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SPECIAL ISSUE: THE SEMIOTICS OF HYBRID NATURES

Semiotic Fitting and the Nativeness of Community

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Abstract

The concept of 'semiotic fitting' is what we provide as a model for the description and analysis of the diversity dynamics and nativeness in semiotic systems. One of its sources is the concept of 'ecological fitting' which was introduced by Daniel Janzen as the mechanism for the explanation of diversity in tropical ecosystems and which has been shown to work widely over the communities of various types. As different from the neo-Darwinian concept of fitness that describes reproductive success, 'fitting' describes functional (sign) relations and aboutness. Diversity of a semiotic system is strongly dependent on the mutual fitting of agents of which the semiotic system consists. The focus on semiotic fitting means that, in the analysis of diversity, we pay particular attention to decision making (choice), functional plasticity, recognition windows, the depth of interpretation of the agents, and the categories responsible for the structure of the semiotic system. The concept of semiotic fitting has an early analogue in Jakob von Uexküll's concept of '*Einpassung*' (as different from '*Anpassung*', meaning 'evolutionary adaptation'). The close concepts of 'semiotic fitness', introduced by Jesper Hoffmeyer and by Stéphanie Walsh Matthews, 'semiotic selection', introduced by Timo Maran and Karel Kleisner, and 'semiotic niche', introduced by Hoffmeyer, provide different versions of the same model. If community is constructing itself on the basis of (relational) fitting, then nativeness of the community is a product of fitting, not vice versa. Nativeness is a feature that deepens in the course of community succession. The concept of 'semiotic fitting' demonstrates the possibility to analyse the role of both indigenous and alien species or other agents in a community on the basis of a single model.

Keywords Coevolution · Coexistence · Community · Consortia · Ecological fitting · Fitness

We define 'semiotic fitting' as the agent's capacity for making and preserving the local semiotic bonds, meaning the agent's functional or communicational match with its surrounding. Semiotic relations differ from other relationships due to their specific

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mediatedness, which means they are empirically detectable. The semiotic aspect of the concept carries the functional and meaningful quality of adaptedness that became lost in the concept of 'evolutionary fitness' as a result of the formalization of the mechanism of natural selection. In this article we explore some core aspects of the concept of 'semiotic fitting'.

The Reality of Community

In order for a system to be a *whole* — and in that sense real — it requires reciprocally generated constraints (see Montévil and Mossio 2015; Deacon 2011). We focus here on the modelling of biological communities, because these are the systems in which fitting occurs.

In the dominant formal models of species coexistence based on the island biogeography approach or the concepts of metapopulation and species pool, the set of species that coexist in a certain space is derived from the balance between immigration, reproduction, and extinction, modified by environmental conditions and habitat diversity (for instance, Wu and Vankat 1991; Hubbell 2001). The set of species[1] in such models of dynamic balance (called 'neutral theory' — see Leibold and Chase 2018: 27) may simulate the species' composition in an area rather well. However, the set of coexisting species in this type of models should not yet be called a community, because these models do not require specific functional (communicational, semiotic) bonds between the species that would turn the set of species into a kind of functional whole.

We define community as a set of species that are functionally linked, i.e. linked by restorable mediated bonds. By these bonds we mean the relations based on processes of recognition (like, for instance, the recurrent relations between a predator and prey, flower and pollinator, root and mycorrhiza fungus, etc.). Thus, the community is real if its members (coenopopulations) are linked by self-restorable[2] mediated bonds. Since the restorable mediated bonds or relations of recognition are the same as code-relations or habits, we receive a further version to define a community: it is the local set of code-related species. The codes or habits that are responsible for the functioning of the community would be called ecological codes (Kull 2010).

In this way, defining community as the functionally related set of species — i.e. as a self-restorable (which also means inheritable) network of species, as consortia, as we will later see — implies that there could be species in a territory that do not belong to the community. These ex-community species commonly include irregular migrants, but not only and not always. For instance, if a territory is inhabited exclusively by herbs of several species in a sterile soil, then there is no community, because different plant specimens commonly cannot have direct functional relations with each other. Common resources usually cannot serve as a mediator that creates specific links. Functional relations between plants almost always require non-plant organisms for mediation. This means that the set of vascular plant species may form a real community almost only due to non-plant organisms that are responsible for functional relations: fungi, animals, microbiota. The core of the community is a linked set of consortia.

