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Opinion

A User's Guide to Metaphors In Ecology and Evolution

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Biologists energetically debate terminology in ecology and evolution, but rarely discuss general strategies for resolving these debates. We suggest focusing on metaphors, arguing that, rather than looking down on metaphors, biologists should embrace these terms as the powerful tools they are. Like any powerful tool, metaphors need to be used mindful of their limitations. We give guidance for recognizing metaphors and summarize their major limitations, which are hiding of important biological detail, ongoing vagueness rather than increasing precision, and seeming real rather than figurative. By keeping these limitations in mind, metaphors like adaptive radiation, adaptive landscape, biological invasion, and the ecological niche can be used to their full potential, powering scientific insight without driving research off the rails.

Highlights

Biologists constantly debate specific terms in biology, but rarely discuss general strategies for resolving these debates. Most vexed biological terms are metaphors; so thinking about metaphors is a good starting point for devising such strategies.

Metaphors are not just colorful ways of explaining science to the public. They are key tools that are vital to science. As such, they need to be deployed with awareness of their strengths and weaknesses.

Metaphors inspire research and unite researchers of diverse disciplines, but their dark side is that they can hide important biology, their vagueness can lead to misunderstanding, and it is easy to regard them as real rather than metaphorical.

Recognizing metaphors is a key step for researchers to figure out how to use biological terminology to its greatest effect, driving research and inspiring collaborative action.

Biological Laboratory Equipment: Microscopes, Pipettes . . . and Metaphors

Biology pulses with **metaphors** (see Glossary). Molecular clocks tick along the branches of phylogenetic trees, selection pressures push red queens over adaptive landscapes, and organisms, snug in their niches, communicate information advertising rewards and defenses [1–4]. Much is made of the limitations of metaphors – surely thinking about science in terms of imaginary forces, make-believe landscapes, and fictional royalty, however evocative, must distort scientific practice. Accordingly, scientists are ever more frequently cautioned to be circumspect in deploying metaphors [5–9]. Metaphors in biology are usually regarded as second-class citizens, stand-ins to be discarded when the real biological phenomena are rigorously characterized [10]. However, this view is incompatible with the way metaphors are actually used by biologists, as powerful tools as much a part of science as microscopes, pipettes, and mathematical models [11–20]. Yet unlike these traditional tools, metaphors provoke constant debate between biologists.

War of the Words

Debates over terminology bedevil the biological literature [1–3], but are anything but 'mere **semantics**'. Instead, these debates are extraordinarily consequential for both scientific practice and the relationship between science and society [21]. They are consequential for science because debates over terminology shape what gets studied and what does not. Regarding 'niches' as real entities [22] and 'conservatism' as a real process leads to the study of niche conservatism [16,23,24] and, some argue, neglect of the ways that organisms themselves shape the conditions of natural selection that act on them [2,16,25] or aspects of development that limit evolutionary change in habitat preference [23]. In the same way, there are reasons to think that biological 'invasion' talk, rather than helping manage ecosystems, could instead promote complacency regarding the role of humans in creating habitat for non-natives [9,18,26]. Mismanagement of terminology is also consequential for the relationship between public perception and science [5,6,13,21,27]. Overenthusiastic use of genetic 'blueprint', 'book of life', and similar metaphors perpetuate painful nature–nurture debates in human

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sexuality, in which it is implied that if a given trait is 'written in the DNA', the trait is inevitable and thus justifiable, and if not, it is potentially morally suspect [28]. Similarly, debates over the ethics of synthetic biology are shaped by metaphors such as 'programming life' in 'DNA software', 'editing', or even 'hacking' into it [7,14,17,29]. At a global scale, scientists debate whether earth is at its ecological 'tipping point' or is pushing planetary 'boundaries' [30–33]. These and other current debates not only seem to have no end in sight, but with both scarce scientific resources and important societal issues in the balance, addressing these debates is more urgent than ever. Yet, while biologists spend a lot of time debating specific terms, we spend little time discussing general strategies for resolving terminological debates. A rewarding first step is to recognize that the most highly debated terms in biology are metaphors.

Metaphors are the main vehicles for communicating science to non-scientists, and their use in this context is much discussed and well studied [13,21]. We focus here on a less-discussed aspect, the crucial role of metaphors as tools in science itself [16–20]. This perspective is important because scientists ask very different things from metaphors in their own work than they do when talking to civilians. Among biologists, there is constant debate over particular terms [9,17,24,25,34–36]. However, there has only rarely been recognition in a work directed at scientists of metaphors as desirable tools for research, and discussion of metaphors in general rather than a debate over a single metaphor [16,17,20].

