

## **Hierarchy: The Source of Teleology in Evolution**

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“Zebbras evolved stripes in order to discourage biting flies.” Evolutionists everywhere cringe. Language like that is forbidden in evolutionary discourse. We do not allow teleological talk, the “in order to” in that first sentence. Such language suggests that the evolution of zebra stripes was goal-directed, purposeful. Teleological language seems to imply that zebras in their evolution somehow sought out an end-state—detering biting flies—or worse, that the end-state of deterring biting flies was the cause of the changes tending that way. Both are impossible. In our present worldview, species do not seek. Their present behavior is not guided by some vision of the future, for they have none. Nor does the future itself guide them. End-states do not reach back in time and cause evolutionary change. The future does not cause the past.

Still, there is a reason that we are tempted this way, a reason why we slip so easily into thinking about adaptive evolution in teleological terms. It is that the close fit of organism to environment seems to demand purpose. After Darwin, we think we know better, of course. We know that blind variation and selective retention creates the appearance of purpose. What we might say about the zebra is that in some ancestral population of unstriped or less-striped zebra ancestors, the variants with more striping were better able to deter flies (Caro et al. 2014), suffered fewer bites, perhaps contracted fewer diseases, and therefore left more surviving offspring, a process that was repeated over many generations leading to a descendant species with greater striping. Or something like that. Apparent teleology is explained by blind mechanism.

Oddly, and a little ironically, however, it turns out that our original pre-Darwinian intuitions were not far off. There is, I argue, a structural similarity between the process of adaptive evolution and all the other processes we commonly think of as teleological. Simple organismal tropisms, physiological homeostasis, the movement and patterning of cells in development, and even the behavior of human-made, goal-directed devices—all of these seemingly teleological systems are structured hierarchically. They are nested physically. They consist of a small thing that moves or changes inside a stable big thing, inside a field of some kind. In all of these systems, the apparent seeking behavior of the small thing is guided hierarchically, from the top down. The upper-level field directs the lower-level small thing moving within it. Likewise for evolving species. The species lineage leading to modern zebras is a small thing relative to its environment—in other words, relative to the environment within which it changes. That environment, that context, is a big thing. It is a kind of ecological field. And to the extent that a species evolves adaptively, it is guided from above by that ecological field.

In what follows, I explain why seemingly teleological systems are structured hierarchically in this way. I also argue that the teleological view of adaptive evolution has certain payoffs, and that it unsettles—in intriguing ways—our thinking about a process we imagine to be already well understood. For one thing, it unifies a wide range of biological processes, bringing together seemingly disparate aspects of behavior, physiology, development, and adaptation into a single explanatory scheme. For another, it provides a novel and expansive view of the process of adaptation, one that relegates natural selection to the role of mechanism, at least in principle replaceable by other mechanisms. And third, it highlights certain requirements for adaptive evolution, especially variation and environmental constancy, requirements that have been long recognized but have been underappreciated. In the teleological view, variation and environmental constancy emerge as special cases of requirements for teleological systems generally—namely, lower-level freedom and upper-level stability.

I am using the word *hierarchy* here in its structural sense—that is, to refer to nested physical objects, things within things. In my usage, hierarchy overlaps strongly with terms like integrative level (Feibleman 1954; Haber 1994), ecological hierarchy (Eldredge and Salthe 1984), scalar hierarchy (Salthe 1985, 2009), constitutive hierarchy (Valentine and May 1996), and compositional hierarchy (Wimsatt 1994). Importantly, however, hierarchy in my sense does not imply any functional relationship between parts and the whole, nor does it imply that wholes are emergent in any sense. A

helium-filled balloon, consisting of gas molecules plus the plastic skin that encloses them, is a hierarchical system. So is a pile of rocks, although not a very interesting one (see below). Also, hierarchy here does not include hierarchies in time, in which one entity gives rise to several, which in turn give rise to more, and so on. In other words, genealogical hierarchies are excluded. Also excluded are specification hierarchies, such as postal addresses, and command or control hierarchies, such as military chains of command. In none of these is there necessarily any physical nesting of objects within objects. (See Zylstra [1992] for a useful discussion of the distinctions among the various aspects of hierarchy.) This is not to say that structural hierarchies cannot also have control-hierarchy features and vice versa—that control is not built into the concept of hierarchy that I'm using here.