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[1] The expression 'set of species' means in this article "the local set of organisms that belong to various species" (which is equivalent to 'set of coenopopulations').

[2] I mean that sign relations (and codes) are preserved due to restorable mediators.

In conclusion, the reality of *community* is largely analogical to the reality of *species*. A species is real if it is based on the pairwise recognition between individuals (thus forming a category of the family-resemblance kind in Ludwig Wittgenstein's sense — see, e.g., Kunz 2012: 60–61). The recognition species concept (Paterson 1993) and the biosemiotic species concept (Kull 2016) meet this criterium, while phylogenetic and typological species concepts do not. Both in case of species and of community, their reality stems primarily from fittting, not from boundaries (which are secondary and fuzzy).

Co-Evolution Versus Ecological Fitting

A community of organisms, if the community is real (in the sense described above), has a structure based on mutual relationships between individuals of different species. There are parasites and hosts, plants and pollinators, predators and prey, roots and their fungal symbionts, etc. In order to explain how such structures came about, ecologists Paul R. Ehrlich and Peter H. Raven introduced the concept of 'coevolution' (Ehrlich and Raven 1964). The definition of 'coevolution' says that there is coevolution if a trait in one species has evolved as a response to a change of a trait in a second species, which again has influenced the evolution of the second species. The concept quickly became popular and coevolution was seen as the main mechanism explaining the congruence or conformity of species in communities.

16 years later, in 1980, Daniel Janzen published a two-page article in the journal *Evolution*, in which he claimed that this is not at all obvious. He wrote (Janzen 1980: 611):

> It is commonly assumed that a pair of species whose traits are mutualistically congruent have coevolved. For example, it is quite possible that the fruit traits of a mammal-dispersed seed coevolved with the mammal's dietary needs. However, it is also quite possible that the mammal entered the plant's habitat with its dietary preferences already established and simply began feeding on the fruits of the species that fulfilled them. When this occurs, it is those species that are most exactly congruent which will appear most coevolved yet are likely to be the least coevolved.

And he concluded (Janzen 1980: 611–612):

> I plead for the retention of the usefulness of 'coevolution' by removing it from synonymy of usage with 'interaction', 'symbiosis', 'mutualism', and 'animal-plant interaction'. A bee is not necessarily coevolved with the flower it pollinates, a caterpillar is not necessarily coevolved with its sole species of host plant, and a bruchid beetle[3] is not necessarily coevolved with the protease-rich legume seeds that it preys on.

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[3] The same example with bruchid beetle (*Bruchus pisorum*) was used by Jakob von Uexküll when arguing for *Einpassung* (e.g., von Uexküll 1928: 219–220; 1957: 68–69). Janzen confirmed that he provided this example independently, as he had not read Uexküll (Kull 2018a).

Daniel Janzen is a tropical ecologist who has worked for a long time in Costa Rica. He has discovered and described several co-dependent relationships in tropical communities and published a series of books about the nature of Costa Rica. One of the earlier results of his work is known as the Janzen-Connell effect. This is a widely accepted explanation for the maintenance of the biodiversity of tree species in tropical rainforests.

The Janzen-Connell effect is based on the observation that parasites or herbivores that feed off the seeds of a particular tree species are gathered more than proportionally at the places where the food source is highest — close to that species of the tree. As a result, renewal of the species of the tree will not take place close to the mother tree, but more often within a certain distance from it, where parasite density is lower (Janzen 1970). Another ecologist, Joseph Connell, proposed a similar explanation (Connell 1971). Connell (1975) also suggested that the role of competition is overestimated, and food relations play a much bigger role in the establishment of community structure. The Janzen-Connell hypothesis is among the most important models put forward to explain species coexistence in species-rich communities. This hypothesis predicts that the probability of offspring survival should increase with the distance from conspecific adults, and decrease with conspecific offspring density, due to predation by host-specific pests near the adults. It has been shown to work widely over the ecosystems of various types (Agosta and Klemens 2008; Bever 2003; Petermann et al. 2008), however, it is not the sole mechanism responsible for the spatial pattern of a plant community (Zhu et al. 2013).

