effects of perch diameter and incline on the kinematics, performance and modes of arboreal locomotion of corn snakes (*Elaphe guttata*). J Exp Biol 210: 3862–72.

Bahlman JW, Swartz SM, Riskin DK, Breuer KS. 2013. Glide performance and aerodynamics of non-equilibrium glides in northern flying squirrels (Glaucomys sabrinus). J Roy Sco Interface 10:20120794.

Barnett JR, Bonham VA. 2004. Cellulose microfibril angle in the cell wall of wood fibres. Biol Rev 79: 461–72.

Bauer U, Poppinga S, Müller UK. 2020. Mechanical ecology—taking biomechanics to the field. Integr Comp Biol 60: 820–8.

Bauer U, Poppinga S. 2022. New insights and opportunities from taking a biomechanical perspective on plant ecology. J Exp Bot 73: 1063–6.

Biewener AA. 1989. Scaling body support in mammals: limb posture and muscle mechanics. Science 245: 45–8.

Carrington E, Waite JH, Sarà G, Sebens KP. 2015. Mussels as a model system for integrative ecomechanics. Ann Rev Mar Sci 7: 443–69.

Carrington E. 2002. The ecomechanics of mussel attachment: from molecules to ecosystems. Integr Comp Biol 42: 846–52.

Chang JJ, Crail JD, Combes SA. 2016. Wind alters landing dynamics in bumblebees. J Exp Biol 219: 2819–22.

Chown SL, Gaston KJ, Robinson D. 2004. Macrophysiology: large-scale patterns in physiological traits and their ecological implications. Funct Ecol 18: 159–67.

Clemente CJ, Dick TJM, Wheatley R, Gaschk J, Nasir AFAA, Cameron SF, Wilson RS. 2019. Moving in complex environments: a biomechanical analysis of locomotion on inclined and narrow substrates. J Exp Biol 222: jeb189654.

Combes SA, Dudley R. 2009. Turbulence-driven instabilities limit insect flight performance. Proc Natl Acad Sci 106: 9105–8.

Costello JH, Strickler JR, Marrasé C, Trager G, Zeller R, Freise AJ. 1990. Grazing in a turbulent environment: behavioral response of a calanoid copepod, *Centropages hamatus*. Proc Natl Acad Sci 87: 1648–52.

Coutand C, Chevolot M, Lacointe A, Rowe N, Scotti I. 2010. Mechanosensing of stem bending and its interspecific variability in five neotropical rainforest species. Ann Bot 105: 341–7.

Crall JD, Chang JJ, Oppenheimer RL, Combes SA. 2017. Foraging in an unsteady world: bumblebee flight performance in field-realistic turbulence. Inter Focus 7: 20160086.

Crowell HL, King KC, Whelan JM, Harmel MV, Garcia G, Gonzales SG, Maier PH, Neldner H, Nhu T, Nolan JT. 2021. Thermal ecology and baseline energetic requirements of a large-bodied ectotherm suggest resilience to climate change. In press. Ecol Evol 1–13. DOI: 10.1002/ece3.7649.

Cryan PM, Gorresen PM, Hein CD, Schirmacher MR, Diehl RH, Huso MM, Hayman DTS, Fricker PD, Bonaccorso FJ, Johnson DH, Heist K, Dalton DC. 2014. Behavior of bats at wind turbines. Proc Natl Acad Sci 111: 15126–31.

Denny M, Gaylord B. 2010. Marine ecomechanics. Ann Rev Mar Sci 2: 89–114.

Denny M, Helmuth B. 2009. Confronting the physiological bottleneck: a challenge from ecomechanics. Integr Comp Biol 49: 197–201.

Denny M. 2016. Ecological mechanics: principles of life's physical interactions. Princeton (NJ): Princeton University Press. p. 530.

Denny MW. 1988. Biology and the mechanics of the wave-swept environment. Princeton (NJ): Princeton University Press. p. 344.

Domenici P, Seebacher F. 2020. The impacts of climate change on the biomechanics of animals. Conserv Physiol 8: coz102.

Doncieux S, Bredeche N, Mouret J-B, Eiben AE (Gusz). 2015. Evolutionary robotics: what, why, and where to. Front Robot AI 2: 4.