Metaphors are extraordinary tools used by scientists in all phases of research [14,19], and like any powerful tool, they must be deployed with knowledge of their strengths and limitations [12,17]. Scientists accept these limitations because of the advantages that metaphors bring. To help biologists use metaphors to their maximum potential, we draw on recent work [18,19,37] to propose a general strategy for biologists to address debates over scientific metaphors. We start by highlighting the beneficial roles that metaphors have in scientific research, as well as their main pitfalls.

Metaphor Power

Metaphors often provide the only means of access to new scientific territory [17,38]. However, even in mature fields, metaphors chug along apparently indefinitely, spinning off novel insights for decades with no end in sight [11]. So, while it is true that metaphors can sometimes lead scientific thinking into the weeds, metaphors need not, indeed cannot be, discarded by scientists in their daily work [14]. The power of metaphors lies in two main attributes.

'Go West': Metaphors As Guides to Discovery

The most apparent benefit of metaphors is their **expressiveness**. Metaphors are not simply verbal models but cognitive tools that evoke thinking about possible attributes and relations of novel entities or phenomena [19]. The expressiveness of metaphors drives this thinking. 'Landscape' and evolutionary 'force' metaphors vividly spawn thinking about how the factors that generate variation in populations yield variants that survive or reproduce differentially [4,39–41]. Even metaphor mismatches are useful – the genetic 'blueprint' metaphor strikingly highlights that there is no representation of the adult immanent within an embryo [42,43], a crucial insight in understanding development [43,44]. The ability of metaphors to guide discovery is sufficiently valuable to justify their use, but they do have another remarkable benefit.

A Big Enough Umbrella

A second and often unacknowledged benefit of metaphors is their extraordinary ability to bring together scientists from diverse perspectives [4,6]. Because they can be interpreted in many different ways, scientific metaphors group an often vast array of phenomena under a single

Glossary

Metaphor: analogical projections of ideas to situations in which they do not literally apply. In biology, aspects of familiar systems are used to construct models to understand a target biological system better, guided by the familiar aspects in the source system [62,63]. Most metaphors continually inspire new interpretations, and as a result, their fans of meaning and application continually widen, making them vaguer over time.

Metaphor diagnostics: inspired by the work of philosopher Stephen Yablo [37], the following diagnostics help identify whether a term is a metaphor. 'Expressiveness' is the ability of a term to evoke analogies in the system onto which it is projected. Phenomena evoked by the metaphor of 'radiation' include notions of divergence from a common ancestor, just as electromagnetic radiation emanates from a point source. 'Paraphraseability' highlights that replacing a metaphor results in increased, not decreased, precision. Replacing protein in a sentence will usually make it more cumbersome. Not so metaphors: 'evolution of articulated laticifers' is far more precise than 'evolution of defense'. 'Silliness' highlights that metaphorical terms evoke properties that clearly do not project to the target system, in ways that nonmetaphorical terms do not. Clades do not buy yachts, no matter how successful they are. Although playful sounding, this diagnostic is anything but frivolous. Nonapplicable aspects are important signs of a metaphor.

Operationalization: the practice of creating an *ad hoc* measurement to quantify aspects of interest inspired by a vague term. Any given metaphor can be operationalized in countless ways.

Reification: regarding an imaginary entity as though it were real. All quantitative tests of 'adaptive radiation' reify the metaphor [11]. The similarity of ecological preferences between closely related species is a pattern requiring explanation. Calling this pattern 'niche conservatism' and thinking that it is a process that can explain evocative label. Biologists studying phenomena as diverse as speciation and extinction rates, morphological disparity, phylogenetic tree shape, or the organism–environment fit can all claim to be studying different aspects of adaptive radiation, for example [11,45]. The **vagueness** of metaphors is thus one of their virtues, allowing them to foster cross-pollination among biological perspectives. The prodigious benefits of metaphors, however, come with limitations [6,39], and we examine three.

Metaphor Pitfalls

Highlighting Some Features, Hiding Others

The first limitation is that even while highlighting some aspects of a phenomenon, metaphors hide other, potentially important details [7,17,46,47]. Using metaphors to their maximum potential requires keeping in mind aspects that might be hidden [17]. For example, the 'tree of life' metaphor vividly evokes common ancestry and nested patterns of relationship [48]. For all its vividness, the term hides that different species concepts result in different trees, and different molecular regions tell differing stories, making talk of a single tree of life dubious [49,50]. Hybridization, horizontal gene transfer, and symbiogenesis question whether a tree is even an appropriate metaphor at all [51,52]. Another metaphor that clearly hides crucial biology is the adaptive landscape [4,40,53], which evokes 'peaks' and 'valleys' of low and high fitness. Yet fitness–trait combinations can shift constantly, unlike real landscapes [53,54], and real populations can likely jump between distant points through n-dimensional space, unthinkable in real landscapes [4,42,55]. Despite the limitations of the metaphor, there are more papers on biological landscapes than ever [4,40,53], and, for that matter, on phylogenetic trees, illustrating how metaphors can drive research despite hiding important aspects of nature. This tendency for metaphors to hide crucial biology is their greatest drawback, but not their only one.

