

Fitness Meets Niche Construction and Symbiosis

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Abstracts

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Fitness Under Niche Construction

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In this talk, I will lay out the different ways niche construction can challenge a common conception of evolutionary fitness. To fix ideas, I will capture the common notion with a simple causal model. This causal model not only underpins many philosophical interpretations of fitness, it also reflects the intuitions driving colloquial and the usage of natural selection in other disciplines.

According to the causal model, *differences* in fitness are the result of *differences* in the (1) non-accidental, (2) intrinsic, (3) comparable features of traits or individuals, ensured in part by the presence of a (4) common environment. I will show that niche construction (and in some cases, massive symbiosis as well) challenges each component of this model.

My analysis has an important implication for the „counterexample” debate over the Propensity Interpretation of Fitness (PIF). PIF is a probabilistic interpretation of the fitness value in mathematical evolutionary models. The PIF is based on a specific causal model of fitness, which, I argue, is a species of the simple causal model outlined above. Past critiques of the PIF have focused on mathematical models inconsistent with PIF’s probabilistic representation of fitness. Responses to these counterexamples have either tried to fix the PIF’s probabilistic representation or abandon it while retaining the PIF’s causal model. I argue that causal counterexamples from niche construction share unifying features with the mathematical counterexamples and reject the PIF’s causal model. The problem with PIF is thus not just its specific representation of fitness as a kind of propensity, but also the causal structure of fitness that accounts for its propensity.

From individual interactions to population growth: Demographic definition of fitness and causal structures underlying evolutionary processes from the game theoretic point of view

Krzysztof Argasiński

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The talk will be focused on the definition of Darwinian Fitness as the measurable quantity related to the physical process of self-replication. It will be based on the latest development in mathematical models of evolutionary game theory. Organisms are regarded as replicators that produce copies of themselves and can be removed from the population in effect of death. Thus the two opposing physical forces shaping the size and the composition of the population are the fertility and the mortality. Reproduction and death of the individual depends on the interactions with other organisms or other elements of the environment. This leads to the possibility of trade-offs between different outcomes of the interaction, resulting from the causal structure of that interaction (for example when reproduction occurs after danger stage such as mating fight, only survivors can win and reproduce). Those interactions also affect the state of the individual (energy level, accumulation of damages) leading to life history mechanisms shaping its life cycle. This approach naturally leads to the demography as the basic conceptual toolbox. Individuals, which are rather „chemical reactions” of finite duration than „particles” with constant properties, constitute populations undergoing ecological and selection processes responsible for their size and composition. Those, processes may (or may not) lead to the population level dynamic equilibria, which in effect determine the fate of the contained individuals. This closes the feedback loop. Therefore, we can explain the natural phenomena in terms of „population machines” emerging from the local interactions (such as outcomes of pairwise encounters) or aggregated collective behaviour (for example bacterial quorum sensing).

Argasinski, K., and M. Broom. „Ecological theatre and the evolutionary game: how environmental and demographic factors determine payoffs in evolutionary games”. *Journal of mathematical biology* 67.4 (2013): 935-962.

Argasinski, K., and M. Broom. „Evolutionary stability under limited population growth: Eco-evolutionary feedbacks and replicator dynamics” *Ecological Complexity* 34 (2018): 198-212.

Argasinski, K., and M. Broom. „Interaction rates, vital rates, background fitness and replicator dynamics: how to embed evolutionary game structure into realistic population dynamics”. *Theory in Biosciences* 137.1 (2018): 33-50.

Doebeli, Michael, Yaroslav Ispolatov, and Burt Simon. „Point of view: Towards a mechanistic foundation of evolutionary theory”. *Elife* 6 (2017): e23804.

The Language of Adaptation and Niche Construction: Watchout a Metaphoric Snowball

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How should „fitness” be treated? This paper deals with the philosophical and linguistic aspects of the issue. In many cases, notions like „fitness” or „adaptation” work as teleological metaphors. According to Rosenberg and McShea, an explanation is said to be teleological when it resorts to notions such as ends, goals, purposes, or objectives (Rosenberg & McShea 2008). The deconstruction of metaphors, as I am going to argue, can disclose the ascribed teleology and prevent from much confusion.