Dugauquier J, Godefroid M, M'Zoudi S, Terrana L, Todinanahary G, Eeckhaut I, Dubois P. 2021. Ecomechanics of black corals (Cnidaria: Anthozoa: Hexacorallia: Antipatharia): a comparative approach. Invertebr Biol 140: e12347.

Ecological morphology: integrative organismal biology. 1994. In: Wainwright PC, Reilly SM. editors. Chicago (IL): Chicago University Press. p. 376.

Ecology and biomechanics: a mechanical approach to the ecology of animals and plants. 2006. In: Herrel A, Speck T, Rowe NP. editors. Oxfordshire: Taylor and Francis Publishers. p. 350.

Ennos AR. 1997. Wind as an ecological factor. Tree 12: 108–11.

Fandel AD, Garrod A, Hoover AL, Wingfield JE, Lyubchich V, Secor DH, Hodge KB, Rice AN, Bailey H. 2020. Effects of intense storm events on dolphin occurrence and foraging behavior. Sci Rep 10: 19247.

Ferrario F, Beck MW, Storlazzi CD, Micheli F, Airoldi CCS, Airoldi L. 2014. The effectiveness of coral reefs for coastal hazard, risk reduction and adaptation. Nat Commun 5: 3794.

Finelli C. 2000. Velocity and concentration distributions in turbulent odor plumes in the presence of vegetation mimics: a flume study. Mar Ecol Prog Ser 207: 297–309.

Foster KL, Higham TE. 2012. How fore- and hindlimb function changes with incline and perch diameter in the green anole (*Anolis carolinensis*). J Exp Biol 215: 2288–300.

Foster KL, Selvitella AM. 2022. Alessandro Maria Selvitella, Kathleen Lois Foster, The Spring-Mass Model and Other Reductionist Models of Bipedal Locomotion on Inclines. Integrative and Comparative Biology icac047, https://doi.org/10.1093/icb/icac047.

Fournier M, Stokes A, Coutand C, Fourcaud T, Moulia B. 2006. Tree biomechanics and growth strategies in the context of forest functional ecology. In: Herrel T, Speck A, Rowe N. editors. Ecology and biomechanics: a mechanical approach to the ecology of animals and plants. Boca Raton (FL): CRC Press. p. 1–34.

Frazier PA, Jamone L, Althoefer K, Calvo P. 2020. Plant bioinspired ecological robotics. Front Robot AI 7: 79.

Frey DL, Gagnon P. 2015. Thermal and hydrodynamic environments mediate individual and aggregative feeding of a functionally important omnivore in reef communities. PLoS One 10: e0118583.

Garland T, Jr Bennett AF, Rezende EL. 2005. Phylogenetic approaches in comparative physiology. J Exp Biol 208: 3015–35.

Gaylord B, Barclay KM, Jellison BM, Jurgens LJ, Ninokawa AT, Rivest EB, Leighton LR. 2019. Ocean change within shoreline communities: from biomechanics to behaviour and beyond. Conserv Physiol 7: coz077.

Gaylord B, Denny MW, Koehl MAR. 2008. Flow forces on seaweeds: field evidence for roles of wave impingement and organism inertia. Biol Bull 215: 295–308.

Gerald GW, Mackey MJ, Claussen DL. 2008. Effects of temperature and perch diameter on arboreal locomotion in the snake *Elaphe guttata*. J Exp Zool A Ecol Gen Physiol 309A: 147–56.

Harley C. 2013. Linking ecomechanics and ecophysiology to interspecific interactions and community dynamics. Ann NY Acad Sci 1297: 73–82.

Harter TS, Damsgaard C, Regan MD. 2022. Linking environmental salinity to respiratory phenotypes and metabolic rate in fishes: a data mining and modelling approach. J Exp Biol 225: jeb243421.

Herrel A, Perrenoud M, Decamps T, Abdala V, Manzano A, Pouydebat E. 2013. The effect of substrate diameter and incline on locomotion in an arboreal frog. J Exp Biol 216: 3599–3605.

Higham TE, Clark RW, Collins CE, Whitford MD, Freymiller GA. 2017. Rattlesnakes are extremely fast and variable when striking at kangaroo rats in nature: three-dimensional high-speed kinematics at night. Sci Rep 7: 40412.