Vagueness

Above, we celebrated the vagueness of metaphors as permitting a vast array of biologists to unite under an expansive umbrella term. However, amplitude of interpretation means that biologists can use the same term while talking about different things. Ask five colleagues for their definition of 'constraint' and chances are you will get five different answers. Some biologists intend constraint to refer to factors that impede the production of variants that would be favored by selection. From this point of view, constraints are in opposition to selection [23,56]. Others see patterns of trait covariation, often forged by selection, as constraints [45]. Still others regard the environment or even selection itself as constraints [56]. Using 'constraint' without defining it usually leads to different biologists understanding different things and, far too often, talking past one another.

Worse yet, in addition to simply talking past one another, biologists often bicker over the correct interpretation of a metaphor. As originally coined, adaptive 'radiation' applied to clades with many species [11]. By all accounts satisfying this original notion, Rift Lake cichlids are a celebrated and much-studied adaptive radiation, having over 1000 species [57]. However, Darwin's finches, also a paragon of adaptive radiation, have barely over a dozen species [58], hardly an impressive number. In maximal disagreement, some workers regard all of life an adaptive radiation, whereas others think that single species show adaptive radiation [11,59]. Recognizing that the radiation in question is metaphorical and thus lacking a single correct interpretation would avoid such unresolvable squabbling. Instead, it directs research efforts to the core biological issues of interest, in this case, the processes producing the entire range of diversification rates, clade sizes, and levels of morphological disparity [60]. This focusing of research effort away from vain debates over the single correct definition of a metaphor and

evolutionary patterns [23] is another example of a reified metaphor.

Semantics: how words correspond to the world, one of the central efforts of science. The phrase 'mere semantics' refers to trivial quibbling over different terms to refer to the same thing, but semantics in the true sense is anything but 'mere'.

Teleology: imputing goal-directed agency to non-sentient systems. Many biological metaphors, such as 'adaptation', 'advertising', 'competition', 'defense', 'function', and 'selection' make it harder rather than easier to envision that these processes are not consciously goal-directed [44].

Vagueness: refers to the open-ended definition of a concept, meaning that there are different ways in which a concept can be interpreted and used. This means that there is no single correct interpretation, in contrast to concepts having a more or less fixed definition whose conditions of application are more clearly stated, for example, protein, pollination, biomass, etc. That a metaphor can have many interpretations is a great benefit, because it means that researchers with diverse interests can come together under a single expansive banner. It means, however, that biologists must be careful to specify what they mean when using a metaphor, and to recognize that operationalization simply implements a given interpretation of the metaphor and does not dispense with vagueness.

toward the most productive research efforts requires recognizing that a given vexed term is a metaphor, complete with its cargo of vagueness.

Recognizing the vagueness of biological metaphors can be surprising, because as scientists, we often regard precision as the hallmark of our terminology. Yet a look at the literature shows that metaphors continually spin off new interpretations, with each new interpretation widening the fan of meaning of a metaphor, making it less rather than more precise over time. Inspired by the metaphor of the 'niche', Grinnell's notion highlights combinations of habitat and behavior, Elton's niche consists of considerations such as animal food preferences, and Hutchinson's version of the niche is defined by the environmental and resource variables that a given biologist happened to regard as important [24,61]. Niche interpretations proliferate to this day [61–63], leading to an ever-larger set rather than convergence on precise consensus regarding a real entity in nature [11,22]. Adaptive radiation is more than a century old and its fan of meaning also widens by the year [11,45,59,64]. The vagueness of metaphors provides grand umbrellas under which biologists can unite. However, overlooking the vagueness of metaphors leads into traps of talking past one another and arguing about the correct definition of a term where none exists.

Reification

A final downside to the use of metaphors is that it is often easy to forget that they are metaphors at all and come to regard them as real aspects of nature. This occurs via a fallacy known as **reification**. Reification is the treating of an imaginary construct as though it were real [27]. 'Adaptive radiation' is reified in every study that attempts to identify quantitatively a clade as representing adaptive radiation or not [11]. These studies specify a statistical threshold above which clades are considered adaptive radiations and below which they are not. These thresholds can involve variables such as species number, clade imbalance, speciation rate, or morphological disparity, for example, 'an adaptive radiation is a situation in which one clade has 90% of the species with respect to its sister taxon' [64]. Crucially, in each author's

Box 1. Diagnose a Metaphor in Three Easy Steps

Debates over metaphors are maximally consequential for the field and for society at large. Should ecologists concerned about ecosystem degradation rally around global 'tipping points' or instead focus on 'planetary boundaries' [30–33]? Recognizing that a concept is a metaphor helps decide whether it is better to avoid debating the correct interpretation of the term in favor of focusing discussion on how to maximize the benefits of the metaphor (Box 2). That most high-stakes terminological debates in biology center on metaphors makes it essential for biologists to build a common language for discussing them. This common language starts by recognizing that a given term is a metaphor.