An example of the use of metaphors in biosciences can be delivered by minimal intellect studies. Some recent research evidence may make one admit that diverse adaptive responses of creatures lacking neural system, like plants, to environmental cues display their „cognitive abilities” (Gross 2016; Trewavas 2016), and against all odds - plant’s „neurology” (Alpi et al. 2007; Calvo 2016; Msimang 2016). This leads to the deflation of the notion of “cognition” and „intelligence”, and hence, to the revision of a larger scope of scientific vocabulary. Similar thing happens to the discourse of fitness and adaptation, where figurative contexts ascribing functions and goals while explaining the evolution of communities have for a while prevailed over seeing their co-evolution.

The developments in scientific vocabulary and competition of theoretical and conceptual framework are quite normal and even a necessary thing. Furthermore, it is worth noting, that the scientific language is full of metaphors, which is hardly avoidable. Hence, the deconstruction of terms will probably not undermine the basic means of scientific communication. It is more likely, that putting a lot of effort in sorting out the old metaphors a scientific community creates new ones.

Characteristically, the so-called „teleological thinking” has been remaining pervasive in the discourse of fitness. The concepts of „co-evolution” and „niche construction” differ from the concept of „adaptation” to the environment conditions, but the discussion remains largely teleological in the principle. Some epistemic implications of this fact will be further analysed.

Speciation drives speciation or extinction? The parallel between the evolution of the concept of ecological niche in ecological modelling and of causality in evolutionary biology

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There is an ongoing discussion (especially in *Nature*) between two hypotheses. The first one says that speciation drives extinction (ex. Whittaker 2007). Here, the ecological modelling is based on the famous MacArthur-Wilson (1963, 1967) theory of island biogeography, which says that speciation and extinction depend on spatial properties of the environment (such as island size and isolation). In other words, speciation and extinction depend on properties extrinsic to the species being modeled. The second hypothesis says, on the contrary, that species diversity itself drives speciation and that the higher number of endemic species, the higher the speciation rate (Emerson & Kolm 2005). In this model, speciation and extinction depend on properties intrinsic to the species being modeled. I argue that the first hypothesis goes in line with the adaptationist, externalist 'lock and key' supposition that the discontinuity of species results from the discontinuity of environments to which species get adapted, while the second hypothesis goes in line with the supposition that the discontinuity of species results from the discontinuity of variation which now gets popular. I will show that there is a parallel between the evolution of the concept of ecological niche and the way we understand the causality in evolution.

Symbiosis of the fittest: Why function is more important than taxonomic composition

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While the number of microbial cells has been recently updated to roughly being the same, the number of genes of the microbiota still outweighs that of the human host by far. Thus, the host has a large repertoire of potential biochemical activities in addition to its own hereditary material at its disposal - at least to some extent. The host provides niches for certain microbes to colonize. From the host's perspective, it is less important which taxa are present, but rather that certain functions will be taken care of, e.g. digesting dietary fiber, while others are kept at bay, e.g. infection. At the same time, the microbes may re-shape and actively construct their niche by their activities.

Viewing the microbiota „as an ecosystem on a leash”, Foster et al. „therefore, expect natural selection to favour hosts that act as ecosystem engineers that influence not only individual species but also community-level properties, such as stability and productivity” (2017, p. 48). I suggest that *function* in the form of biochemical repertoire is such a community-level property that is more important - and persistent - than *taxonomic composition*. Taxonomic profiling still remains the major

way in which microbiota are being characterized. However, a frequent observation in microbiota studies is the fact that functional repertoire is more conserved across individuals than taxonomic composition:

This observation of similarity in habitat (niche) use with respect to functional genes, but not species, together with the relative ease with which bacteria share genetic material, suggests that the key level at which to address the assembly and structure of bacterial communities may not be „species” (by means of rRNA taxonomy), but rather the more functional level of genes. (Burke et al., 2011, p. 14288)

Therefore, I suggest to modify idea of measuring ecological fitness as persistence through time (Bouchard, 2008) by addressing differential persistence of functional aspects rather than taxonomic lineages. The focus on function has consequences for both evolutionary and physiological questions, where the co-evolution and development of microbiota and host is not pictured as passive colonization; instead, the active construction of niches from both parties constitutes fitness investments that impact each other's fitness and shape the dynamics of their symbiotic relationship. An important aspect in this enterprise will be the role of the immune system in monitoring niche colonization and construction by the microbiota. The interplay of functions results in a feedback-dialog such that host and microbiota „invest” in each other's fitness for optimal functionally fitting niches, together maximizing the persistence - and fitness - of the holobiont.

