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Review

Linking ecomechanical models and functional traits to understand phenotypic diversity

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Physical principles and laws determine the set of possible organismal phenotypes. Constraints arising from development, the environment, and evolutionary history then yield workable, integrated phenotypes. We propose a theoretical and practical framework that considers the role of changing environments. This 'ecomechanical approach' integrates functional organismal traits with the ecological variables. This approach informs our ability to predict species shifts in survival and distribution and provides critical insights into phenotypic diversity. We outline how to use the ecomechanical paradigm using drag-induced bending in trees as an example. Our approach can be incorporated into existing research and help build interdisciplinary bridges. Finally, we identify key factors needed for mass data collection, analysis, and the dissemination of models relevant to this framework.

Highlights

All organisms must comply with physical laws, which place rigid or hard constraints on survival and reproduction. Ecomechanics is the expression of that interplay, and assumes a central role when considering organismal development, ecology, and evolution.

How organisms will respond to changes in the environment, such as human-mediated climate change, will depend strongly on ecomechanics.

Functional traits are commonly used to investigate the consequences of ecological variation. Ecomechanical models that incorporate functional traits and environmental variables are key to deciphering the rules of life and expand upon functional trait studies.

The use of the ecomechanical framework is illustrated using multiple examples (e.g., wind-induced bending mechanics in trees and gecko adhesion in the real world). We emphasize safety factors as a key metric when assessing the evolution of form and performance. Biologists can apply our framework to many other systems.

We offer suggestions for constructing and tailoring the data pipeline for future ecomechanical models to enhance their availability and utility for various disciplines.

Using the ecomechanical approach to understand the rules of life

All forms of life must comply with physical laws, resulting in a series of 'universal' or 'hard' **constraints** (see Glossary) [1,2]. Although these constraints limit the possible phenotypes, 'local' or 'soft' constraints emerge as a consequence of ecological, developmental, and evolutionary processes that determine which phenotypes are adaptive. Thus, any realized phenotype is the result of: (i) physical principles and processes; (ii) the context in which the organism performs the manifold tasks required for growth, survival, and reproduction (i.e., organism–environment interactions); and (iii) its evolutionary history [1,3].

Function is a key concept at the intersection of developmental biology, ecology, and evolution [4]. Function interacts with ontogenetic and reproductive changes, and thus profoundly affects survival and fitness [5,6]. It also affects community and ecosystem-level processes, as well as macroevolutionary patterns of diversity including biogeography, diversification rates, and speciation [7]. Therefore, the concept of function bridges all levels of biological organization. Indeed, there is growing momentum to connect **functional traits (FTs)** and mechanics of organisms to their environments (i.e., **ecomorphology** and **ecomechanics**) in order to predict survival, reproduction, and community structure [8–13].

We aim to reinvigorate an integrative approach that incorporates physics as the basis for organismal FTs [14]. FTs are morphological, phenological, and physiological characteristics affecting an individual's fitness [15]. They are often measurements of convenience (i.e., defined *a priori* based on ease of collection), but one way to formalize the function of a trait is to use **biophysical models** to identify relevant traits and quantify how these traits contribute to overall performance. These models can reveal integrated or compound FTs that provide greater insight

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than any single FT taken in isolation [16]. However, understanding the limits to organismal survival, which necessarily includes abiotic as well as biotic factors, requires a mechanistic model that includes such factors [17]. This differs from many approaches that are solely reliant on intrinsic features of an individual (Figure 1), such as the Newtonian mechanics governing animal motion. Our framework focuses on the former [i.e., models that include individual traits and environmental variables (EVs) (Figure 1)], which we term **ecomechanical models**. Key EVs in these models include fluid speed (wind or water), temperature, and habitat structure, all of which have strong effects on organismal form and function.