Philosopher Stephen Yablo [37] has devised useful criteria for recognizing metaphors, and his work inspires the three we offer here. Expressiveness refers to the evocativeness of a metaphor. In a biological context, analogies to terms such as 'landscape' in adaptive landscape, 'radiation' in adaptive radiation, and 'niche' in ecological niche immediately spring to mind, expressiveness that is a good sign of a metaphor. **Paraphraseability** is a powerful diagnostic based on whether a term can be replaced with alternative terminology. Replacing a metaphor always results in more precise expression. 'This clade is an example of an adaptive radiation' could be replaced by different authors as 'this clade speciated very rapidly into a very large number of species', 'this species includes morphs that are very different ecologically', or 'this clade has 90% more species than its sister taxon'. All these examples are far more precise than 'adaptive radiation', paraphraseability that is an important sign of a metaphor. What Yablo refers to as **silliness** highlights that metaphors have aspects that clearly do not apply to the target system. These aspects can be entertainingly put as silly questions or statements [37]. Chaperone proteins clearly do not accompany other ones to ensure decorous behavior. Radiating species do not cause ionization. Selection pressures are not measured in pounds per square inch. Genetic blueprints do not specify their scale in meters. Moonlighting proteins do not have to hide their night function from their day one. These aspects that do not apply help reveal that a concept is a metaphor. With diagnostics of expressivity, paraphraseability, and silliness in mind, biologists can identify metaphors to see how they might help and hinder scientific research. Box 2 helps decide what a metaphor's best use is.

Table 1. Example of Metaphors in Ecology and Evolution, Metaphor Diagnostics, and Examples of How They Can Hinder Research

Metaphor	Expressiveness: what the metaphor evokes from the source domain	Paraphraseability: examples of how the metaphor can be replaced with more precise terminology	Silliness: aspects that do not apply	Metaphor pitfalls: examples of ways that the metaphor can hinder research	Refs
Adaptive 'landscape'	Evokes high and low positions connected by continuous series of intermediate points	Some trait combinations have higher fitness than others; current fitness is informative with regard to changes that will increase or lower fitness	When the population crossed the valley, it got its feet wet in the river	Probably most or all real selection spaces are wholly or otherwise unintuitive, fostering incorrect expectations regarding the action of drift and selection	[40,55]
Adaptive 'radiation'	Evokes rapid divergence from a common ancestor in a multitude of forms and lifestyles	Clades differ in speciation rate, species number, and morphological and functional disparity	The radiation diminished with the square of distance	Easily reified, in the form of quantitative thresholds that arbitrarily designate yes/no 'adaptive radiation' categories	
Advertising (flowers, males, aposematism, etc.)	Some actors (pollinators, females) select others (flowers, males) based on cues that may or may not correlate with quality	Selection favors some trait associations over others, e.g., red flowers with nectar, and not others, e.g., red flowers with no nectar	Worldwide, flowers spend over a billion dollars on billboards alone	Can lead to teleological formulations rather than thinking in terms of real biological processes	
Synthetic biological 'chassis'	Evokes visions of a standard minimal base on which custom constructions can be straightforwardly built	Synthetic biologists strive to identify minimal sets of genes and other cellular resources that give them maximum versatility	The Golgi apparatus fell off the chassis because it was not bolted on properly	Critically hides that the 'minimal' set of genes for cell maintenance depends on culture media and conditions	[17]
Competition	Evokes the willful effort of vying parties to control finite resources	An element of the selective environment of species A, insofar as it affects resources important to species A, is species B	Zebra mussels won Best Invasive 2018 by beating the native species	Can lead to erroneous comparisons of fitness or performance between species rather than within, which is where natural selection really acts	
Conservatism (phylogenetic, niche)	Evokes resistance to forces that would otherwise provoke change	Some aspects of some lineages vary markedly between species whereas other features vary little	With their great regard for tradition, the coelacanths remain proudly morphologically conservative	Leads to misplaced explanation of a given pattern (e.g., niche similarity across species) by appeal to another pattern (phylogenetic relatedness) rather than a process	[23]
Constraint (e.g., evolutionary, developmental, phylogenetic, ecological)	Evokes powerful limits to change in the face of factors that would otherwise be expected to provoke change	Some factors bias or limit what can be produced in development, sometimes in ways that do not seem plausibly accounted for by selection	Wherever evolution takes humans, chimps are constrained to follow, explaining their similarity	Almost always invites cross-talk because different workers understand different things by 'constraint'; often vague code for selection	
Ecological 'tipping point'	Evokes displacement of center of gravity to a point of no return, followed by a rapid crash	It is possible that sufficient quantitative damage to the ecosphere might lead to rapid qualitative deterioration of ecosystem services	After it tipped, the ecosphere hit with a loud bang	Different authors can have different notions of what a tipping point is; as a result, ecologists can waste effort debating the metaphor rather than addressing ecosystem decline	
Ecosystem 'health'	Evokes populations not at risk of extinction, habitats free of human produced toxins, and ecosystems that recover readily from perturbation	Speaking in terms of the specific variables intended (e.g., lead content, species composition) will always lead to more precise expression.	The ocean has been feeling much healthier since it has been playing water polo and cutting down on salt	Because the term is so vague, its use will easily lead to different scientists talking past one another	
Environmental 'filtering'	Filter implies that some external condition determines which species can live where	Different species can persist in different conditions of natural selection	The ocean cleans its environmental filters three times a year	Misleadingly implies that a 'filtering' process distinct from known processes such as selection exists	