Higham TE, Ferry LA, Schmitz L, Irschick DJ, Starko S, Anderson PSL, Bergmann PJ, Jamniczky HA, Monteiro LR, Navon D, et al. 2021. Linking ecomechanical models and functional traits to understand phenotypic diversity. Trends Ecol Evol 36: 860–73.

Higham TE, Jayne BC. 2004. Locomotion of lizards on inclines and perches: hindlimb kinematics of an arboreal specialist and a terrestrial generalist. J Exp Biol 207: 233–48.

Higham TE, Rogers SM, Langerhans RB, Jamniczky HA, Lauder GV, Stewart WJ, Martin CH, Reznick DN. 2016. Speciation through the lens of biomechanics: locomotion, prey capture and reproductive isolation. Proc R Soc B Biol Sci 283: 20161294.

Higham TE, Russell AP, Niewiarowski PH, Wright A, Speck T. 2019. The ecomechanics of gecko adhesion: natural surface topography, evolution, and biomimetics. Integr Comp Biol 59: 148–67.

Higham TE, Schmitz L, Niklas KJ. 2022. The Evolution of Mechanical Properties of Conifer and Angiosperm Woods. Integrative and Comparative Biology icac103. https://doi.org/10.1093/icb/icac103.

Higham TE, Stewart WJ, Wainwright PC. 2015. Turbulence, temperature, and turbidity: the ecomechanics of predator–prey interactions in fishes. Integr Comp Biol 55: 6–20.

Hwang J-S, Costello JH, Strickler JR. 2014. Copepod grazing in turbulent flow: elevated foraging behavior and habituation of escape responses. J Plankton Res 16: 421–31.

Irschick DJ, Jayne BC. 1999. A field study of the effects of incline on the escape locomotion of a bipedal lizard, *Callisaurus draconoides*. Physiol Biochem Zool 72: 44–56.

Janot KG, Unda F, Mansfield SD, Martone PT. 2022. Evolutionary Patterns in Chemical Composition and Biomechanics of Articulated Coralline Algae. Integrative and Comparative Biology, icac021, https://doi.org/10.1093/icb/icac021.

Jayne BC, Ellis RV. 1998. How inclines affect the escape behaviour of a dune-dwelling lizard, *Uma scoparia*. Anim Behav 55: 1115–30.

Jayne BC, Irschick DJ. 1999. Effects of incline and speed on the three-dimensional hindlimb kinematics of a generalized iguanian lizard (*Dipsosaurus dorsalis*). J Exp Biol 202: 143–59.

Johansen JL, Akanyeti O, Liao JC. 2020. Oxygen consumption of drift-feeding rainbow trout: the energetic tradeoff between locomotion and feeding in flow. J Exp Biol 223: jeb220962.

Klittich MR, Wilson MC, Bernard C, Rodrigo RM, Keith AJ, Niewiarowski PH, Dhinojwala A. 2017. Influence of substrate modulus on gecko adhesion. Sci Rep 7: 43647.

Koehl M.A.R. 2022. Ecological biomechanics of marine macrophytes. J Exp Bot. 73: 1104–21.

Koehl MA. 1999. Ecological biomechanics of benthic organisms: life history, mechanical design and temporal patterns of mechanical stress. J Exp Biol 202: 3469–76.

Koehl MAR, Wainwright SA. 1977. Mechanical adaptations of a giant kelp. Limnol Oceanogr 22: 1067–71.

Koehl MAR. 1996. When does morphology matter? Ann Rev 27: 501–42.

Krishnan A, Socha JJ, Vlachos PP, Barba LA. 2014. Lift and wakes of flying snakes. Phys Fluids 26: 031901.