### **Teleology and Hierarchy**

One signature of all seemingly teleological systems is their persistence (Sommerhoff 1950; Nagel 1979). A homing torpedo launched at a target ship shows persistence. If it deviates from the path toward the target ship—say, if it momentarily detects a passing pod of whales—it returns to a trajectory toward the ship. If a bacterium climbing a food-concentration gradient deviates, say when local currents drag it to lower concentration, it returns to an up-gradient trajectory. In human physiology, when blood pressure falls too low, the secretion of renin induces angiotensin, which constricts blood vessels, restoring the pressure. In a developing sea urchin embryo, primary mesenchyme cells migrate from the south pole of the blastula to the subequatorial region, where they merge and secrete the larval skeleton. If displaced from their trajectory toward the equator, say by an experimenter, the cells return to that trajectory. Deviation and return, error and correction, create the impression of an entity or a variable that is directed, headed somewhere, purposeful. It persists.

A related signature property of teleology is plasticity, the ability to find a given trajectory from a wide range of alternative starting points (Sommerhoff 1950; Nagel 1979). The torpedo can find a trajectory toward the target ship from any starting point within the sound field emanating from the ship. The primary mesenchyme cells of the sea urchin embryo can find their trajectory toward the equator from virtually any starting point within the embryo.

Any theory of teleological behavior must account for these two properties (Nagel 1979). In an earlier paper (McShea 2012), I developed a

hierarchical view of teleology, arguing that persistence and plasticity in a biological entity are the result of what I call upper direction—that is, direction by a higher-level field within which the entity is immersed. The bacterium is upper directed in that its movements are directed by the food gradient within which it is immersed. The bacterium's persistence and plasticity are explained by the fact that the field is present over a large area, so that wherever the bacterium wanders, or wherever it starts, the field is there, directing the bacterium to an up-gradient trajectory. Direction, in other words, comes from something that is larger than and envelops the teleological entity (see also Feibleman 1954). In the human example, the persistence and plasticity of blood pressure is directed by a larger structure, an organ system that includes the kidneys and the blood vessels of the circulatory system. In the sea urchin, the persistence and plasticity of the primary mesenchyme cells is directed by a large-scale developmental structure, probably a gene activation field or a morphogen field (Ettensohn 1990; Ettensohn and McClay 1988; see Weiss 1971 and Korn 2002 on fields in development generally). The homing torpedo is upper directed in that it is guided by the sound field emanating from the target ship, a field that is larger than the torpedo and within which the torpedo is immersed.

I intend nothing mysterious by this notion of a field. Fields are physical structures. Their action on the entities they contain is direct and local, but fields can be present over a wide area. In some cases, the size of the field is evident only when the pattern of local effects is observed at larger spatial or temporal scales. For a single bacterium, the field would be evident if the bacterium deviated frequently from an up-gradient trajectory, so that its persistent behavior could be observed over a large spatial range. Or we could release a thousand bacteria into the gradient all at once and see the field instantaneously in the plastic and persistent behavior of the entire population. Again, fields as I understand them are physical—not idealizations, not abstractions, and not in any way transcendent. Or at least, they are no more transcendent than an ordinary gravitational field, or for that matter, a field of corn.

What about causation? I chose the phrase upper direction in order to distance this discussion from (what I see as) the unproductive debate in the philosophy of science over “downward causation.” The debate is between reductionists who claim that all causation is necessarily lower level and antireductionists who leave some scope for higher-level causation. The tone of the argument here is antireductionist, but reductionists can rest assured that nothing mysteriously emergentist is being invoked. The causal

processes at work in upper direction are no different from the ones routinely invoked in everyday explanation. Consider these examples of upper direction. (None are framed as teleological, although they could easily be modified to make them so.) The gas molecules in a round balloon are directed from above by the plastic skin of the balloon to remain within a fixed radius of the center. The movements of rats in a maze are directed by the walls of the maze, forcing the animals to stay inside the maze and restricting their movements to the walled paths. Cars are directed by the spatial pattern of the roads. National interest rates on home mortgages direct the decisions of individuals thinking about purchasing or selling homes, inducing or discouraging buying or selling. The balloon skin, the walls of the maze, the pattern of the roads, the national interest rate—all of these are fields, spatially distributed physical structures that direct the entities contained within them (gas molecules, rats, cars, and potential home buyers/sellers).