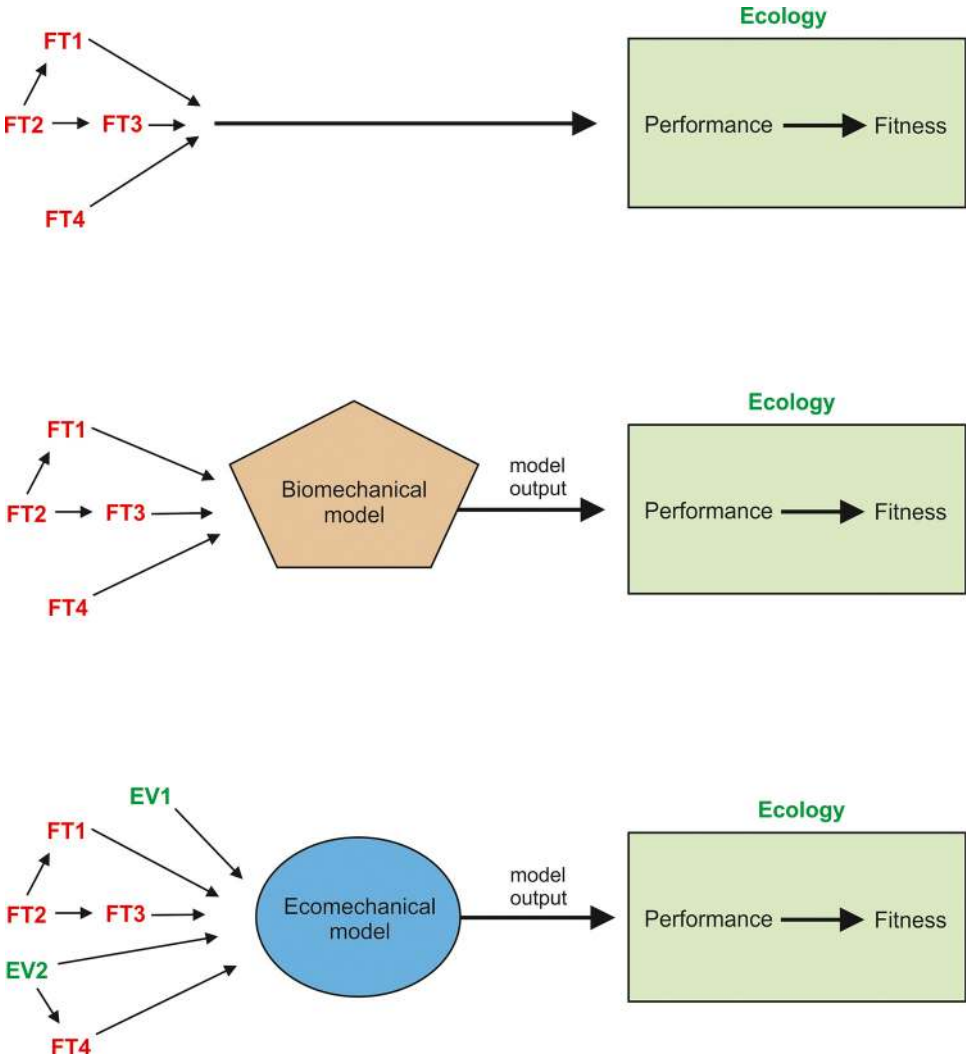

Figure 1. Three ways in which to use functional traits (FTs) in biology. The top example indicates that FTs, and interactions among them, can be used to estimate performance (and ultimately fitness) within a given ecological context (green box). The middle example incorporates a biomechanical model that includes FTs as inputs. The output of the biomechanical model is used to predict performance in a given ecological context. The bottom example, which we are proposing as most useful in the study of organisms, incorporates an ecomechanical model. In this case, the inputs are both FTs and environmental variables (EVs), and the output of the model is again used to predict performance in an ecological context. Not only can FTs interact with one another, but EVs can also alter the properties of FTs (see text for details). This integrative approach is ideal for understanding ecological performance.

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The general framework of our approach is outlined in Figure 2. A trait, or series of interacting traits, will, based upon one or more biophysical laws, dictate the **ecological performance** of an organism. The trait-to-performance link can occur rapidly, in 'real' time, ranging from nanoseconds to minutes. However, this framework extends to changes in environmental conditions (represented by environments 1, 2, and 3 in Figure 2) over short (e.g., seasons) or long periods of time (e.g., millions of years). Additionally, our framework accounts for developmental time, which can change the way in which the organism interacts with and within its habitat. This framework, therefore, builds upon the form–function–fitness paradigm by considering ecomechanical performance over relevant timescales. Later, we highlight the novelty of ecomechanical models, and expand on these timescales: rapid, ecological, evolutionary, and developmental. We illustrate the utility of our framework using **bending mechanics** as an example, since it is broadly applicable across nearly all organisms. This example illustrates the critical role of stochastic EVs and FTs in ecomechanical models.

Ecomechanical models and organismal safety factor

Organismal performance relies upon the coordinated response of multiple FTs in a given ecological context. Importantly, an ecomechanical framework permits the prediction of survival in the face of changing conditions using a quantitative framework [18]. A prime example, which we highlight later in our case study, is maximum breaking stress in plants (Box 1, and Figure 3). This model can be applied to any cantilevered organism, such as coral (Figure 3), and includes morphological traits (diameter, length, etc.) and characteristics of the ambient fluid (air or water), such as velocity and density.

Key to understanding survival is the determination of an organism's **safety factor**, both within the bounds of current conditions and predicted future conditions. Safety factors represent a margin of protection against failure; for example, a safety factor of 2 indicates the maximum load that can be withstood without material failure is twice the load actually experienced by the organism. Higher safety factors are, therefore, beneficial and may be more common in systems with unpredictable loading regimes; however, they can be costly to maintain, as doing so often requires additional investment in material. These periodic moments of excessive **force** have been considered potential drivers of evolution. For example, amphisbaenians and skinks that burrow may occasionally encounter sharp-edged objects that result in very high local stress, requiring a reinforced skull to avoid failure [19].

Ecomechanical models provide an opportunity to explore safety factors under current and predicted environmental conditions. A classic example is the prediction of dislodgement of mussels by wave-induced forces using a combination of time-varying hydrodynamic forces and mussel attachment strength [17]. Knowing the attachment ability of mussels and the magnitude of wave forces then provides a critical tenacity that must be achieved to remain attached to the substrate. Models of future changes in wave action can then be incorporated to determine the biomechanical robustness of the system.

Bending and breaking: organisms in fluids as model systems

There are two ways in which a fluid (water, air, or both; Figure 3) can exert force on an organism: pressure and friction. In turn, this force can reach sufficient magnitude to cause an organism attached to a substrate (e.g., sponges and trees) to bend or, as highlighted previously, be dislodged from the substrate. A bending moment is the product of a distance or length (e.g., tree trunk or branch), and an external force. On land, two predominant external mechanical

Glossary

Bending mechanics: the behavior of a slender structural element subjected to an external load applied perpendicularly to it longitudinal axis.
Biomechanics: the study of the mechanical design of organisms.
Biophysical models: simulations of biological systems using mathematical formalizations of the physical properties of that system.
Constraint: anything, internal or external to an organism, that limits the production of new phenotypes.
Drag: the force exerted by a moving fluid on an organism.
Ecological performance: the ability to execute an ecologically-relevant behavior.
Ecomechanics: the study of the mechanisms underlying the interactions of organisms with their biotic and abiotic environment.
Ecomechanical models: models that include individual traits and environmental variables (EVs).
Ecomorphology: the study of the relationship between the morphology of an organism and its environment.
Force: mass multiplied by acceleration.
Functional traits (FTs): morphological, phenological, and physiological traits affecting an individual's fitness.
Isometry: the maintenance of shape with changes in size.
Ontogenetic change: changes attending the growth and development of an organism that can alter an organism's interactions with its environment and how the environment interacts with the organism.
Reynolds number (Re): a dimensionless number that describes the quotient of inertial and viscous forces.
Safety factor: in biology, refers to the dimensionless quotient of a structure's ability to resist mechanical stresses, and the maximum stress that it is likely to experience over its lifetime in its environment.