References

- Bouchard, F. (2008). Causal processes, fitness, and the differential persistence of lineages. *Philosophy of Science*, 75(5):560–570. doi:10.1086/594507.
- Burke, C., Steinberg, P., Rusche, D., Kjelleberg, S., and Thomas, T. (2011). Bacterial community assembly based on functional genes rather than species. *Proceedings of the National Academy of Sciences*, 108(34):14288–14293. doi:10.1073/pnas.1101591108.
- Foster, K. R., Schluter, J., Coyte, K. Z., and Rakoff-Nahoum, S. (2017). The evolution of the host microbiome as an ecosystem on a leash. *Nature*, 548:43–51. doi:10.1038/nature23292.

Ecological 'Inception': Can organism be a niche?

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Recent development of technology allowed to consider influence of bacteria on hosts biology. Among invertebrates the most influential are endosymbiotic bacteria that cause number of phenotypic and even genotypic effects on hosts populations. As a consequence, these bacteria can affect not only current ecological relations or host physiologies, but also causing evolutionary effects, e.g. contributing to speciation. In the world of insects, there are a number of endosymbiotes, of which the following types deserve special attention: *Wolbachia*, *Cardinium*, *Spiroplasma* and *Rickettsia*. All of them characterizes a similar effect on the biology of their hosts.

Among these bacteria *Wolbachia* is the most frequent and best known endosymbiote. This intracellular bacterium is known to cause a number of manipulations of hosts reproduction through male-killing, cytoplasmic incompatibility, parthenogenesis induction, and feminization of genetic males to increase its own fitness. However recent discoveries showed that it also can protect its host from RNA viruses or be bacteriocyte-associated nutritional mutualist. For long time it was believed that *Wolbachia* can be only inherited in mothers line. Currently we have numerous evidences that it also can be transmitted horizontally to previously uninfected specimen through common food source, predation or through parasitism.

In my studies I use molecular tools to investigate whether there are dependencies in the ecological and evolutionary context between the occurrence of endosymbiotic bacteria and beetles. Beetles species can be found in almost all freshwater and land-based ecosystems, they are a very ecologically plastic group in which representatives of almost all life strategies can be found. On the micro level single specimen can be consider as a niche for resident microorganisms, collectively known as the microbiota. My aim was to answer the question: what shapes the microbiota composition of host and which (if any) of its traits make it more prone to be infected by endosymbiotic bacteria. My results indicate that *Wolbachia* is the most common endosymbiont with 27% infection level and *Rickettsia*, *Spiroplasma* and *Cardinium* were much less prevalent as they infected: 8%, 3% and 2%, respectively. Co-infection by different endosymbionts occurred rarely and was limited mostly to two bacteria taxa within one host. Moreover hosts that share some biological/ecological traits were more often infected by *Wolbachia* than others. Trophic affinity (as well as habitats and microhabitats, which are correlated with trophy) is probably the most important explanation for *Wolbachia* occurrence in beetles. *Phytophagous* and saprophagous species had the highest infection rate (38.6% and 34.3% respectively) whereas predators were the least infected ones (17.6%). Such phenomenon is probably associated with horizontal transfer of bacteria. This findings correspond to my other studies in which I found preliminary evidence for horizontal transfer of *Wolbachia* among *Crioceris* leaf beetles through host *Asparagus* plant. On the other hand such pattern did not occurred in predatory ground and rove beetles which share the same habitat and probably feed on similar pray. Finally my findings indicate that hosts microbiome is shaped by both phylogenetic affinity and diet and less by endosymbionts presence.

Fitness and complexity

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Derived from the theory of information, the notion of complexity, or more specifically functional complexity, provides a widely applicable measure that could help explain a plethora of biological phenomena, including consciousness (Tononi et al. 2016). The notion of complexity is important also with relation to evolution and fitness - in the theoretical biology and philosophy of biology there has been a lively discussion over understanding the direction of evolutionary change either in terms of increase of fitness or in terms of increase of complexity (Saunders & Ho 1976, Joshi et al. 2013).