This notion of a field as directing lower-level behavior is a fairly commonplace one, although the language used varies enormously. In some cases, such as the bacterium pursuing food, we ordinarily call the field providing upper-level direction a gradient. In other cases, such as the rat in a maze, the field is a boundary, establishing limits on change or movement. In both cases, they might be described as upper-level “constraints” on the entities contained within them (Eldredge and Salthe 1984; Salthe 1985). Fields can also be thought of in some cases as contexts, which guide or channel their contained entities. In still other cases, such as the effect of interest rates, fields might be biases on the direction of change occurring within them. Here I use all these words as near synonyms. Fields can be gradients, biases, boundaries, constraints, or contexts, depending on the situation. I realize that I am violating some norms of usage here in using the words “field” and “upper direction” to cover concepts with very different connotations, some implying an active tendency and others a passive one, some implying limitation and others a driving force. For present purposes, however, the perhaps jarring effect of this violation is useful if it draws attention to the two features that all these different systems share: containment and the causal power that containment makes possible. In other words, it draws attention to hierarchy.

Notice that in many of the examples given, the fields are simple. The food field is a simple gradient. But an organ system governing blood pressure is a more complex structure. As will be seen, the ecological fields that direct evolutionary change may be more complex yet. The point is that

the appearance of teleological behavior is not a function of the complexity of the field. Rather, it flows from the hierarchical relationship between the field and the contained entity.

So far, the analysis has considered only two levels, the field and the contained entity. But as Salthe (1985, 2009) and others have pointed out, complete causal stories for hierarchical systems typically require at least three levels: the focal entity, the next higher level, and the next lower level. Here the teleological entity lives at the focal level, the upper-level structure is the field, and the lower level is the domain of what we call mechanism (Feibleman 1954). Mechanisms play a critical causal role in teleological behavior. The behavior of a bacterium in a food field, or an individual in a housing market, is partly the result of its internal mechanisms. For the bacterium, these are its signal-transduction mechanisms. For the human individual, these are the motivations and other mental mechanisms underlying home-buying decisions. Lower-level mechanisms explain why and how the entity is affected by the field. I downplay these mechanisms here because in conventional explanations in biology they are commonly the sole focus, with the existence and causal necessity of upper-level structure taken for granted. I shift the focus in part to redress the imbalance.

### *Two Perhaps Obvious Further Requirements for Teleological Behavior*

The first is stability. The upper-level field must be stable, or more precisely, it must be roughly constant on a timescale that is long relative to change or movement in the teleological entity. And it must be constant on a spatial scale that is large relative to the movements of the entity. If the food gradient varies greatly in space, the bacterium will become “confused,” so to speak—unable to discern which way the gradient increases—and its trajectory will not be persistent. If a morphogen gradient is changing quickly, cells that are guided by it will not find their target locations.

The second requirement is freedom. The teleological entity must be at least somewhat free to change or move independently of the upper-level field. Persistence is error and correction, and an entity that has no freedom will make no errors and therefore will not appear to persist. If I throw a rock, a molecule within the rock rigidly follows the trajectory of the rock. The molecule is directed from above, by the rock of which it is a part, but in this case—as in all solid objects—the direction is too complete, too perfect, to support the appearance of teleology. Lower-level freedom is essential for teleological behavior.

### *A Near Requirement*

In all the examples of teleological systems I discuss, including the evolutionary ones in the next section, the field is spatially continuous. The guiding field in the embryo occupies a discrete portion of space, and the primary mesenchyme cells behave teleologically within that space. As Campbell (1958), Simon (1962), and other systems thinkers have recognized, spatial continuity is what makes possible some of the most interesting properties of hierarchical systems. And it would seem to be important for teleology. At least, it is easy to see how a spatially continuous field can arise naturally and how it can provide direction wherever (within the continuous space) the teleological entity happens to wander. Still, spatial continuity is not an absolute in-principle requirement. One can imagine a field that is spatially dispersed, such as the web, which exerts its influence on teleological entities (people) through widely scattered web-connected devices.