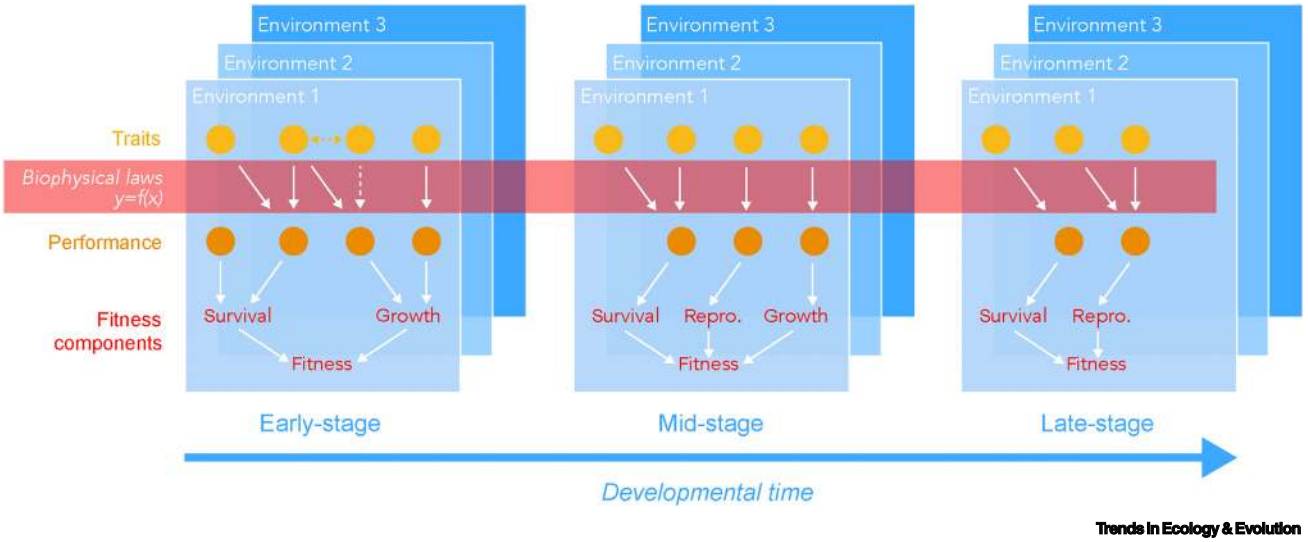

Figure 2. Framework for linking functional traits (FTs) to the environment and evolution. The relationships between FTs and fitness depend strongly on the environment (shown as Environment 1, 2, and 3 at each developmental stage) and developmental stage of the organism. In the case of development, it might be that the organism interacts differently with a similar environment as it grows, or the environment itself might change as an animal grows (e.g., habitat shifts). Traits not only combine, in some cases, to define a specific level of performance, but traits can also act indirectly through another trait (shown as broken yellow and white lines on left panel).

forces are gravity and **drag**. The acceleration of gravity is a constant force that organisms respond to and accommodate as they grow in size. By contrast, the magnitude of drag changes with flow speed (Box 1). In addition to the fact that organismal diversity has likely been shaped significantly by fluid forces, fluid (air and water) speeds are commonly projected to change as a consequence of climate change [20], leading to altered hydrodynamic and aerodynamic forces.

Be it a bone or a branch, bending is ubiquitous among plants and animals [21,22]. Bending can be advantageous, as in elastic energy storage mechanisms and in drag reduction, or it can be detrimental, resulting in breakage. The observed bending (or breakage) is defined by functional attributes, many of which are provided in online databases. For plants, resisting bending, or at least failure, is important to maintain normal loads (e.g., the weight of a leaf lamina extending from a petiole [23]). Excess force, as might occur in variable environments, presents a situation that could result in breakage (safety factor <1), such as drag-induced bending moments due to an extreme wind event [24]. That said, being able to deflect energy is also critical for some plants, leading to a reduction in drag by orienting the bulk of the structure parallel to the direction of the fluid (Figure 3). These examples are dynamic, which means that a model explaining the role of the FT and the range of forces being experienced are necessary.

Community ecology and biomechanics

In 2010, Vellend proposed that all community level processes can be classified into four key categories: dispersal, selection, drift, and speciation [25]. With the exception of drift, each of the remaining processes is strongly tied to biophysics and organismal function. Thus, our ecomechanical framework can be applied to almost all community-level processes. Dispersal may be broadly defined as the movement of individuals through space either by passive or active transport (e.g., the wind dispersal of seeds and fruits, or the flight of insects and birds). The laws of diffusion, for example, define dispersal–distance curves [26], in which propagule concentration is highest near the source [26,27]. Many organisms have evolved dispersal mechanisms that take advantage of fluid dynamics and moving air or water currents. Examples include the timing of

spawning events in intertidal mussels (*Mytilus*) [26] and corals (Cnidaria) [27], as well as the elaborate winged fruits of maples (*Acer palmatum*) [28], and the ovulate scales of pinecones (*Pinus*) creating airflow patterns directing pollen toward receptive surfaces [29].

Migration is another important (passive or active) component of dispersal. In the ocean, long-distance dispersal is commonly linked to buoyancy [30,31]. In habitat-forming brown algae (e.g., kelps), buoyancy is a convergent trait shared by multiple lineages [32,33]. Buoyant algae can form large rafts known to travel across reefs [34] or even across oceans [35]. In some corals, and some terrestrial plants, asexual reproduction occurs through fragmentation and subsequent vegetative growth of the fragments that are transported elsewhere [36], highlighting the role of mechanics.

Environmental conditions affect the composition of communities by filtering, or limiting the survival and presence of, organisms adapted to their local environments [37,38]. This selective process has two components, abiotic gradients (e.g., temperature, precipitation, and light) [39–42] and biotic factors (e.g., interspecific competition and prey–predator interactions) [43,44]. Ecomechanical models connect abiotic and biotic factors and provide the ability to predict community composition in the present, past, and future.

