Evolutionary Pressures and Environment's Building

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ABSTRACT. In the last fifteen years the idea of *Evolution* as two different *pressure* directions, from the environment to the organisms' morphology and from organisms to environmental niches, has relentlessly caught on. Starting from this approach, the paper tries to put together Niche Construction Theory with Elisabeth Vrba's Habitat Theory, by means of the concept of *Umwelt*, developed by German physiologist Jacob von Uexküll. Furthermore the idea of *Umwelt* will be used as a reply to some of Samir Okasha's critiques to the evolutionary soundness of Niche Construction.

1. Fragmentation

The first step is to examine the idea of *fragmentation*- the very evolutionary trigger- as considered by the strong environmentalism of paleontologist Elisabeth Vrba and Niche Construction's (*NC*) approach to organisms' action.

Vrba worked extensively on the environmental influences, both direct and indirect, upon the evolutionary processes, (Vrba, 1994; 1995): particularly stressing out the concept of *vicariance* (e.g.: Vrba, 1985; 1993), considered as

"the process of subdivision of a formerly continuous distribution of a species" (Vrba, 1985, p. 229),

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or rather a subdivision of a formerly continuous species into discontinuous "islands", within the boundaries of the habitat of the species. Vicariance, considered as the fragmentation of species, is only an intermediate response inbetween the environmental changes (pressures and selections) and the final reply of the species towards the mutated conditions (i.e. extinction, speciation, stasis, intraspecific evolution). Vicariance closely depends on environmental conditions:

"from the point of view of organisms, a small change in salinity, pressure, temperature or vegetation can represent an obstacle every bit as formidable as a gross topographic barrier" (id, p. 233).

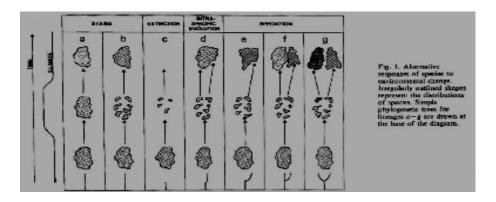
It is only after *vicariance* that others phenomena, such as migration or extinction, may occur: "while vicariance sensu strictu involves subdivision of species' distributions by the *appearance of barriers*, migration occurs when *barriers disappear*" (id, p.233). The issue is that

"each species has a particular <u>tolerance range</u> for each habitat component that may or may not be identical to that of other species and a combination of such ranges for all its requirement that is unique".

From the environmental point of view, the fragmentation of habitat and species can determine (as *one* of possible consequences) speciation and evolution, because "under the habitat theory, physical change is hypothesized to be the 'kick' that initiates speciation, while the nature of the change depends on interactions among the inherited properties of lineages and the physical and biotic context" (id, p. 21). But physical change must be enough strong

"to bring about disjunction of previously continuous populations for a sufficiently long interval if the irreversible change implied by speciation are to occur" (id, p. 24).

Alternatively, the reconstitution of previous species can verify (fig.1, b) (Vrba, 1985, p. 233).



Niles Eldredge's "Sloshing Bucket" theory explains more consistently this idea: "extinction of entire major groups—prompting the evolution of other large-scale groups" (Eldredge, 2008, p.14) can only happen when the relationship between species, their habitat and ecosystem is strongly deteriorated. Otherwise, if the degradation is restricted, there will not be significant evolutionary changes; if it is of medium-level and size, the ecosystem will be reconstructed from adjacent demes, thus miming the swinging movement of the bucket.

Habitat Theory considers only one direction of fragmentation, conversely, according to NC the processes ultimately leading to speciation events, have to be considered as moving in two opposite directions inside an "evolutionary niche", thought as "the sum of all the natural selection pressures to which the population is exposed" (Odling-Smee, Laland, Feldman, 2003, p.40). According to NC theory, fragmentation of habitats and species entails that organisms are not only subject to the pressures of environmental changes, they are also subject of the struggle against changes in their habitat/ecosystem, countering environmental changes in order to "restore a match between their previously evolved features and their environment's factors" (id, p.46). Odling-Smee et al. calls this particular category of NC "counteractive" (id, pp. 44-50). Facing habitat's fragmentation and mutation, organisms "respond [...] by moving to or growing into a more suitable place" (id, p. 47) ("counteractive" relocation, e.g. seasonal migration), or modifying their surrounding physically ("counteractive" perturbation, e.g. thermoregulation of nests). Alternately, NC can be Inceptive: organisms, as niche-builder, start the environmental alteration modifying their surroundings (Inceptive Perturbation, e.g. beavers' dams, earthworms behaviour) or moving to a new place, exposing themselves to novel, different selective pressures (Inceptive Relocation, e.g. choosing a place for a nest). In this sense, organisms are responsible for fragmentation and vicari-