### *Three Perhaps Necessary “Course Corrections”*

First, there is no such thing, in our current worldview, as a system that is literally “goal-directed.” No behavior is literally directed by something in the future, and from the perspective of a teleological entity, goals exist only in the future. If they were present for the entity now, they would not be goals. Concretely, the homing torpedo is not directed by the actual target ship. It cannot be, because the target ship is not present for it. The ship lies only potentially in its future. Rather, the torpedo is directed by a sound field emanating from the target ship, a field that is present for the torpedo right now and at every moment. Even human goal directedness is entirely governed by present motivations and ideas. (I have proposed elsewhere that the motivations driving seeming goal-directed behavior in us are brain states that are structured as fields of some kind [McShea 2012, 2013].) When we act purposively, we are governed by imagined or anticipated futures that are present in our minds right now. The actual future never causes anything in the actual present. It is for this reason that I modify the word *teleology* with *apparently* and *seemingly*. These words are not intended to imply that teleological behavior is somehow unreal. Persistence and plasticity are real and require explanation. *Apparently* and *seemingly* are simply an acknowledgment of the impossibility of future causation.

Second, it should be obvious, but perhaps needs saying anyway, that not all upper-level structures are capable of upper direction, and there-

fore not all hierarchically embedded entities behave teleologically. A pile of rocks is a higher-level structure, one that consists of the rocks that constitute it, but the pile cannot provide much direction to the contained rocks. One reason is that the pile does not have much integrity. The forces that hold the pile together are far too weak to provide upper direction, as would be obvious if, for example, one tried to move the pile as a whole. The whole thing comes apart. The parts, the rocks, would show no persistence. Their trajectories would not track the pile very well. The point is simply that many (most?) hierarchical systems are not especially teleological.

Finally, one might object to the whole line of argument here, pointing out that among the hierarchically structured systems that do show persistence and plasticity, some are not what we would call teleological. For example, a ball released from the lip of a bowl will find a trajectory toward the bottom from any point on the inside surface of the bowl. Further, once released, if it is displaced—by, say, a nudge from a finger—it returns to a trajectory toward the bottom. The ball is persistent and plastic, and it is directed by a larger field, gravity, within which it is immersed. But few would call its behavior teleological. One way to respond to this objection would be to tweak the conditions, requiring that the system in question attain a certain level of complexity—that they be difficult to understand—to qualify as teleological (McShea 2012), a threshold that the ball in the bowl does not reach. Along the same lines, I could argue that teleology is a matter of degree, that the bacterium in the food gradient is highly teleological while the ball in the bowl is just barely teleological. Or I could simply point out that providing necessary and sufficient conditions for teleology is not the mission here. This is not a project in analytical philosophy. It is not an explication of our usage of a term. Rather, it is an engineering analysis, in the style of Wimsatt (2007), intended to reveal how seemingly teleological systems actually work. And if—in addition to explaining the systems we are inclined to call teleological—that analysis also happens to cover some systems that do not move us to use that word, so be it. Perhaps we need to revise our language.

## **Adaptation and Hierarchy**

For evolution, the hierarchical view invites us to take a top-down perspective—to look down, so to speak, from high above the species, with geography and time collapsed onto a scale suited to our imaginative capacities. From this perspective, looking down on a mid-Cenozoic horse lineage as



it traverses the last forty million years, we see body size increasing and number of toes decreasing, molded by a chilling climate and the transformation of the animal's habitat from forest to open plains. This view invites us to see the ecological field, the combined biotic and abiotic context within which the lineage evolves, as a set of forces, or pressures, that act on the phenotype. Permitting myself considerable license with language, the ecological field is a pair of hands that envelopes each species, delicately shaping the phenotype—to the limited extent allowed by internal constraints and stochasticity—in a way that supports survival and reproduction. Nothing in this view contradicts the standard organism-centered or population-centered view of natural selection. It is simply a higher-level view of the same process.