Box 1. The evolution of drag-induced bending mechanics and safety factors in trees

The use of ecomechanical models is illustrated by assessing the ability of a tree to resist the bending moments resulting from the drag forces induced by oncoming wind (Figure I). For simplicity, the geometry of a tree's canopy is modeled as a vertical prolate spheroid with a projected sail area, S, equal to $\pi ab/4$, where a and b are canopy height and canopy width, respectively (Figure 3A). The maximum bending stress, σ_{max}, at the base of a trunk is given by the formula

$$\sigma_{max} = 4M/\pi r^3, \quad [I]$$

where M is the bending moment and r is the radius of the trunk at its base. The bending moment is equal to the product of the drag force, F_d, exerted by the oncoming wind and the effective height of the canopy, H_e, for example,

$$M = F_d H_e, \quad [II]$$

and the drag force is given by the formula

$$F_d = 0.5\rho S U^2 C_d, \quad [III]$$

where ρ is the density of air, U is wind speed, and C_d is the drag coefficient. Thus, substituting Equations [II] and [III] into [I] yields the formula

$$\sigma_{max} = \rho a b U^2 C_d H_e/2r^3. \quad [IV]$$

The safety factor, SF, against wind-throw equals the quotient of the critical breaking stress, σ_{crit} (i.e., the maximum stress that the wood at the base of the tree can sustain before breaking) and the maximum bending stress at the base of the trunk. Thus,

$$SF = \sigma_{crit}/\sigma_{max} = 2r^3\sigma_{crit}/(\rho a b U^2 C_d H_e). \quad [V]$$

Three of the parameters in Equation [V] can be asserted *a priori* (i.e., the density of air at 15°C is 1.225 kg/m^3, the drag coefficient of a prolate spheroid subjected to turbulent airflow is 0.20 (unitless), and the average critical breaking stress of greenwood across a broad spectrum of eudicot trees is 9.7 GN/m^2). Specifying the remaining variables in Equation [V] clearly depends on the dimensions of the tree and the ambient wind speed. Our estimates of safety factor may be considered exceptionally high because they assume that the trunk has a uniform radius, that the wood has no flaws, and that the wind speeds are steady. They also neglect uprooting due to root–crown oscillations, and ignore the additional loading resulting from rain and flying debris. Nevertheless, it provides an upper boundary condition and reveals which biotic and abiotic factors influence windthrow and safety factors.

In addition to this ecomechanical model (drag-induced bending in trees), there are numerous models that could be leveraged to explore developmental, ecological and/or evolutionary questions. For many of the existing models, trait inputs are available in online databases, as are historical and current environmental variables (EVs). These models can be used to define which functional traits (FTs) should be measured moving forward, along with the relevant ecological variables. Examples include gecko adhesion (Box 2), running on water in lizards, bite force in mammals and other groups, and aerodynamics of flight in birds and bats (Figure S1 in the supplemental information online).

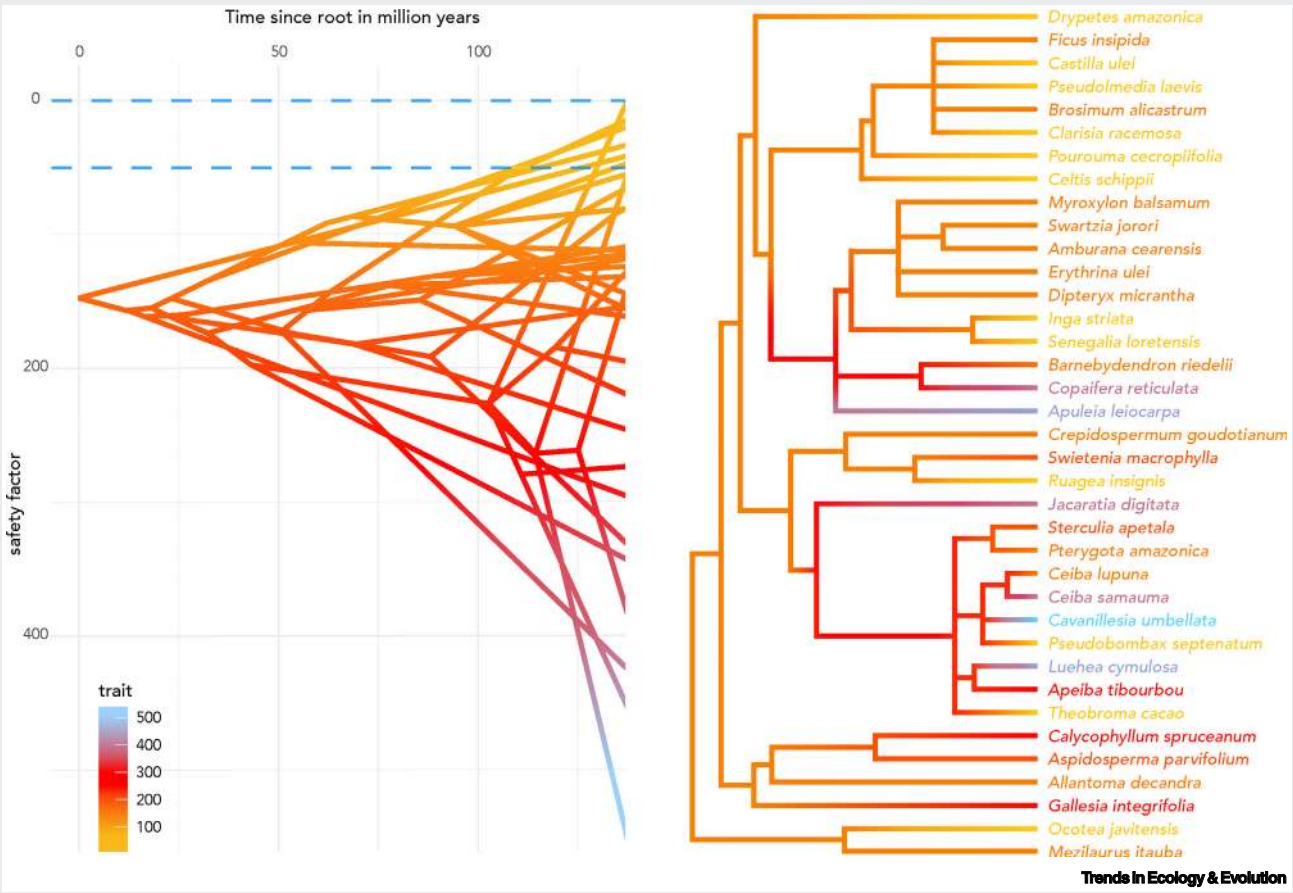

Figure I. The evolution of safety factor among 37 extant tree species from Peru [101], illustrated through an evolutionary traitgram on the left and a mapping of ancestral states on the right. We pruned a time-calibrated molecular phylogeny for angiosperms [102] to match our data, and visualized the estimated safety factors through functions in the phytools [103] and ggtree [104] packages for R. The evolutionary traitgram is a projection of a phylogeny calibrated to time (x-axis) in a space defined by safety factor (y-axis). Based on data on living species alone, the traitgram suggests an increase in maximum safety factor over the last 100 million years. A safety factor of 0 (top blue broken line) is the point at which a tree is considered susceptible to damage, and only very few species have safety factors less than 50 (lower broken line). Most species appear to be overbuilt. The mapping of ancestral states underscores this pattern and suggests that the traits underlying large safety factors (>400) evolved several times independently.

