LIMITS TO DARWINISM

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Natural selection exemplifies the physical principle of maximal energy gradient dispersion, is unable to alter early ontogeny, cannot be responsible for generating development including senescence, and is unable to explain convergent evolution of more than a single dimension.

'Self-organization proposes what natural selection disposes.' This catchphrase (Batten, et al. 2009) is well exemplified in Linde's paper. Her association with Stuart Newman's developmental biology program exposed her to the work of material self-organization in developing embryos, as carried on by generic physical mechanisms mediated by direct and indirect products of the genes of the 'developmental toolkit,' in the form of 'dynamical patterning modules' (DPMs).

The broader framework here considers living systems to be dissipative structures (Prigogine, e.g., 1980), acquiring form (*eidos*) spontaneously as they accumulate around flows of energy. Each living form extends from within, as mediated by DPMs, while being limited externally by ecological constraints enfolding its available energy sources. These external limits are the province of evolutionary biology. Living systems are organized to facilitate the flow of energy through them (Bejan and Lorente 2010), utilizing genetic information, acquired historically, to refine the channeling of these flows. In this physical perspective we follow Cuvier's view that form follows function, and we note that all dissipative structures function, from the universal point of view, to mediate the dispersal of energy. Each form emerging during development increases its energy flow throughput (Odum and Pinkerton 1955).

Some might think that the viewpoint expressed above is reductionist, but this would be mistaken if 'reduction' is interpreted, as usually in biology, to mean reducing life to molecular interactions. Life might logically be held to be a kind of chemistry, but that would leave out its meso- and macroscopic aspects (cells, organisms, populations, species, and bi-

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This article comments the article of Marta Linde Medina, "Natural selection and self-organization: A deep dichotomy in the study of organic form," published in this issue (pp. 25-56).

Ludus Vitalis, vol. XVIII, num. 34, 2010, pp. 227-235.

omes). My physical viewpoint here extends from the microscopic (heat energy production) through the other levels, all of which are kinds of dissipative structures) and extends further, to the earth itself and out into the cosmos. The universe can be assumed to be globally engaged in the process of thermodynamic equilibration, as a consequence of the ongoing Big Bang having produced so much order—so many forms—by way of gravitation and its sequelae. Our activities link directly to the cosmos.

My perspective here is certainly physicalist, and in one sense, as shown in this hierarchy

{physical world {material world {biological world}}}

is more reductionist than the materialist approach of Newman and his co-workers. Such conceptual reductions are inevitable if we are to place biology within an intelligible framework, which is what we attempt to do in natural philosophy. The physical world is much bigger, as well as much smaller, than any level where biology extends its reach, and so we might say that the physicalist approach not only reduces biology, but *extends* it to physics. Entropy production locally is a universal affair in our non-equilibrium universe.

Let us examine whether my perspective here actually is very far from the current understanding in evolutionary biology. Many biologists take natural selection to be the key concept of biology. Darwinism in evolutionary biology can be defined as the view that natural selection is the most important concept in understanding biological evolution. It is, as Fisher's (1929) model demonstrates, the idea that the kinds in a population that reproduce fastest will come into dominance in that population. But this is just an extension of the physical idea that possible energy flow channels that mediate the fastest dissipation of energy gradients will come to dominate the world of dissipative structures (e.g., Matsuno and Swenson 1999; Annila and Salthe 2010). Reproduction, as with any production, is energy intensive, and maximizing its rate tends necessarily to increase the associated entropy production (Salthe 2009). So then we can see that natural selection, as revealed in Fisher's model, is physically a more complicated version of a principle referred to as the 'maximum entropy production principle' (MEPP) (Swenson 1997; Lorenz 2002; Dewar 2003; Mahulikar and Herwig 2004; Sharma and Annila 2007; Kleidon 2010).

MEPP (which biases the choices of energy flow pathways toward the most energetically costly via the fastest possible work) can also be postulated to entrain developmental activities to take the quickest routes through ontogeny consistent with a species' life history. This point of view, suitably modified for application to local activities as the 'maximal energy dispersal principle' (MEDP) (Annila and Salthe 2010), has yet to inform developmental biology, but I would guess that it could contribute to understanding, for example, the standard forms of vertebrate embryonic stages up to the phylotypic stage (Hall 1997). These stereotypical forms may be thought of as the generic external result of an internal struggle to acquire form as rapidly as possible by self-organization in an out-of-equilibrium universe. Tentative evidence for this may be found, for example, in the formation of the primitive steak in the chicken embryo, where this is accompanied by "large-scale vortical cell flows" (Vasiev, et al. 2010). The vortex, along with branching tree forms, is a spontaneous pattern of convective flows that often accompanies increased energy dissipation.