I will try to make the contrast in perspectives more concrete. Consider the evolution of neck folding in turtles. In modern cryptodires and pleurodires, the neck has two hinged connections, one between each of two adjacent pairs of neck vertebrae, enabling them to fold the neck and pull the head under the protective umbrella of the shell. Mesozoic amphichel-ydean turtles did not have these hinges or this capacity (Rosenzweig and McCord 1991). From the standard perspective, we would say that in some ancient population of non-neck folders, random variation produced some individuals with proto-neck-folding capability, and because this capability provided some advantage, say some protection from predators, the variant individuals were more likely to survive and reproduce. Notice that even from this lower-level viewpoint, the persistence of the trajectory of the population would be evident. From generation to generation, random variation constantly threatens to carry the population off track, away from proto-neck folding. But the differential survival of individuals with proto-neck-folding capability brings the population back to an adaptive trajectory. (Notice that my use of the word *persistence* is different from the usual one in evolutionary discourse. Here it means error and correction [in the sense of Sommerhoff and Nagel], the signature of teleology, not endurance or mere survivorship.)

From an upper-level perspective, persistence is even clearer. Let us represent an evolving species as a time-series of points in a phenotype space. Also within the space, vectors representing the selective forces—for example, predation—imposed on the species by the environment point toward a neck-folding phenotype. With the passage of millions of years, the points become a line, roughly following the vectors and moving toward a local adaptive peak, neck folding. I say roughly because the intensity of

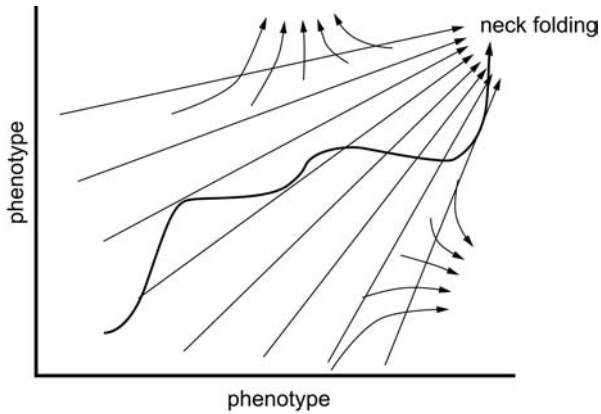


FIGURE 4.1 A turtle species evolving under the direction of an ecological field that drives it generally in the direction of neck folding. See text for discussion.

predation doubtless varies a bit in time and space, and the phenotype is in any case prone to drift. So what we actually see is not a straight line from non-neck folding to neck folding but a trajectory with series of a deviations and corrections. We see persistence. And the cause, the source of overall direction, is the predator-containing ecological context within which the species is moving (figure 4.1). The size and stability of the upper-level ecological field are both critical for persistence. The field must extend over a large portion of the accessible phenotype space. In other words, neck folding must be advantageous over a large-range of variants. (Notice that while the representation here of the phenotype space is abstract, the interaction between phenotype and field—between a real organism and its ecology—is real and physical, not at all abstract.) In addition, neck folding must be advantageous, on average, over a sizable chunk of the physical space over which the population might wander, or over which it might propagate. Finally, the ecological field must be stable in time. Neck folding needs to be stably advantageous, on average, over the entire course of the adaptive process. If the source of advantage is predation, then predation pressure needs to be present most of the time. Of course, no ecological field is perfectly constant. More properly, the requirement is for stochastic constancy, leaving considerable latitude for random variation.

The nice thing about the turtle example is that turtles as a group also show plasticity. (Notice that *plasticity* is being used here in the Sommerhoff-Nagel sense—entities adopting similar trajectories from

multiple alternative starting points—not in the usual biological sense, to refer to ecophenotypy.) The paleontological evidence indicates that neck folding evolved at least two times independently, in the cryptodires and in the pleurodires, taking somewhat different paths in each group (Rosenzweig and McCord 1991). The pleurodires fold their necks in a horizontal plane, while cryptodires fold them in a vertical plane, with the hinges located at different places along the neck, between different adjacent vertebral pairs, in the two groups. Still, the adaptations are convergent in the sense that they confer the same neck-folding capability. In evolution, teleological plasticity is convergence.