Ecomechanics through the lens of time

Rapid organismal-level events

The expression of a FT, which is important for ecomechanical models, is often rate-dependent. Thus, considering how FTs respond to varying loading rates will be of prime importance when predicting how organisms function in their environment. For example, force and energy are linked to prey capture and feeding through their transfer from the predator to its prey via an attack [45,46]. However, the time frame over which force (or energy) is transferred to a target differs widely, from chewing in mammals [46] and crushing in coconut crab claws (*Birgus latro*) [47] to high-speed strikes in snakes (*Crotalus sp.*) [48], aquatic bladderworts (*Utricularia sp.*) [49], and mantis shrimp (*Odontodactylus scyllarus*) [45]. Identifying the rate of force–energy transfer between predators and prey is essential to evaluating traits such as bite force or strike energy because materials, especially biological materials, respond differently when loaded at different rates [50–53].

Box 2. Real world gecko adhesion as a future ecomechanical model

Dry adhesion, an attachment mechanism found in a variety of invertebrates and squamate reptiles, has a rich history in engineering and biological sciences [93]. Despite the widespread appreciation of the adhesive apparatus in geckos (Figure II), few attempts have been made to incorporate ecological aspects, such as humidity and substrate roughness, with a few exceptions [94,95]. However, these factors are likely determinants of both the origin, evolution, and function of the system [96]. Several models have been used to describe adhesion, especially in geckos. The Johnson, Kendall, Roberts (JKR) model describes the force F required to pull an elastic sphere, with a radius R, from a flat surface [97]. Predicted adhesion is then calculated by:

$$F = \left(\frac{3}{2}\right)\pi R\gamma, \quad [VI]$$

where γ is the adhesion energy between the sphere and the surface. Expanding on this, Arzt *et al.* utilized the JKR model to examine the role of setal density in adhesion from insects to geckos [98]. They note that adhesion force is relative to a linear dimension of the contact. Thus, dividing the contact area into a number of n subcontacts (in this case, setae), each with a radius of $R/\sqrt{n}$ (reflecting self-similar scaling), adhesion increases to:

$$F' = \sqrt{n} \cdot F \quad [VII]$$

As noted by [99], the force of adhesion (F_C) can be largely explained in both natural and synthetic systems through the following equation in which G_C is defined as a measure of surface energy as defined by the material to which adhesion occurs (see [99] for more details), A is the area of the adhering pad, and C is system compliance. In an analysis across 14 orders of magnitude, [99] showed that stiffer materials produce more powerful adhesion.

$$F_C = \sqrt{G_C} \cdot \sqrt{\frac{A}{C}} \quad [VIII]$$

Natural surface topography will alter the A in the previous equation, with rough surfaces reducing A, thereby reducing F_c. For example, on rough sandstone surfaces, only 1.1–3.6% of the surface in the uppermost 30 μm is available for the establishment of the adhesive bond [100]. By contrast, almost 100% of this same region is available on artificially smooth surfaces. As a validation of this reduction in force, geckos from the genus *Phelsuma* exhibit a reduction in adhesion with increasing roughness (Figure II). Future work could incorporate these basic models in tests of adhesion across spatiotemporal gradients. This ecomechanical approach will be critical when trying to understand the evolution of adhesion.

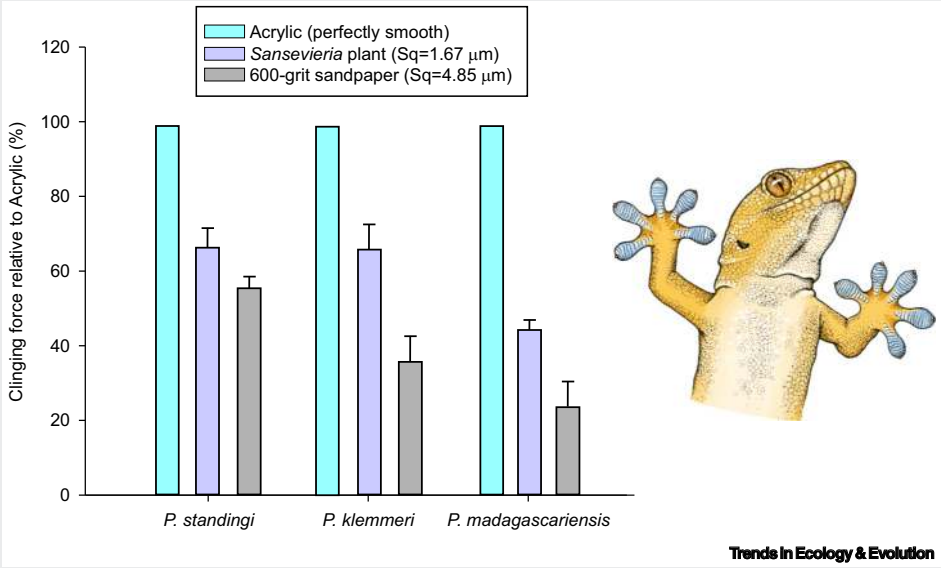

Figure II. Gecko adhesion on different surfaces. Presented here is clinging performance for three species of day geckos (genus *Phelsuma*) on surfaces varying in roughness. Shown are data for Standing's day gecko (*P. standingi*), the yellow-headed day gecko (*P. klemmeri*), and the Madagascar day gecko (*P. madagascariensis*). *Sq* represents area roughness. Clinging force measurements are from [94].