Turning now away from physics, I call attention to an observation on animals and plants that involves specifically *biological* information as clearly as any problem currently taken upon evolutionary biology, which is dominated by the 'descent with modification' perspective of Darwinism. The Darwinian perspective understands phylogeny to be an invasion of living systems into a plethora of ecological niches as its key image, cladogenesis. This is fundamentally another elaborate version of the increase in entropy as visualized in physics. It represents in particular an increase in the informational entropy of living systems overall—the Maxent principle (e.g., Brooks and Wiley 1988)—which also tends to multiply the dissipation of diverse energy gradients as each species becomes specialized ecologically.

Well, what, then, is the observation that directs our attention in a conceptual direction opposite to the Darwinian program and its implicit physical support—and so is now largely ignored by evolutionary biologists? Contrary to the usual image of 'descent with modification,' it is convergent evolution (e.g., Willey 1911; Conway Morris 2003). Here is a short list of examples:

1. Jellyfish, squids and vertebrates have focusing eyes on the same plan. It is known that the clear protein that makes up the lens is coded for by different genes in these cases. The genes are different, but the form and function are the same. Amazingly, the same form is found as well in the eyespot of single-cell dinoflagellates (Leander 2008).

2. Both old man's beard (a lichen) and Spanish moss (a flowering plant) live as finely dissected grayish masses draped over the branches of trees in misty coastal environments, the first in northeastern North America, the second in southern coastal regions. They are organized so as to capture water from mist, and minerals from dust.

3. Both the very primitive hagfish in the oceans and an Amazonian catfish live by burrowing into large rotting corpses that have drifted into deep waters. Their bodies have converged upon a muscular eel shape covered in slime, which can tie itself into knots.

4. The primitive freshwater fish Polyodon and the basking shark have evolved the same body form, mouth structure and behavior for feeding upon plankton. It should be noted in this case that there are other kinds of body designs for this same economic activity, notably in the whale shark and among whalebone whales. That is, we cannot explain these similarities by claiming that there is only one possible way to achieve this particular way of life, in which case natural selection would have been sufficient to explain the similarities.

5. The New World vultures have evolved from hawks, while Old World vultures evolved from storks.

6. Hummingbirds and hummingbird moths have evolved the same body form, general size and hovering behavior allowing them to feed upon nectar in flowers. Other birds and butterflies have achieved this economic activity in quite different ways.

7. Large complicated underground nests with tall chimneys for air conditioning have evolved both in some tropical ants, related to wasps, and in some tropical termites, related to cockroaches.

8. A stunning larger scale example is found in comparing the many body shapes and lifeways of marsupial mammals with those of eutherian mammals. The faunas of each, which evolved independently on separate continents, duplicate the same major forms and lifeways, like those of wolves, mice and badgers—even saber tooth tigers. We do find a few very specialized kinds in each group that were not duplicated in the other fauna, like the eutherian bats. Also, while the lifeways of kangaroos compare closely with those of antelopes and deer, their body forms and progression are different, and so not all the ecological duplicates in this general example are as closely similar as most of them are. Google 'Tasmanian Tiger' to watch how closely this animal appears doglike.

9. An even larger scale example is found in the fossil record, when early paleoniscoid fishes were replaced, after a mass extinction, by holostean fishes, and when these were replaced after another large scale extinction by modern teleost fishes. All of these faunas evolved the same panoply of body forms—minnows, pikes, eels, flatfish, panfish, and so on. This pattern of replacement has been called 'iterative evolution,' Again, there are some unique forms, like teleostean seahorses, not found in the earlier faunas.

10. Agriculture was evolved separately by humans, ants, termites and bark beetles.

11. Another large scale example is the evolution of similar vegetations in different regions, while the species are all different. A well-known example is the Mediterranean vegetation profile found also in the Andes Mountains, South Africa, California and in Australia. In this case the

similarity clearly involves factors larger in scale than organisms and their genes.

As can be seen, convergence has been significant during biological evolution. But where could such 'anti-entropic' information reside in the living world? As a first guess, it might be carried internally as genetic information, which, then, holds more kinds of information than only that relative to particular local external circumstances.

As the old saying goes—'there's more than one way to skin a cat'—so how could distantly related species sometimes access quite similar forms when adapting to new habitats? Now, certain similarities acquired by several distant phyla would not be problematic for the selectionist view—for example, streamlined body shapes in species that move swiftly through water. Classical adaptive scenarios suffice to explain such very general similarities in a single functional dimension, as seen in this case in squids, sharks and porpoises. If it could be shown that there could be only one way to access a general ecological niche (sensu Elton 1927), then convergence would cease to be an issue. Failing that, the Darwinian principle of increasing morphological disparity accompanying the generation of new ecological niches does not explain evolutionary convergence.