The upper-level view reveals a species directed, persistently and plastically, by its ecological context, by the ecological field within which it moves. The view emphasizes the causal role of the field. In contrast, the conventional lower-level view emphasizes the causal properties of the evolving organism or population—gene frequencies, developmental constraints, and the mechanistic details of the organism-environment interaction. Obviously those properties are important. Many terrestrial vertebrates with tough integuments evolved in an ecological field similar to the one in which turtles evolved, but they did not evolve neck folding. (Sadly, I should say, because it is hard to imagine a more endearing phenotype than a neck-folding baby hedgehog or pangolin.) Something in the genetic structure, the anatomy, the life history, and the developmental constraints and potentialities of turtles leant itself to variation of the appropriate sort to produce neck folding. And these factors are just as important in explaining the species' trajectory as the bacterial signal transduction pathways are in explaining the bacterium's trajectory. What the top-down view does is reduce all these factors to the level of mechanism. And as we zoom out, the mechanistic details disappear from view, leaving us with biological entities, species, with certain variational properties, moving in space and time and guided by the ecological fields within which they move. The details of the underlying mechanism are not ignored exactly, just black-boxed (Odum 1971; Valentine and May 1996).

The argument has so far been focused at the level of an evolving species and the evolution of adaptations at the level of phenotype. But the question naturally arises whether the same reasoning applies at larger scales, to macroevolutionary entities like clades and to properties such as speciation and extinction rates. At present, I don't see why not. The argument should be completely general, applying to evolving entities at all scales. Long-timescale entities also move and change within ecologies, and these ecologies have certain features that are stochastically constant, stable,

on those timescales, and therefore ought to be able to provide consistent upper direction. The Paleozoic Era had an average climate, one that was warmer—for example—than the average climate of the Cenozoic. Ecological contexts become more general, with parameters that are defined more broadly, as the timescale increases. And they become perhaps harder to imagine, to think about in concrete terms. But there is no reason to think they become less real, less able to act causally on the entities they contain.

Importantly, nothing in this view requires that upper-level control be absolute. It is true that the walls of the maze absolutely prevent the rats from taking shortcuts or from wandering out of the maze altogether. But the direction that ecological fields provide to species is probabilistic. The field probabilistically biases the direction of species movement without precisely determining it, just as the gradient probabilistically biases the movement of the bacterium or the interest rate probabilistically biases the decision of the potential home buyer. In figure 4.1, the two smaller fields on the side are a recognition of the probabilistic nature of adaptation, of the fact that other adaptive pathways were undoubtedly available and neck folding was not inevitable.

Finally, nothing in the upper-level view implies that selection pressures are somehow organism independent. The ecological field that molds a species is a function of the properties of the species being molded, just as the fields that affect a moving particle are a function of the properties of the particle. An uncharged particle is not moved by an electric field. A turtle with no shell evolving in a predation-intensive environment would be under no pressure to evolve neck folding. A shell-less turtle is a different kind of turtle, with different ecologically relevant properties, and it therefore experiences a different ecological field, which presumably would take it in a different direction, perhaps toward greater speed afoot. And of course, as the phenotype changes, so do the relevant dimensions of the ecological field. As very small organisms become large, for example, gravity joins the ecological field, becoming relevant in ways that it is not for very small organisms. Thus as a species changes, the ecological field it experiences changes.

## **Adaptation and Teleology**

There is a deep connection, I argue, between adaptive evolution and other teleological processes, including goal-directed behavior, physiology, and

development in organisms. And the connection is not merely linguistic or metaphorical; it is structural. All these teleological processes have the same general physical structure—a smaller lower-level entity directed by a larger enveloping field. And this is the main virtue of the hierarchical view, the conceptual unification it achieves.

In addition to revealing a structural commonality among these disparate systems, this view also makes sense of apparent teleology. It pulls aside the wizard's curtain, revealing how the magic of seeming future causation works. It shows how hierarchically structured systems create the appearance of being directed by their outcomes—how the bacterium swimming up a food gradient can seem to be directed by a food source that it has not yet found (and may never find), how an acorn can appear to be guided in its development by the oak tree that it will become (but is not yet), how the striping of zebras can appear to evolve for the future purpose of deterring flies. The secret, the hierarchical view reveals, is that the end-state does not direct the teleological entity at all. What directs the entity is the field within which the entity moves, a field that is large and present for the entity at each moment, right now, as the entity is moving or changing.

The viewpoint also presents certain long-known necessary features of the adaptive process in a new light. Just as the food field must be large and stable in order to direct the bacterium, ecological fields must be large and reasonably stable in order to direct adaptation. In evolution, this is true in two senses. Ecological fields must be large and stable in space—that is, over at least the physical range of movement of the population. And finally, they must be “large” in time—in other words, roughly constant over the duration of the adaptive process. In sum, the field must be large enough to be present wherever the entity's wanderings take it and stable enough to be reliably present whenever the entity arrives there.