Lailvaux SP, Mishra A, Pun P, Kabir MWU, Wilson RS, Herrel A, Hoque MT. 2022. Machine learning accurately predicts

the multivariate performance phenotype from morphology in lizards. PLoS One 17: e0261613.
Lan Y, Huang N, Fu Y, Liu K, Zhang H, Li Y, Yang S. 2022. Morphology-Based Deep Learning Approach for Predicting Osteogenic Differentiation. Frontiers Bioeng Biotechnology 9:802794.
Lauder GV. 2022. Robotics as a Comparative Method in Ecology and Evolutionary Biology. Integrative and Comparative Biology, icac016, https://doi.org/10.1093/icb/icac016.
Li Y, Nowak CM, Pham U, Nguyen K, Bleris L. 2021. Cell morphology-based machine learning models for human cell state classification. NPJ Syst Biol Appl 7: 23.
Lieber L, Langrock R, Nimmo-Smith WAM. 2021. A bird's-eye view on turbulence: seabird foraging associations with evolving surface flow features. Proc R Soc B Biol Sci 288: 20210592.
Losos JB, Sinervo B. 1989. The effects of morphology and perch diameter on sprint performance of *Anolis* lizards. J Exp Biol 145: 23–30.
Losos JB. 1990. The evolution of form and function: morphology and locomotor performance in west Indian Anolis lizards. Evolution 44: 1189–203
Marshall KL, Chadha M, deSouza LA, Sterbing-D'Angelo SJ, Moss CF, Lumpkin EA. 2015. Somatosensory substrates of flight control in bats. Cell Rep 11: 851–8.
Martone P. 2007. Kelp versus coralline: cellular basis for mechanical strength in the wave-swept seaweed *Calliarthron* (Corallinaceae, Rhodophyta). J Phycol 43: 882–91.
Martone PT, Boller M, Burgert I, Dumais J, Edwards J, Mach K, Rowe N, Rueggeberg M, Seidel R, Speck T. 2010. Mechanics without muscle: biomechanical inspiration from the plant world. Integr Comp Biol 50: 888–907.
Mendes S, Turrell W, Lütkebohle T, Thompson P. 2002. Influence of the tidal cycle and a tidal intrusion front on the spatio-temporal distribution of coastal bottlenose dolphins. Mar Ecol Prog Ser 239: 221–9.
Newcomb LA, Cannistra AF, Carrington E. 2022. Divergent Effects of Ocean Warming on Byssal Attachment in Two Congener Mussel Species. Integrative and Comparative Biology icac111, https://doi.org/10.1093/icb/icac111.
Niklas KJ. 1992. Plant biomechanics: an engineering approach to plant form and function. Chicago (IL): University of Chicago Press.
Niklas KJ. Spatz H. 2010. Worldwide correlations of mechanical properties and green wood density. Am J Bot 97(10):1587–94.
Nikora V. 2010. Hydrodynamics of aquatic ecosystems: an interface between ecology, biomechanics and environmental fluid mechanics. River Res Appl 26: 367–84.
Nourani E, Bohrer G, Becciu P, Bierregaard RO, Duriez O, Figuerola J, Gangoso L, Giokas S, Higuchi H, Kassara C, et al.. 2021. The interplay of wind and uplift facilitates over-water flight in facultative soaring birds. Proc R Soc B Biol Sci 288: 20211603.
Nudds RL, Ozolina K, Fenkes M, Wearing OH, Shiels HA. 2020. Extreme temperature, combined with hypoxia, affects swimming performance in brown trout (*Salmo trutta*). Conserv Physiol 8: coz108.
O'Donnell MJ, MN George, Carrington E. 2013. Mussel byssus attachment weakened by ocean acidification. Nat Clim Change 3: 587–90.
Pennycuick CJ. 1972. Animal flight. Victoria Embankment: Edward Arnold Ltd. Publisher. p. 68.
Phillip JM, Han K-S, Chen W-C, Wirtz D, Wu P-H. 2021. A robust unsupervised machine-learning method to quantify the morphological heterogeneity of cells and nuclei. Nat Protoc 16: 754–74.
Podos J, Hendry AP. 2006. The biomechanics of ecological speciation. In: Herrel A, Speck T, Rowe NP. editors. Ecology and biomechanics: a mechanical approach to the ecology of animals and plants. Oxfordshire: Taylor and Francis Publishers. p. 350.
Ravi S, Crall JD, Fisher A, Combes SA. 2013. Rolling with the flow: bumblebees flying in unsteady wakes. J Exp Biol 216: 4299–309.
Rogers JS, Monismith SG, Koweek DA, Torres WI, Dunbar RB. 2016. Thermodynamics and hydrodynamics in an atoll reef system and their influence on coral cover. Limnol Oceanogr 61: 2191–206.
Rowe N., Speck T. 2005. Plant growth forms: an ecological and evolutionary perspective. New Phytol 166: 61–72.
Safi K, Kranstauber B, Weinzierl R, Griffin L, Rees EC, Cabot D, Cruz S, Proano C, Takekawa JY, Newman SH. et al. 2013. Flying with the wind: scale dependency of speed and direction movements in modelling wind dupport in avia flight. Mov Ecol 1:4.
Santana SE, Grossnickle DM, Sadier A, Patterson E, Sears KE. 2022. Bat Dentitions: A Model System for Studies at the Interface of Development. Biomechanics, and Evolution, Integrative and Comparative Biology icac042, https://doi.org/10.1093/icb/icac042.
Schmitt D. 1994. Forelimb mechanics as a function of substrate type during quadrupedalism in two anthropoid primates. J Hum Evol 26: 441–57.
Schubert PJ, Dorkenwald S, Januszewski M, Jain V, Kornfeld J. 2019. Learning cellular morphology with neural networks. Nat Commun 10: 2736.
Surapaneni VA, Schindler M, Ziege R, de Faria LC, Wölfer J, Bidan CM, Mollen FH, Amini S, Hanna S, Dean MN. 2022. Groovy and Gnarly: Surface Wrinkles as a Multifunctional Motif for Terrestrial and Marine Environments. Integrative and Comparative Biology icac079, https://doi.org/10.1093/icb/icac079.
Titocci J, Bon M, Fink P. 2022. Morpho-functional traits reveal differences in size fractionated phytoplankton communities but do not significantly affect zooplankton grazing. Microorganisms 10: 182.
Tunnicliffe. V. 1982. The effects of wave-induced flow on a coral reef. J Exp Mar Biol Ecol 64: 1–10.
Valentina Di Santo. 2022. EcoPhysioMechanics: Integrating Energetics and Biomechanics to Understand Fish Locomotion under Climate Change. Integrative and Comparative Biology icac095, https://doi.org/10.1093/icb/icac095.
Vettori D, Nikora V. 2019. Flow-seaweed interactions of *Saccharina latissima* at a blade scale: turbulence, drag force, and blade dynamics. Aquat Sci 81: 61.
Vilensky JA, Moore AM, Libii JN. 1994. Squirrel monkey locomotion on an inclined treadmill: implications for the evolution of gaits. J Hum Evol 26: 375–86.
Wainwright PC. 1991. Ecomorphology: experimental functional anatomy for ecological problems. Am Zool 31: 680–93.
Wainwright SM. 1976. Mechanical design in organisms. San Francisco (CA) John Wiley & Sons, Inc.p. 423.