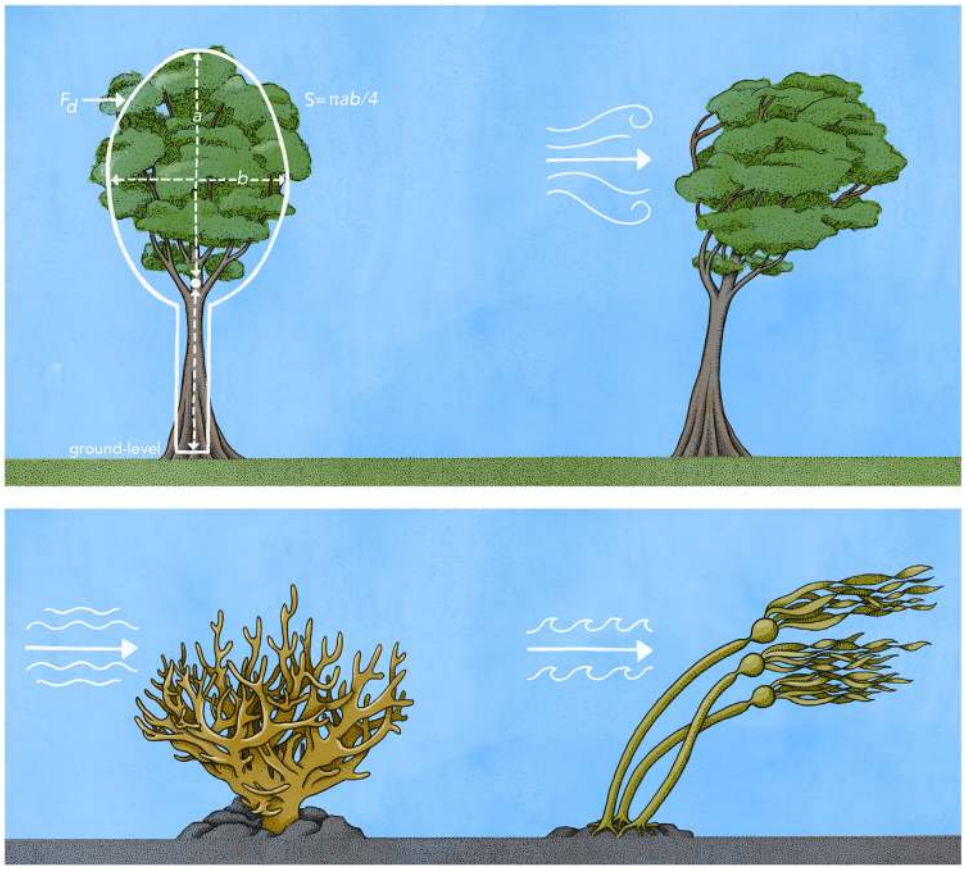

Figure 3. The interaction between fluid flow (air or water) and organisms. Trees will bend as wind speeds increase (upper panel), coral will resist bending (lower left), and bull kelp will bend and align with the direction of flow in water (lower right). Our model is superimposed on the tree in the upper left, where F_d is the drag force, S is the area of the canopy, a is the height of the crown, and b is the width of the crown.

Generally, when strain rates increase, biological materials become stiffer [50,54] as a consequence of their viscoelasticity. Thus, a material that undergoes deformation under a static load will deform much less under the same force applied at higher speeds. The consequences of strain rate on force–energy transfer have been explored in high-speed puncture tests where the volume of deformed material is inversely proportional to the strain rate [55], and higher speeds allow for greater puncture depth before the macroscopic deformation of test materials [56]. From a biological perspective, it is less clear how the bite force of an animal measured under static conditions might change with different jaw closing speeds. It is certainly the case that animals will close their jaws at different speeds given varying external conditions affecting the feeding interaction. Jaw-opening in fish is another example of rate-dependent function, as it is fundamentally different when performed at different speeds. However, only sudden, high-speed gape opening and cavity expansion leads to suction production, which is essential for prey capture in many vertebrates [57] and even in some plants [58]. These examples illustrate the need to properly parameterize ecomechanical models with realistic EVs and FT values.

The environment in which an organism lives often changes through time (Figure 2), which causes it to continually experience varying rates of applied forces. Examples of this include varying wind conditions at the edge of a forest and varying water flows in an intertidal zone. How FTs respond

to varying loading rates will therefore impact responses to global change [59]. The environment (e.g., wind speed) not only affects how a FT will contribute to performance, but also potentially alters the properties of the FT itself (Figure 1). For example, higher wind speeds will increase drag forces on a bending tree, but may also increase the stiffness of the tree through rate-dependent material properties discussed previously.

The response of an organism to changes in the environment can lead to performance thresholds being crossed, such that an organism shifts to a different micro-environment where performance is enhanced. For example, the rate of fluid movement affects the interplay between inertial and viscous forces [designated by the **Reynolds number (Re)**]. Faster speeds can allow small organisms to transition to higher Re regimes, allowing them to overcome viscous forces in a new microenvironment [60,61].

Development/ontogeny (individual-level timescale)

As noted, organism–environment interactions are constantly in flux. This not only arises from a variable environment, but also a variable organism (i.e., organisms experience their environment differently as they develop, and most organismal traits depend on size). Organism–environment interactions should be considered relative to directionality: both the effect of the environment on the organism and the capacity of the organism to perform in the environment may be altered in response to **ontogenetic change**. Ecomechanical models provide the framework for investigating how developmental changes will influence performance in a changing environment.

Size influences almost every aspect of an organism's biology, including biomechanical relationships (e.g., [62]). As such, changes in size over time will affect organism–environment interactions. In an aquatic environment, Re, as discussed previously, is not only influenced by speed, but also size. Therefore, escaping the viscous regime can be accomplished by increasing swimming velocity and/or by increasing size. In fact, it appears that many fish invest in quick growth to avoid problems associated with viscosity, rather than adapt to the viscous flow regime [63]. This example highlights just one way in which development can play a critical role in determining the relationships between **biomechanics**, behavior, and responses to changing ecological conditions.