Unfortunately, the most popular formalisms developed within the information theory, computer science, and physics, e.g. the Kolmogorov complexity (Kolmogorov 1968), are not easily fitted to living organisms (Deacon & Koutroufinis 2014). It seems however, that with the advent of Karl Friston's free energy principle (and the associated active inference framework, Ramstead et al. 2018, Kirchhof et al. 2018) and the work that is being done within this framework on niche construction (Constant et al. 2018) it became possible to provide an accurate, intuitive, and formal definition of functional complexity.

The free energy principle is a normative rule that aims to provide a unified account of the processes of life and cognition happening on multiple timescales: evolutionary, phylogenetic, ontogenetic and real-time (Ramstead et al. 2018). Its key claim is that systems, defined by their enclosure in a Markov blanket, aim to minimize the difference between their model of the world and the actual state of their environment. This difference is measured in information theoretic terms as surprisal. However, since the systems cannot directly access the actual amount of surprisal, they have to minimize the upper bound on it, provided by the free energy (Friston 2010). This minimization, according to the active inference framework, is an active process that can be (with certain reservations) described analogously to the process of scientific hypothesis testing.

In the paper I will propose a formal definition of complexity derived from the free energy principle that realizes the following intuitions: it is a continuous, additive function; it is closely related to the processes (past and future) happening in the living organism; it is applicable both to biological systems and to informational systems; it is intuitive (in the sense of the Deacon's „frog soup” problem); it is a real property of the analyzed system. I will try to show that this definition unites the notions of complexity and of fitness.

References

Constant, A., Ramstead, M. J. D., Veissière, S. P. L., Campbell, J. O., & Friston, K. J. (2018). A variational approach to niche construction. *Journal of The Royal Society Interface*, 15(141), 20170685. <https://doi.org/10.1098/rsif.2017.0685>

- Deacon, T., & Koutroufinis, S. (2014). Complexity and Dynamical Depth. *Information*, 5(3), 404–423. <https://doi.org/10.3390/info5030404>
- Friston, K. (2010). The free-energy principle: a unified brain theory? *Nature Reviews Neuroscience*, 11(2), 127–138. <https://doi.org/10.1038/nrn2787>
- Joshi, N. J., Tononi, G., & Koch, C. (2013). The Minimal Complexity of Adapting Agents Increases with Fitness. *PLoS Computational Biology*, 9(7), e1003111. <https://doi.org/10.1371/journal.pcbi.1003111>
- Kirchhoff, M., Parr, T., Palacios, E., Friston, K., & Kiverstein, J. (2018). The Markov blankets of life: autonomy, active inference and the free energy principle. *Journal of The Royal Society Interface*, 15(138), 20170792. <https://doi.org/10.1098/rsif.2017.0792>
- Kolmogorov, A. N. (1968). Three approaches to the quantitative definition of information. *International Journal of Computer Mathematics*, 2(1–4), 157–168. <https://doi.org/10.1080/00207166808803030>
- Ramstead, M. J. D., Badcock, P. B., & Friston, K. (2018). Answering Schrödinger’s question: A free-energy formulation. *Physics of Life Reviews*, 24, 1–16. <https://doi.org/10.1016/j.pprev.2017.09.001>
- Saunders, P. T., & Ho, M. W. (1976). On the increase in complexity in evolution. *Journal of Theoretical Biology*, 63(2), 375–384. [https://doi.org/10.1016/0022-5193\(76\)90040-0](https://doi.org/10.1016/0022-5193(76)90040-0)
- Tononi, G., Boly, M., Massimini, M., & Koch, C. (2016). Integrated information theory: from consciousness to its physical substrate. *Nature Reviews Neuroscience*, 17(7), 450–461. <https://doi.org/10.1038/nrn.2016.44>
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Why the evolution of heritable symbiosis neither enhances nor diminishes the fitness of a symbiont?