Webb PW. 2002. Control of posture, depth, and swimming trajectories of fishes. Integr Comp Biol 42: 94–101.

Weihs D. 2002. Stability versus maneuverability in aquatic locomotion. Integr Comp Biol 42: 127–34.

Williams BM, Borron D, Liu R, Zhao Y, Zhang J, Lim J, Ma B, Romano V, Qi H, Zheng Y. et al.. 2020. An artificial intelligence-based deep learning algorithm for the diagnosis of diabetic neuropathy using corneal confocal microscopy: a development and validation study. Diabetologia 63: 419–30.

Wolf Zane, Lauder GV. 2022. A Fish-Like Soft-Robotic Model Generates a Diversity of Swimming Patterns. Integrative and Comparative Biology icac039, https://doi.org/10.1093/icb/icac039,

Yanagisawa H, Koshimura S, Miyagi T, Imamura F. 2010. Tsunami damage reduction performance of a mangrove forest in Banda Aceh, Indonesia inferred from field data and a numerical model. J Geophys Res Oceans 115: 1–11. doi:10.1029/2009JC005587.

Zaaf A, Van Damme R, Herrel A, Aerts P. 2001. Spatio-temporal gait characteristics of level and vertical locomotion in a ground-dwelling and a climbing gecko. J Exp Biol 204: 1233–46.