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Evolutionary 'success'	Evokes many species and lifestyles, e.g., fish are the most successful group of vertebrates	Fish represent the largest clade of extant vertebrates	The fish enjoyed their success by relaxing a million years on their yacht without speciating	'Success' biases attention to speciose clades, rather than why there is a range of species number across clades	
Function	Evokes proper role of a trait (e.g., the heart pumping blood) vs malfunctions (defibrillation) and incidental properties (audible heartbeat)	Trait variant X is prevalent in populations because bearers of Y reproduced disproportionately compared to other variants	The hopeful monster's novel jaw structure was supposed to function in defending it against lions but did not work	In addition to the risk of **teleology**, 'function' can hide that the causal interaction between performance and selective regime causing traits to become differentially expressed is often unknown	
Genetic 'blueprint'	Evokes the 1:1 specification of adult structure in the genome, as in a blueprint to scale	Some features, e.g., some amino acid sequences, can sometimes be predicted from DNA sequences	The application for a new Bauplan was rejected because the genetic blueprints weren't turned in on time	Erroneously implies that adult features are prefigured, homunculus style, in the genome	
Genetic 'information'	Evokes nucleic acids containing messages that are independent of the substrate (i.e., information in DNA could be in a different form)	Selection favors some sequences of nucleic acids because they participate as crucial resources in producing proteins and in other developmental processes	With so much information in their nuclei, cells are very wise	Reliance on the 'information' metaphor dramatically hides the fact that, far from being neutral codes that could just as well have a different form, nucleic acids are in fact scaffolds on which other macromolecules are built	[68]
Herbivore 'resistance', 'defense' (e.g., hairs, latex, or toxins)	Evokes the notion of plant–herbivore arms races, in which plants direct substantial reserves of finite resources into deterring would-be attackers	In some plants, features such as hairs, latex, or toxins are favored by selection in the presence of some insects	Plants resist oppressive herbivores that want to impose their arthropod way of life on them	Subject to all the problems of identifying the proper 'function' of a trait (see in this table), as well as the risks of teleological interpretations of adaptation (also see adaptation)	
Herbivore 'tolerance' (fast growth rather than defense)	Evokes coexistence and flourishing despite offenses	Rapid growth can compensate for tissue removed by herbivores	Plants tolerate diverse viewpoints, including those of herbivores, even though they might not agree with them	Easily leads to reification of 'tolerance' as a feature that can be acted upon by selection as distinct from growth rate, when in fact this is unlikely	
Biological 'invasion'	Evokes unwanted, aggressive displacement of native species by non-natives, resulting in environmental degradation	Non-native species often become abundant in novel environments, and are often associated with lowering of population numbers of native species	The invading mussels lost the battle but won the war	The 'invasion' metaphor could deflect attention from the role of humans in moving non-native species and in priming habitats for non-natives	
Molecular 'chaperones'	Evokes accompaniment in a crucial and sensitive process	Some proteins interact with nascent polypeptide chains in reliably producing some folding patterns over other possible ones	The proteins did not kiss because they were worried that Hsp70 would tell their parents	Vague in that which molecules are considered indispensable for correct folding can differ between researchers	
Molecular 'clock'	Evokes the precise marking of time by the regular movements of a clock	Given known substitution rates, differences in nucleotide sequences between species can date events on a phylogeny	The trilobites went extinct because they forgot to wind their molecular clock	There is nothing in the 'clock' metaphor that highlights that substitution rates are likely not constant along or between lineages	

Table 1. (continued)