Maintaining geometric similarity (similar shape) is referred to as **isometry**, whereas the change in one or more aspects of shape relative to body size indicates allometry. Isometric growth can have negative consequences, which will ultimately place constraints on the biomechanics of an organism. A common example is stress on support elements in a terrestrial environment [64]. The forces applied to skeletal elements are directly proportional to body mass. However, cross-sectional area of the element increases as the 2/3 power of body mass. This scaling relationship increases the risk of mechanical failure in larger organisms, although mammals circumvent this issue by larger species exhibiting a more upright posture (increased effective mechanical advantage) [64]. Ecologically-relevant situations, such as food consumption, pregnancy, or carrying young, will exacerbate this problem, potentially reducing the safety factor [65].

Many organismal structures exhibit changes in mechanical properties throughout development [66,67]. A common driver of these changes is altered demand from the organism's environment. Thigmomorphogenesis in plants is a prime example, whereby plants sense and respond to mechanical stimuli, in some cases leading to strengthening of the tissue [68]. Thus, without considering the developmental stage of an organism and its ecology, it would be difficult to interpret biomechanical and morphological phenomena. It is common for organisms to exhibit an increase in structural stiffness through development, which leads to less deformable structures, but also more efficient locomotor systems [69]. Similarly, strength (i.e., maximum stress) commonly

increases throughout ontogeny in plants and animals [70,71] due to microstructural changes such as lignification or calcification/ossification. Like the rate-dependent shifts in FT properties, development must be considered when parameterizing ecomechanical models.

Structural changes can occur as organisms grow and deal with changes in organism–environment interactions, but the environment can also influence the mechanical properties of organisms directly. Ocean acidification, for example, can compromise the structural properties of calcified organisms (e.g., coral) by reducing calcification or increasing dissolution [72]. Interestingly, early developmental stages are often more negatively affected. In addition to calcification, ocean acidification can also influence attachment mechanisms in marine invertebrates. For example, the proteinaceous byssal threads of mytilid mussels are negatively affected, reducing the extensibility, force to break, and tenacity of attachment to hard substrates [73].

Evolution: constraints, convergence, and ecomechanics

The basic laws governing the behavior of mass and energy are invariant, which establishes what can be called 'hard' or 'universal' constraints, boundary conditions that no form of life can trespass. These establish what is physically possible and what is impossible [2]. An excellent example of a universal constraint is that of arm swinging (i.e., brachiation) in gibbons, which generally follows the constraints imposed by a pendulum model [1]. However, pendular mechanics cannot define all aspects of brachiation; transition between handholds involves a loss of mechanical energy that requires input from the animal [74]. All forms of life also face 'soft' or 'local' constraints, the trade-offs that emerge as organisms perform multiple functions to grow, survive, and reproduce. In turn, how these trade-offs are accomplished (phenotypic 'solutions') help inform how biodiversity has evolved [75,76]. When cast in the context of theoretical morphology, hard constraints can be thought of as prohibited regions in a morphospace, whereas soft constraints can be thought of as the roads that lead to adaptive morphologies provided that organisms can evolve ways to navigate them. Unlike hard constraints, soft constraints can change over the lifespan of an organism, or over ecological or evolutionary time just as they can differ in space (local to global) (Figure 4). Most tasks cannot be maximized simultaneously, and must trade off with other performance tasks. However, there are different solutions for achieving the same set of functions, a principle known as many-to-one mapping [77–79].

The direction of evolution is often governed by ecological conditions, thus highlighting the importance of ecomechanical models. Fishes are a prime example, in which body form has frequently diverged along ecological gradients including flow, predation, and habitat structure [80]. Those fish species that evolved in high flow, low predation, and open habitats, often have more streamlined bodies and higher aspect ratio caudal fins for prolonged swimming. Swimming performance (e.g., endurance) is then dependent on both ecology (e.g., flow) and FTs (e.g., body and fin shape). The idea of trade-offs arises here, where these morphological traits are suboptimal in low flow, high predation, and/or highly structured habitats. This has led to widespread convergent evolution in body form across fishes [81], aquatic mammals [82], and aquatic reptiles [105], emphasizing that ecomechanics strongly influences the evolution of phenotypic diversity. Convergence, trade-offs, and many-to-one mapping are prevalent across the tree of life in various environmental scenarios, but ecomechanical models provide the tool to understand them.

Data pipeline and open trait networks

To implement ecomechanical models on a wide scale, we note that databases must be expanded and coordinated, and their accessibility increased. However, the nature of data collection, at present, is inherently slow. Experiments, field observations, and data processing are rate limiting.