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ance or re-acting against them. In all these cases, if actions of *niche-builder* organisms are persistent, they will produce alterations, that can far exceed the boundaries of their singular habitats reaching different niches and species. The next paragraph will inquire the modalities of such alterations.

2. Umwelt

The project to understand *how* the effects of organisms' actions can exceed their original niche stands on what Samir Okashaⁱ tags as *conceptual problem* into *NC theory*. He claims that *NC* principle can be properly applied only when the effects of the "building" alter "the niche of those self-same organisms [the niche-builders]" (Okasha, 2005, p. 2). This *inclusive* meaning of the theory,

"restricting the notion of niche construction to the narrow reading would result in a concept of much less *ecological* significance than **OLF**'s [Odling-Smee, Laland and Feldman] concept, but from an *evolutionary* point of view it might make more sense, given the importance of the distinction between altering one's own selective environment and altering that of others. Perhaps the moral is that the conceptual demands of evolution and ecology are hard to satisfy simultaneously" (id, p. 4).

To be honest, Okasha's idea seems not so appealing: NC theory 's relevance ultimately rests on the effort to re-combine ecology and evolution, recovering Charles Darwin's original idea (Chiesura, 2009; Gagliasso, 2004).

Conversely, the *broad* reading of NC can be assumed if we refer to Uexküll's distinction between the "*Umwelt*" and the "*Welt*". The *Umwelt is* the *perceptive world* surrounding each organism, as a *soap bubble* (von Uexküll, 1934; eng. transl. 1957, p. 5) composed by perceptual cues (*Merkmal*) that the organisms can "detect" into their habitat (consistent with the idea of "*occupation*" in an evolutionary niche, "the 'lifestyle' of organisms, [...]the many different ways in which different organisms survive and reproduce by actively interacting with their environments") (Odling-Smee *et al.*, 2003, p. 40). This *Umwelt* is carved out from the *Welt*, the objective world composed by all the physical objects surrounding the organisms (consistent with the "*address*" in an evolutionary niche, "the real habitat of organisms in real space and time") (id, p. 40).

Using this distinction, it is clear that evolutionary effects of organisms' ac-

tions can be wide and pervasive: certainly, the organisms act *upon* the objects *within* their *Umwelt* only, but theirs actions reverberate *within* the "undetectable *Welt*". Some of the objects inside may be part of the *Umwelt* of other animals: it follows that the activities of or-

ganisms on their niche may mutate other organisms' environmental conditions, changing their selective pressures (for instance the activities of some bacteria that built the atmospheric condition -giving off oxygen- which allowed the evolution of life that we know today).

2. Conclusions

This paper aimed to demonstrate how "Habitat Theory" (Vrba,1992) (Vrba,1995) can be connected with "Niche Construction theory" by means of the idea of *Umwelt*. Only perceptive worlds of animals are *separated* each other (Uexküll, 1920; eng. trasl. 1926), whereas all the *Umwelten* combine together – overlapping at time – in the same complex *Welt*. Consequently, if the sudden and strong environmental change is the *chiquenaude* of morphological evolution of species, the accurate and slow work of many organisms is the *chiquenaude* of climate and selective change: all changes, produced by

¹ The idea of two worlds, the first "transparent" and the latter "translucent", depending on the relationship between behaviors and cues [Kim Sterelny (2003), "Thought in a hostile world", Malden-USA/Oxford-UK/Carlton-Australia: Blackwell Publishing] it's coherent with the idea that the effects of organisms' actions can spread out their own niches. In fact, we can think that the actions' effects are more pervasive if the organisms have a "multiple-cued ways of tracking the environment" (id, p. 17).

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both the climate and the organisms, extending during the time, have evolutionary consequences. More precisely, both these actions *are* the evolutionary process.

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