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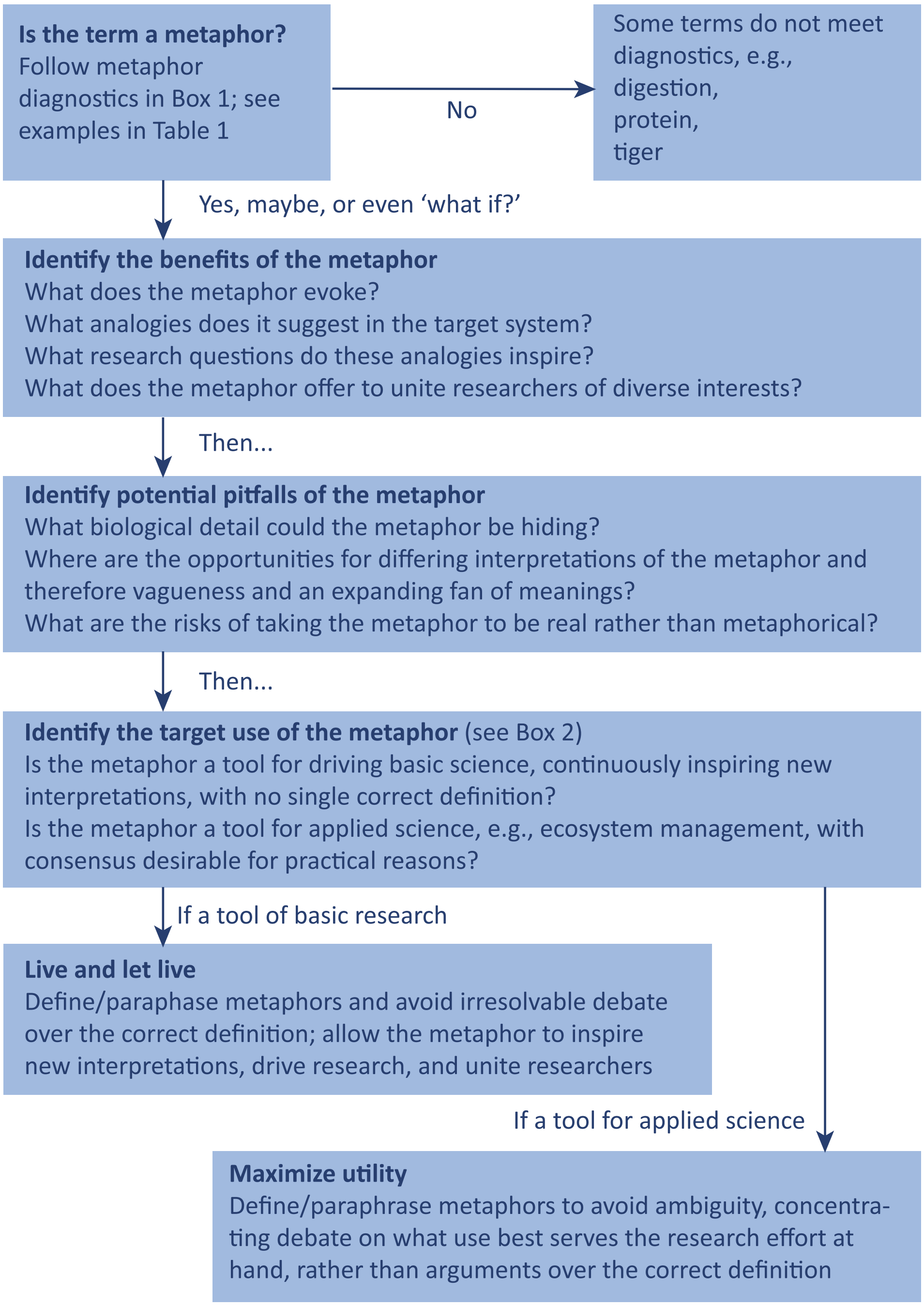
‘Moonlighting’ proteins	Evokes the idea that some proteins have principal roles in addition to less conspicuous or common roles	Proteins often participate in multiple cellular processes, some more frequently than others	Phosphoglucose isomerase got fired when glycolysis caught it working nights as an autocrine motility factor	Hides that there might be no principal versus subsidiary role in terms of biological importance (see function)	
Natural ‘selection’	References the deliberate breeding of certain individuals in artificial selection	Bearers of some heritable variants within a species leave more offspring than others	Mother Nature won Best of Show this year for selection of the best fish species	Dangerously hides the passive nature of the process (see adaptation) and treacherously invites teleology	
Niche	Evokes the notion of a place in nature that perfectly fits a species	Hutchinsonian niche: different species are often characterized by different multivariate combinations of values of environmental variables	This year the lazuli bunting decided to paint its niche green	Strongly evokes the notion of preexisting problems in the world that are independent of organisms, waiting for organisms to solve them	[69]
Selection ‘pressure’	Evokes a force pushing populations through fitness space	See natural ‘selection’	The selection pressure acting on the human sex ratio is 123 pounds per square inch	The ‘force’ metaphor powerfully hides that selection is simply a passive consequence of certain combinations of heritable variation and environmental conditions	
Red queen hypothesis	Evokes the Red Queen of Lewis Carroll’s 1871 children’s book *Through the Looking-Glass* who makes a reference to running ‘to keep in the same place’	The conditions of natural selection can change constantly	Populations can work up quite a sweat running over the ever shifting adaptive landscape	‘Staying in the same place’ hides that there is often no meaningful fixed reference point analogous to the ‘same place’. Often invokes competition and is vulnerable to the dangers of that metaphor as well	
Stress	Conditions causing lowered performance relative to other conditions, which are perceived as ‘optimal’	Some conditions form part of the selective regime of a given species; these conditions are associated with low fitness in some individuals	The Black Forest was drinking too much alcohol and having bad dreams because of drought stress	Hides that the optimum against which ‘stress’ is assessed is an imaginary one, and that the term is a vague and confusing reference to natural selection	[70]
Genetic ‘toolkit’	Evokes a versatile and minimal set of genetic elements necessary for development	Some genetic loci are involved in many processes, others in fewer processes	Frogs keep their toolkits under a lily pad, humans keep theirs in the garage	Hides the fact that most of the genes of the genome are required to produce a new individual, not just a privileged set	