The complement of upper-level field stability is lower-level freedom. Just as the seemingly teleological behavior of the homing torpedo requires that it be able to move to some degree independently of the sound field of the target ship, so species must be able to move to some degree independently of the ecological field in which they are evolving. In evolution, lower-level freedom is guaranteed by the omnipresent tendency in organisms to vary. At the population level, this variation takes the form of mutation and drift. At a larger scale, it can be either drift or change under the influence of selective forces independent of the adaptation in question (McShea and Brandon 2010). Turtle necks were doubtless under selection

for capacities other than folding, selection that must have deflected the evolution of folding at various times. From the perspective of the neck-folding field, these deflections also count as “errors.” In any case, whatever the source of variation, a certain amount of it is necessary for persistence. To follow an error-and-correction trajectory, it must be possible to make errors. That said, it is worth noting that lower-level freedom must not be tuned too high. Too much freedom, too much variation and drift, and the ecological field would be unable to restore the species to its adaptive trajectory. Persistence would fail.

Finally, a point with uncertain consequences. It has been claimed (e.g., Rosenberg and McShea 2007) that natural selection is the only known route to adaptive evolution. Factors such as constraints and phenotypic plasticity have long been recognized as important influences on variation, and new routes to inheritance, such as epigenetic inheritance, have recently entered the evolutionary discourse. But none of these on its own is sufficient for adaptation. And so the original claim remains true: no process—other than blind variation and selective retention—is known that can produce a fit between organism and environment. The hierarchical view of adaptation does not challenge this. But it does open the door to other as-yet-unidentified possibilities. Natural selection is a lower-level mechanism. It is a mechanism by which organisms can be remodeled by the environment on evolutionary timescales. Any lower-level mechanism that allows for environmentally driven remodeling on long timescales would do. Perhaps there are self-organizing mechanisms that can produce the same sort of remodeling. In any case, what the hierarchical viewpoint reveals is that the heart of the process that creates the organism-environment fit, the factor that gives the process its teleological “feel,” is the hierarchical relationship between the ecological field and the evolving species and not the particular mechanism by which the species is made malleable. In other words, adaptation in evolution does not, in principle, require natural selection. Of course, again, at present, it does, but simply because no other mechanism of malleability is known.

## Conclusion

Kant famously said there would never be a Newton for a blade of grass—in other words, no one would ever provide a thoroughly mechanistic account of biological teleology (Rosenberg and McShea 2007). But, one might

ask, doesn't natural selection provide just such an account, showing how all biological goal-directed systems could have arisen? Wasn't Darwin that Newton? The answer is both yes and no. Natural selection does explain the *origin* of organismal tropisms, physiological homeostasis, and the seeming goal-directedness of development. But it does not explain how these systems work, how they are able to create the appearance of goal directness. It does not tell us how persistence and plasticity are achieved. The answer—the knockout punch following Darwin's jab at Kant—is hierarchy: large fields giving direction to smaller entities nested within them. Further, the process of natural selection is itself structured in this way. Selection is species changing within and directed by ecological fields. And it is that hierarchical structure that gives selection its teleological flavor.

This may seem like a strange inversion. We think ordinarily of selection as the source of hierarchy in biology rather than a consequence of it. For example, consider the trend in organismal hierarchy, in levels of organization, from bacterium to eukaryotic cell to multicellular individual to colony and society (McShea 2001). Conventionally, we imagine that selection is what drives these so-called major transitions (Maynard Smith and Szathmáry 1995). That might or might not be true. There are other ways that hierarchical structure can increase besides natural selection. For example, the natural aggregative tendencies of chemical systems, the slight bias toward bonding over dissociation, might be enough to power such a trend (Wicken 1987; see also Simon 1962 and Fleming 2012). But whether or not selection is the driving force, hierarchy must have come first. For one thing, higher-level units must arise before they can be selected (Fleming and Brandon 2015; Simpson 2012). For another—and what the argument here makes plain, I hope—selection itself requires hierarchy. In order to even think about selection in biological entities, we must first suppose them to be nested within ecologies and those ecologies to have causal powers. In other words, hierarchy is conceptually and ontologically prior to selection. It is more fundamental.

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