In 1985, Janzen published another very short article, “On ecological fitting”. He suggests that: “[…] a major part of the earth’s surface may be occupied largely by organisms that are rich in ecological interactions and have virtually no detailed evolutionary history with one another” (Janzen 1985: 309).

Thus, there are two major explanations to inter-species links — one based on coevolution, and another based on search-and-find behaviour. As Janzen and others have suggested, in most cases it is not co-evolution that is responsible for species-specific links. The formation of communities is a relatively quick process that does not require evolutionary time. Ecological fitting means that organisms search and find what fits them — that is, the conditions that correspond to their needs and the cohabitants with whom they match — and then stay connected with them.

Anpassung or *Einpassung*

In this respect it is relevant to recall what Jakob von Uexküll wrote about evolution. Uexküll made a distinction between two kinds of relations which he called *Anpassung* and *Einpassung*. In Tobias Cheung’s wording: “The I-tone of an organism that acts in its specific umwelt is not the result of a gradual “adaptation” (*Anpassung*) in time (as “Darwin” thought) or of the influence of the environment on the individual development of an organism (as “Lamarck” thought), but of its “adjustment” (*Einpassung*)” (Cheung 2004: 160, with reference to von Uexküll 1928: 317–321).

As Uexküll emphasises, *Einpassung*, or fittedness, is rather qualitative — there is no more or less fittedness, or a higher and lower level of it. *Einpassung* is just a match (sometimes, however, quite complex). This emphasis on the reciprocity of interactions in living systems is an important aspect for understanding Uexküll's views, among them his views on evolution. Evolutionary adaptation or *Anpassung* is a slow change, in which natural selection may play a role; it takes many generations for natural selection to be effective. Ecological fitting or *Einpassung* is quick; its time scale is that of communication processes. And importantly, '*Einpassung*' is an early version of the concept of 'semiotic fitting'.

Fitness Versus Fitting: How Fitness Lost its Meaning (and how to Recover it)[4]

What we just mentioned is exactly why we speak about ecological fitting, not fitness. Fitness is defined in the neo-Darwinian theory as the quantitative measure of reproduction ("reproductive success").[5] Fitting or fittedness is different — it is a qualitative, not a quantitative feature.

There is a well-known story of how the concept of 'information', initially used to describe the content of a message, as a result of formalization and becoming measurable by bits, lost its referentiality, the semantic aspect, the meaning in the sense of aboutness. Afterwards there were many works published on the problem of how to get meaningfulness back. The models that describe meaningfulness, the referential information, are essentially semiotic.

The history of the 'fitness' concept provides an analogical story. Herbert Spencer who retold Charles Darwin's theory by using the term of 'fitness' might still have assumed that fitness included a reference to something that surrounds organisms. However, when the theory of natural selection was formalized, it so occurred that such reference (i.e., the qualitative aspect) is unnecessary for the pure selection model — differential replication (together with random variability) is sufficient. The concept of fitness was cleaned from any referentiality or aboutness since the work of Ronald Fisher (1930). Fitness simply turned into reproductive success, or the measure of survival. Moreover, this also meant that agency is not required for an evolutionary theory based on natural selection. Organism as a complex active developmental system became lost in the neo-Darwinian formalized theory.

How to recover it? Obviously by using a model that can explicitly include reference, aboutness. Without such model we cannot even test whether aboutness or agency may work as a factor in evolution, or in a working of an ecosystem. The reality of reference is what is explained by semiotic models. The reality of reference means that the meaning is not assigned by the researcher, but it is a part of the organism's own being. While described by several biologists (for instance, by Jakob von Uexküll), a more formalised theory of reference was developed by Charles Peirce, and 'relational biology' was introduced by Nicolas Rashevsky and Robert Rosen as a non-reductionistic methodology for biology. We assume that agency, the agential aspect of organisms is what is necessary for aboutness of information, as well as for fitting.

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[4] This title alludes to Terrence Deacon's talk "How information lost its meaning (and how to recover it)" presented at Vienna summit of the International Society for Information Studies (June 2015).

[5] However, in a stationary community, fitness is same in all species — one survivor per capita per generation, independently of population number.

Selection or Choice

As we can conclude, Janzen's view on ecological fitting corresponds well to Uexküll's rather non-Darwinian view on evolution. Observing what is going on in research on theory of evolution in recent decades, we can find even more support for these views of Uexküll and Janzen.