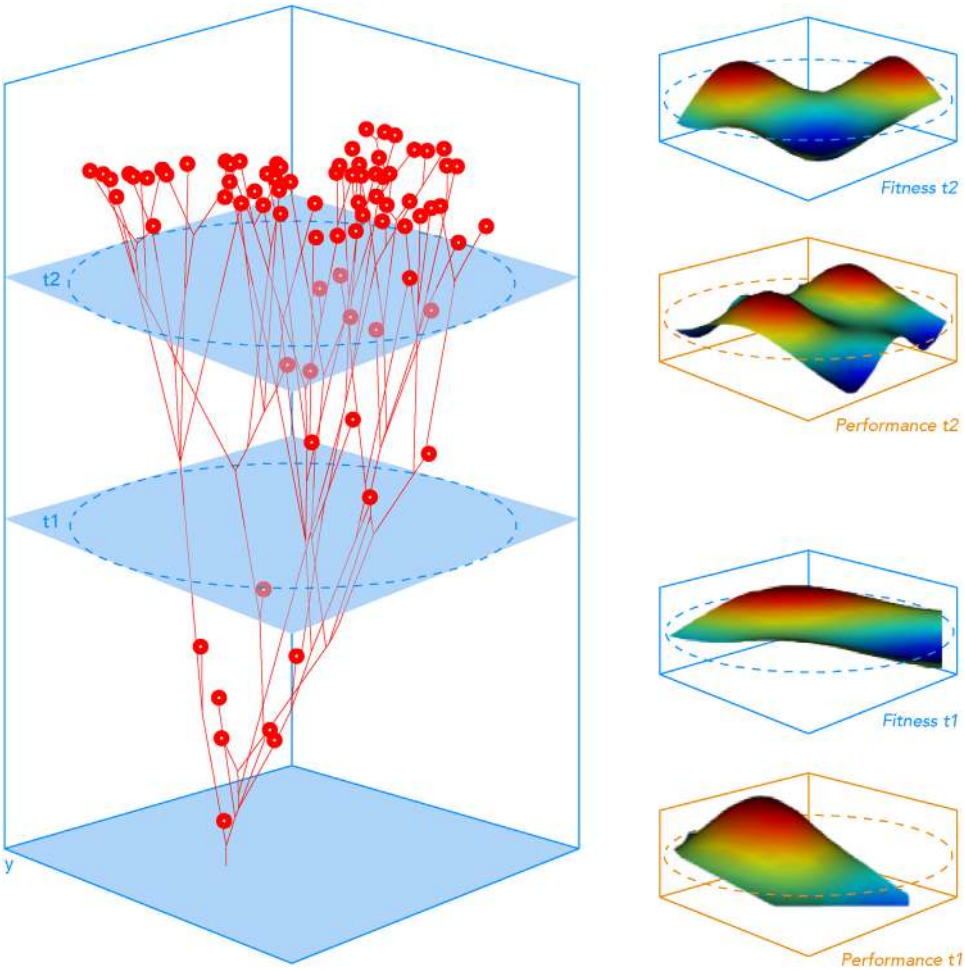

Figure 4. The realized phenotype of organisms is expected to reflect the changes of performance and fitness landscapes through evolutionary time. In contrast to the ecological and developmental time scales in Figure 2, we now consider time points that may be separated by many millions of years. The evolutionary traitgram on the left illustrates phenotypic changes throughout the history of a hypothetical clade, with the phenotype represented by the area defined by x- and y-axis, and time represented by the z-axis. The time slices t1 and t2 represent two different times in history of the clade. The broken blue ellipses represent the limits of realizable phenotypes set by 'hard' constraints which are invariant over time. For each time slice, one can model performance as a function of the phenotype, resulting in performance landscapes that are illustrated in the right panel. The position and number of performance peaks that arise from phenotypes can change through time. Note that the performance peaks for a specific function and phenotype may not equal the fitness peak for the whole organism. As landscapes change, so do the relationships outlined in Figure 2. In other words, the environment might have been dramatically different at t1 than t2, and an ecomechanical model could be used to predict the performance–phenotype relationships across time. Red dots on the left panel indicate the end of a branch, such that lower red dots represent extinct species.

As a result, sharing data needs to become a priority such that the working life of any single datapoint is prolonged beyond a single study [84]. To do this, we must standardize data acquisition, reporting, and archiving, to ultimately ensure that data collection and statistical analyses remain comparable and reproducible across researchers. Given the range of ecomechanical models and organismal systems, it is not possible to detail every aspect here. However, we outline guidelines that should be considered.

A standardized data pipeline would allow us to quickly and easily record data from focal taxa, especially those in natural settings, automatically process those data to return all salient variables, and archive the data in a publicly accessible format. That level of flexibility (e.g., in terms of field recording) and automation for functional data does not currently exist within a single framework. However, aspects of such a pipeline are beginning to take shape, with data acquisition, processing, and archiving tools being added every day. In terms of data acquisition and the ability to capture video in nature, rigs like BeastCam [85,86] permit full 3D point cloud data acquisition. Relatively affordable drone setups for 2D data, as well as video setups for 3D in the field [87] are available. Further, there is enormous potential to engage in community-led science by encouraging those with pit traps and camera traps to share videos with the scientific community. In fact, new advances permit inexpensive high-speed video in combination with an automatic trigger [88]. For data processing, there are already excellent open-source tools that facilitate the extraction of mechanical data. For example, StereoMorph [89] is an open-source alternative for manual tracking, and DeepLabCut [90] automates high-throughput video tracking. What is needed is more coordination among all of these software and hardware elements into easy-to-use, integrated workflows.

This pipeline will only be effective if we use open-source tools with standardized, open file formats and implement best-practices for the inclusion of salient metadata. This has been done extensively for FT data, but has not been extended to higher-level biomechanical traits. For video data, we recommend establishing a standard for reporting camera position, scale, frame rate, and resolution of videos, whether those videos are original works or mined from other sources. Additionally, environmental factors such as physical location, temperature, fluid speed, humidity, size, and date should follow minimum-acceptable metadata standards. This information should be included in video archives and in data reporting, facilitating the integration of FTs and EVs for ecomechanical models. We encourage readers to reference [91], which provides a rubric for data management practices, as well as Darwin Core (DwC) metadata standards. Ultimately, we see that improving access to affordable, high-quality, portable methods of data acquisition, combined with methodological standardization of data collection and analysis, will have a profound impact on our ability to answer the 'big questions' associated with the rules of life.

Concluding remarks

The ecomechanical approach advocated here is critical for understanding patterns of species distributions and interactions, developmental patterns, and evolutionary processes. Although ecomechanical modeling is not new (e.g., [92]), this approach has yet to be adopted on a broad interdisciplinary scale to investigate organism–environment interactions. Here, we highlight how and why such models should be adopted across diverse systems. To facilitate the applicability of ecomechanical models in the broadest context, we must expand FT databases to include biomechanically-meaningful traits, standardize the collection of these biomechanical traits, and increase the access to models using these traits via freely-available online platforms. By doing so, we can start addressing key questions about the phenotypic diversity and the interplay between ecology and biomechanics (see Outstanding questions). We are at a turning point where we can leverage technological advances and big data to further explain the rules of life.

Outstanding questions

How does development influence the ecomechanics of organisms?

How do rapid changes in environmental conditions influence functional traits?

How does the rate of loading indirectly affect performance through changes in functional traits?

How have safety factors evolved across the tree of life, or within individual lineages?

How do soft and hard constraints affect phenotypic diversity?

Can ecomechanical models be used to predict the future in the face of global change?

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Declaration of interests

No interests are declared.

Supplemental Information

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