quantitative **operationalization** of adaptive radiation, rather than a numerical threshold being used to diagnose putatively real entities in nature, the numerical threshold itself *is* the definition [11]. In other words, the artificial idea has become real, has been reified. This example shows that quantification or operationalization by itself is not sufficient to avoid the pitfalls of metaphors. Instead, scientists need to recognize that any single operationalization is just one of innumerable possible translations of a metaphor.

Eating Scientific Cake and Having It Too: Taming Metaphors

With these considerations in mind, biologists can make small changes to their use of metaphors that will bring powerful benefits. Continuing to include metaphors in titles and keywords of scientific papers will attract like-minded readers, making full use of the ability of metaphors to



Trends in Ecology & Evolution

Figure 1. Metaphor Flow Chart. Recognizing that the Majority of contentious biological terms are metaphors reveals a path for addressing terminological debates in ecology and evolutionary biology. The first step involves deciding whether a term is metaphorical or not. Because there is so much to be gained from such an analysis, even if a term does have a technical definition (radiation, selection, etc.), it is still worthwhile entertaining the possibility that a term is a metaphor. This process allows identifying both the benefits of a metaphor, including inspiring novel research and finding scientists with compatible interests, as well as the possible risks posed by a metaphor. These risks include the potential to lead to confusion because different scientists use the same word but mean different things, as well as the potential to regard the

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Box 2. Metaphors for Basic and Applied Science: When to Debate the Correct Definition of a Term

An important step in constructive debates over metaphors is to identify when debate over the correct definition is misplaced versus useful. This depends on the application that scientists want to give a metaphor. There are two main applications in the literature.

Metaphors as Tools of Discovery in Basic Science

The metaphors that drive basic science continually inspire new interpretations. Biologists have been using 'niche' and 'adaptive radiation' for more than a century, and there are more notions of these terms today than ever [11,22]. Niche, understood as different combinations of values in climate database layers, is clearly useful in species distribution modeling [22,62,65,66]. The term just as effectively helps thinking about the mutual shaping of organism and environment, as in niche construction theory [2,67], and even affects how biologists think about inheritance, as in the 'ontogenetic niche' [43]. All of these interpretations serve useful roles driving biological research; argument over a globally correct definition would be pointless. Instead, scientists can recognize that the many interpretations of a metaphor, its very vagueness, is a benefit. This wide fan of meaning means that a metaphor inspires research that continually diverges into novel territory. As research diverges, scientists can still find each other's work and exchange perspectives (e.g., literature searches for metaphors such as 'defense', 'stress', or biological 'information' bring up vast arrays of interpretations). Recognizing a metaphor as tool of basic research thus avoids unresolvable debate over the single correct interpretation while enjoying the power of metaphors to inspire research and bring scientists together.

Metaphors in Applied Science

Sometimes biologists require consensus on the meaning of a metaphor to meet a specific goal, such as maintaining ecosystem resilience or assuring ecosystem services. In these cases, proliferation of meaning might not be desirable. While it might be desirable for the ecological 'tipping point' metaphor [30–32] to spin off new interpretations and generate new debates continually, it could be argued that the most useful meaning of the term is instead the one that allows biologists to unite immediately in avoiding irreversible ecosystem damage. Similarly, biologists might need to rally around a meaning of 'ecological health' or 'invasive' species in meeting their management goals (Table 1). In these cases, it is crucial for biologists to recognize the metaphorical nature of their terminology to avoid irresolvable debates over the correct definition of a term to search instead for the most useful definition for the goal at hand.

bring scientists of diverse viewpoints together. Metaphors can also continue to be used in scientific prose where their metaphorical content inspires the research question. However, at all crucial reasoning steps, as in generating hypotheses or in planning empirical strategies, discussion must be in terms of the actual variables of interest (the Yablo-inspired 'paraphrasing' of Box 1; Table 1 gives examples). Replacing metaphors with the specific variables in question brings greatly increased precision and clarity of reasoning, an easy investment yielding immense benefits.