One such supporting claim was the introduction of the concept of exaptation as an alternative to adaptation, by Stephen Jay Gould and Elizabeth Vrba, already in 1982 (Gould and Vrba 1982; Weible 2013). If evolutionary (Darwinian) adaptation is what begins with a genetic mutation that turns out to be useful, exaptation is what begins with a change in how an existing form is used, that is, a change in function. This contrast can be interpreted as neo-Darwinian versus post-Darwinian theory. What is important in our context is that biological functions are relational features, and change of function is something that can easily happen during an organism's lifetime. Becoming a member of a community means establishing functional relations with some other members of the community.

Living systems are those that make themselves. Life is capable of self-design. This is more than self-organisation, as an old concept that was so popular in the era of cybernetics and that goes back to Hans Driesch's self-regulation concept. This is the capacity of construction and self-construction as dependent on the choices that living organisms make. This also means that community structure and composition are largely based on decisions or choices made by organisms. Natural selection is what may follow. Evolutionary modifications of adaptations will fine-tune functional changes that have become fitted within the community.[6] Choice comes first, selection may work afterwards.

Thus, the point is that in many cases organisms inhabit where they inhabit due to their own capacity to choose, not due to natural selection. The role of ecological fitting has been demonstrated in several communities, even in the case of parasite-host relations, where the conditions for fitting are particularly strongly limited and thus fitting less expected (Brooks et al. 2006; Cipollini and Peterson 2018). It has been concluded that "[…] ecological fitting can be both a precursor to evolutionary diversity or maintainer of evolutionary stasis, depending on conditions" (Agosta and Klemens 2008: 1123).

Semiotic Fitting and its Typology

Organisms are agents, which means that they do work (use free energy) for spontaneous activity. If they can sense and become related with more than one possibility in time, then it follows that they can choose. Choice-making or interpretation is a sign process or semiosis (Kull 2018b). Thus, we get to a semiotic ecology: the ecology that pays attention to the interpretation processes in ecosystems (Kull 2008; Maran 2012a).

Life processes are capable of establishing regular bonds between things of almost any nature. The bonds of life are the relations that living systems first establish

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[6] Because "[…] genes are usually followers, not leaders, in evolutionary change" (West-Eberhard 2003: 29).

coincidentally via semiosis and then may repeatedly convey (epigenetically, genetically, socially, in human case also culturally) as habits (or codes or learned rules).

The mechanism of ecological fitting is choice and learning, which means that it is a semiotic mechanism. Choice is an aspect of semiosis, or interpretation, and learning is the corresponding change in memory as a result of semiosis. Organisms do work, search and find, and as a result design their being. The latter includes niche construction, niche choice, and acclimatisation.

Diversity of a semiotic system is strongly dependent on the mutual fitting of the agents that give form to the semiotic system itself (Kull et al. 2003). The focus on semiotic fitting means that, in the analysis of diversity, we pay particular attention to decision-making (or choice), functional plasticity, recognition windows, the depth of interpretation of the agents, and the categories that are responsible for the structure of the semiotic system.

There are several concepts in biology that have been used to describe the sets of regular semiosic relations. The relational view on community was strongly introduced by the concept of 'consortia'. Consortia are the basic elements of the functional structure of biocoenoses (Reinke 1872; Masing 1981; Kull 2010). As said, the concept of 'semiotic fitting' has an early analogue in Jakob von Uexküll's (1927) concept of '*Einpassung*' (as different from *Anpassung*, the evolutionary adaptation). There are other close concepts, like 'semiotic fitness', introduced by Jesper Hoffmeyer (Hoffmeyer 1997, 1998, see Maran 2012b, 2014) and by Stéphanie Walsh Matthews (2016), 'semiotic selection', introduced by Maran and Kleisner (2010), and 'semiotic niche', introduced by Jesper Hoffmeyer (2008a, b). Terrence Deacon has used the term 'fittedness', defining it as "correspondence [...] to a given extrinsic environmental context" (Deacon 2007: 147). The working of community as based on fitting between its populations is also well described by the concept of 'biophony' — the symbiotic relationship to one another in any given healthy habitat (Krause 2002; Kull 2010; Malavasi et al. 2014).