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One of the current problems in microbiology concerns the understanding of fitness in host-symbiont systems. A great deal of research and conceptual work has analysed how the host benefits from such associations; however, very little of this work has attempted to take the microbial perspective. Nevertheless, some scientists have argued that we should conduct more comparative studies of microorganisms that interact with a host and their free-living counterparts in order to determine whether or not symbiosis is beneficial for these microorganisms. In this paper, by means of analysing heritable symbiosis as a case study, I intend to provide a different perspective on this subject. Mainly, I argue that asking how the fitness of a given microorganism was changed during the evolution of heritable symbiosis may be theoretically unjustifiable, at both the early and late stages of this process. The reason for this, I argue, is that, during the evolution of heritable symbiosis, the fitness of microorganisms becomes incommensurable with that of its free-living counterparts because their contexts become radically different; therefore, comparing their fitness makes little sense. My analysis is driven by the use of the ecological concept of fitness; accordingly, my conclusions are bound to this specific interpretation of fitness.

Holobionts as niche constructors, and how to measure their fitness

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Holobionts are biological assemblages composed by a macroorganism (animal, or plant), plus its symbiotic microbiome. Under the framework of the hologenome concept of evolution, some biologists and philosophers have recently argued that holobionts are biological individuals and that, together with their hologenome, they are a unit of selection in evolution (Rosenberg and Zilber-Rosenberg 2008, 2013; Theis et al. 2016; Lloyd 2017). The thesis that the holobiont and its hologenome constitutes a unit of selection in evolution squares poorly with the scientific evidence, though, as the taxa that compose the microbiome of a host does not seem to get faithfully transmitted transgenerationally (Moran and Sloan 2015; Douglas and Werren 2016; Hurst 2017). Recently, I have argued that the lack of species co-transmission is not problematic if the microbiome is conceived functionally, instead of taxonomically, and holobionts are conceived as units of selection from a multilevel selection 1 perspective (MLS1), instead of from a multilevel selection 2 perspective (MLS2) (Suárez, under review). However, so far, I have not yet developed how the “functional” holobiont could be conceived as a unit of selection from a MLS2 perspective. In this paper, I will argue that it is possible to do so by appealing to the notion of niche construction.

A MLS2 perspective requires the existence of parent/offspring relationship between holobionts. If holobionts are conceived functionally, instead of taxonomically, a MLS2 perspective could be applied to conceive their parent-offspring relationships by studying the patterns of functional similarity between the parental microbiome and the offspring microbiome for a host generation. If the similarity between parent and offspring is higher than between random members of the population, then holobionts would arguably evolve via MLS2 selection. In this paper, I will argue that niche construction can arguably act as a mechanism to guarantee parental/offspring functional similarity concerning their microbiome composition. I will argue that, by constructing their niches for their offspring, hosts undirectededly construct the microbial niche too, and in doing so they increase the likelihood that their offspring bears a sufficiently similar microbiome than the one they bore. Niche construction act, in this sense, as a mechanism to guarantee inheritance relations among holobionts.

I will finally relate this observation to fitness by arguing that niche construction can also be a means to measure the fitness of holobionts to the environment, in so far as it can guarantee that some hosts transmit their microbiome more than other hosts. In the case of the holobiont, there will be two measures of fitness: on the one hand, the fitness of the host (how many offspring it produces); on the other, the fitness of the microbiome (how functionally similar are the different microbiomes in the holobiont population). Niche construction, I argue, would play a role in the later, but not in the former.

Evolution of multicellularity: cheating done right

Walter Veit

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For decades Darwinian processes were framed in the form of the Lewontin conditions: reproduction, variation and differential reproductive success were taken to be sufficient and necessary. Since Buss (1987) and the work of Maynard Smith and Szathmary (1995) biologists were eager to explain the major transitions from individuals to groups forming new individuals subject to Darwinian mechanisms themselves. Explanations that seek to explain the emergence of a new level of selection, however, cannot employ properties that would already have to exist on that level for selection to take place. Recently, Hammerschmidt et al. (2014) provided a ‘bottom-up’ experiment corroborating much of the theoretical work Paul Rainey has done since 2003 on how cheats can play an important role in the emergence of new Darwinian individuals on a multicellular level. The aims of this paper are twofold. First, I argue for a conceptual shift in perspective from seeing cheats as (i) a ‘problem’ that needs to be solved for multi-cellularity to evolve to (ii) the very ‘key’ for the evolution of multicellularity. Secondly, I illustrate the consequence of this shift for both theoretical and experimental work, arguing for a more prominent role of ecology and the multi-level selection framework within the debate then they currently occupy.