Turning again to the developmental aspects of Linde's text, we can note another limitation on natural selection (Salthe 2008), tending to diminish its explanatory power in Evo-Devo biology. Two perspectives on natural selection serve to cast doubt upon its ability to affect ontogeny. First, genetic drift is acknowledged to interfere with selection in small populations, but as a general statistical principle it will also come into play if there is a prolonged interlude between selection and reproduction, during which time subsequent selective factors on viability could vitiate earlier selective results. This is the case in embryos, which go through several very different life stages as they develop. Selection will of course necessarily have its effects at each stage, but since these stages do not reproduce, the effects of selection in earlier stages will gradually become obscured by selection for quite different traits in later stages. These earlier effects of selection, especially in the earliest stages, will 'drift' as a result.

At the same time, the poor 'reproductive value' (RV, of Fisher 1929) of embryos mitigates against any selection acting upon them from having an effect on the population. RV measures the likelihood that a life stage will contribute to a population's reproduction. It is greatest during the earliest reproductive ages and drops off in later age groups, which become increasingly less represented in the population as individuals die off. This effect has been used to devise a Darwinian explanation of aging. From the other end, the RV of embryos gradually increases as the likelihood of any of them contributing to the effective breeding population increases as they continue to develop (i.e., survive). Embryonic and larval mortality rates, high at first, tend to drop off with continued development. And so the RV of the earliest developmental stages is very low. Then the results of any selective pressures acting upon them in regard to their survival could not feature significantly during selection upon the reproductive stages. I have suggested that these constraints on selection are beneficial overall since any effects of selection in the earliest developmental stages, if preserved, might curtail their generative capacity by evolving specializations in what must necessarily be vague embodiments in those whose role in life is solely to develop.

Getting more 'physical' again, development, when viewed broadly from a general dissipative structure perspective, is a property of all dynamic material systems. Here is a table (Salthe 2010) showing the generic changes during development as viewed from the thermodynamic and information theoretical perspectives.

IMMATURE STAGE
- Relatively high energy density (per unit mass) flow rate
- Relatively small size and/or gross energy throughput
- Rate of acquisition of informational constraints relatively high, along with high growth rate
- Internal stability relatively low (it is changing fast), but dynamical stability (persistence) is high
- Homeorhetic stability to same-scale perturbations relatively high

MATURE STAGE (only in relatively very stable systems like the living)
- Declining energy density flow rate is still sufficient for recovery from perturbations
- Size and gross throughput is typical for the kind of system
- Form is definitive for the kind of system
- Internal stability adequate for system persistence
- Homeostatic stability to same-scale perturbations adequate for recovery

SENESCENT STAGE
- Energy density flow rate gradually dropping below functional requirements
- Gross mattergy throughput high but its increase is decelerating
- Form increasingly accumulates deforming marks as a result of encounters, as part of individuation
- Internal stability of system becoming high to the point of inflexibility
- Homeostatic stability to same-scale perturbations declining

It is quite clear that there is no need to suppose that natural selection has produced this generic developmental trajectory in living systems. It belongs to any dissipative structure. Of course, selection will monitor the ways by which members of individual biological species traverse these general stages—except, of course, the earliest and the final (senescent) ones, as noted in the text above.

Finally, I would emphasize that the physicalist perspective need not be mechanistic, which the materialist perspective often does tend to be. For example, non-equilibrium open systems are in principle not predictable in detail (e.g., Annila and Salthe 2010). Energy flows continually change the densities of involved energy gradients, so that no classical computations, for example those based on Gibbs free energies, would be possible. It seems likely that the 'fluctuating asymmetries' (Van Valen 1962) observed in organisms are a sign of the resulting indeterminism during development. The ruling causal power here would be the final cause of the Second Law, the sole physical propensity that is always fully realized, regardless of the material details in any particular case. Epigenesis from this perspective is a hasty 'developing upon' shifting sands that become irreversibly fixed only in transit.

Furthermore, both materialism and physicalism transcend mechanicism when we bring context actively into the picture. For example, protein shapes are not determined solely by the primary sequences of amino acids, but fluctuate with context—a behavior on which their functioning depends. Self-organization is materially a groping through channels of fluctuating contexts, both internal and external, producing individuation of the developing system. As an organism develops, the relative vagueness of an immature system gradually transforms into an increasingly more definite, and particular, embodiment, which, however, never becomes as fully explicit as the models published in the technical literature. These models are generic and meant to represent aspects of a system as they would be in standardized contexts—they are scenarios without story lines.

And yet—despite continuing evolutionary change—we have all those many curious examples of evolutionary convergence! These represent 'stories' that, like mythologies, emerge differently attired in many different (here genetic) contexts. If developmental self-organization is guided by genetic information reflecting past adaptive successes, which have been continually modified over the generations, how can these convergent patterns remain so stable?

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