Fitting of organism or species into a community includes a whole totality of aspects that may be limiting. Decomposing the fitting and describing it as consisting of particular links or semiotic bonds may be a simplification; however, the niche is not provided to an organism in one moment — it is rather sequential along the life cycle. Therefore, the fitting is at least partly decomposable into links that are established in the process of fitting.

Semiotic fitting itself obviously includes various types which correspond to the mechanisms that are responsible for acquiring the habits or establishing the bonds which link the species. We could distinguish, for instance, between four major types of such mechanisms (see also Kull 2019):

(a). fitting by imprinting (iconic, vegetative); organism establishes the relation and keeps it by using its recognition window;
(b). fitting by associating (indexical, animal); organism uses marks that are correlated with the object of linkage in order to find the object of relation;
(c). fitting by imitating (emonic, many vertebrates); organism acquires the means to establish (or keep) the relation by imitating the behaviours existing in the community;

(d). fitting by will and convention (symbolic, humans); organism makes agreements about its links, establishing conventional relations and letting, sometimes violently, others fit to it.

Sign relations are arbitrary, but their freedom is limited by fitting. In other words, fitting is a process that obviously cannot be avoided in establishing sign relations.

Nativeness of Community

Fitting is always local. This means that fitting is forming a local community, establishing the locality of the system, with a tendency towards place-connection, hence an obvious relationship with the aspect of nativeness. There is no sharp boundary between native and non-native species or communities. According to a common definition, native *species* are those that have not been introduced by humans, and that have lived in the area for a rather long time (e.g., over 300 years).[7] This definition cannot be applied for *communities*, because humans usually do not introduce communities, and also because it is often impossible to establish the identity in case of community.

Therefore, we use a different approach to nativeness. Instead of defining nativeness on the basis of origins, we point out relationality as a means of its identification. This would also be in concordance with the definition of community as a set of species that are functionally linked. If community constructs itself on the basis of (relational) fitting, then nativeness of the community is a product of fitting, not vice versa. Nativeness is a feature that deepens in the course of community's succession (assuming there were no severe destruction episodes or large qualitative changes). No identity with the whole is necessary for this.

The mechanism that enables local diversity to persist and increase assumes certain openness to newcomers.[8] Diversity would increase if some additional species establish their place in the network. An important aspect of the fitting concept is that it demonstrates the possibility to analyse the roles of both indigenous and alien species in a community on the basis of the single model.

New relations happen again and again, encountering other members of the local ecosystem, and establishing in this way more and more relationships. Habit-taking — fitting —, however quick at the outset, does not end when a suitable relation is found. Thus, the longer the local history (without destruction episodes), the higher the number of local relations, the stronger the level of nativeness. Studying the natural succession of a community can show us how the context-dependence of its inhabitants and its structure increases. The native community is the most context-dependent community.

As a result, an ecosystem can be native, irrespective of its members having various origins. One is native not because of one's genes or phylogeny, but because of the richness of local semiotic relations. Nativeness is not due to coevolution, it is rather due to deep semiotic fittedness. One is native if one has established rich, multiple and relatively stable relationships with others in certain communicative system. Nativeness

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[7] On a history of the concept, see Chew and Hamilton 2011.

[8] A closed system (i.e. without immigration) in which evolutionary speciation would balance the species extinction should be rather large, e.g. seemingly over 10^5 km^2 for vascular plants (this of course depends on the heterogeneity of the area). This is certainly much larger than the area of local communities.

may appear to correlate positively with ecosystem stability. Since fitting to local diversity is based on functional relationships, it is also the form of development that tends to decrease mutual damage.

Conclusions

One's fitting to a place or to a community seems to include so many aspects, that its description as a set of correspondences seems hopeless, and seems to leave us with one variable only: survival. That is how the problem has been solved in neo-Darwinian models — via the quantity of fitness.

The alternative we propose here is to focus on semiotic relations. These are not entirely discrete; however, these are also not completely continuous. These are the characteristics of which organisms' cognitive umwelt of recognition and action consist. These are the relations that can be analysed and separated due to their mediatedness, also because they are acquired, and their persistence is based on memory.

The concept of semiotic fitting is what we could use as a model for the description and analysis of diversity dynamics and nativeness in semiotic systems. Semiotic fitting makes community real, and it explains the nativeness of an ecosystem.

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