In obtaining these benefits, the following procedure will help (Figure 1). (i) Diagnose the metaphor using the **diagnostics** in Box 1. If a term can be replaced by alternative terminology with an increase in precision, it is likely a metaphor. 'WorldClim climate layers' is vastly more precise than 'niche'. Some terms are hard to paraphrase in this way and are nonmetaphorical, like 'protein', 'digestion', or 'tiger'. Even if a metaphor has a technical dictionary definition (such as radiation, drift, selection, or niche), it is worth proceeding with the following assessments. (ii) What benefits does the term provide in inspiring research and uniting scientists of diverse perspectives? (iii) What pitfalls does it pose in hiding biological detail, in allowing for misunderstanding because of vagueness, and in risking reification? (iv) The most important step involves collective discussion around the use of the metaphor, such as deciding whether it is best used

metaphor as real rather than imaginary. Table 1 gives briefly worked examples of these exercises. Finally, it is important to decide what role is most useful for a metaphor. In driving basic research, it is usually useful to allow the meanings of a metaphor to proliferate unchecked, as the term drives investigation into increasingly novel territory. For applied science, it might be more profitable to find a useful consensus meaning. Either way, no single correct definition exists, meaning that scientists can focus their efforts on the most effective pragmatic use of metaphors. See also Boxes 1 and 2.

as a tool of basic scientific discovery or for applied uses (Box 2). In some situations, time spent debating the correct definition of a vague metaphorical term could be better spent identifying the most useful applications of the term [19]. This would seem likely to be the case for scientific metaphors intended to improve human well-being, such as ecological 'tipping points', ecosystem 'health', or biological 'invasion' (Table 1). As tools for basic research, recognizing metaphors is crucial in avoiding reification, as happens in the case of adaptive 'radiation', 'competition', 'conservatism', the genetic 'blueprint', the ecological 'niche', and many others (Table 1). In this way, the procedure we outline should maximize the benefits of metaphors while keeping a close eye on their dangers.

Concluding Remarks and Future Perspectives

Adaptive radiation, ecological niche, adaptive landscape, biological invasion, and countless other examples (Table 1) illustrate that using metaphors while remaining conscious of their limitations should be a priority for scientists [13,17], because metaphors are here to stay. The procedure we outline (Boxes 1 and 2, Figure 1) will help biologists decide whether the benefits of a given metaphor are worth its dangers, manage those dangers accordingly, and navigate the challenges facing biologists in their use of terminology (see Outstanding Questions). By providing conceptual common ground, our treatment aims to provide direction to virtually all important terminological debates in ecology and evolutionary biology. With so much hinging on evocative metaphors – is the world coming to an ecological 'tipping point'? Is climate change induced 'stress' killing global forests? Should biologists 'hack' genetic 'programs'?– common ground cannot come soon enough.

Outstanding Questions

Can biologists move from debating individual terms to developing general strategies for discussing terminology? Such a process would require substantial time up-front before being able to resolve specific debates.

What benefits would such a metadiscussion have on scientific practice? One benefit would seem a likely reduction in quibbling over the correct definition of a term where no such definition exists, and focusing of efforts where consensus is needed.

Can metaphors lose their second class status in science? Metaphors in biology are often regarded as appropriate for jump-starting research, but destined to be discarded when the real phenomena are understood. This view is often incompatible with the way metaphors are really used by biologists, as tools whose fans of meaning can continually widen, generating new insights indefinitely.

Will biologists resist classifying their preferred terms as metaphors? Few biologists proudly assert that they dedicate their efforts to metaphors, and this is a shame. Metaphors in science are correct and supremely useful, but it remains to be seen whether they can be embraced as such.

Is pragmatic use of metaphors the way forward? In most cases, recognizing that a term is metaphorical leads to pragmatic uses of the term. In powering basic research, it would mean allowing, even celebrating, the ability of a metaphor to generate new ideas even as it becomes vaguer and vaguer, using metaphors in titles and keywords but replacing them with more precise thinking where it counts. For situations such as ecological management, it likely means reaching clarity on a desired goal and using a metaphor accordingly.

Can biologists and philosophers play nice? Most of the vocabulary and tools for thinking about metaphors have been developed by philosophers. But philosophers and biologists often have different concerns, so mutually advantageous collaboration requires keeping these needs in view.

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