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ORIGINAL PAPER

Ecosystems are Made of Semiosic Bonds: Consortia, Umwelten, Biophony and Ecological Codes

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Abstract The paper focuses on the semiotic principles of the organisation of ecosystems, attempting to find concepts that point to relations and not to elements. (1) *Consortium* (the term introduced by Johannes Reinke around 1873) can be defined as a group of organisms connected via (sign) relations, or groups of interspecific semiosic links in biocoenosis. The consortial relations include trophic and topic relations, both implying a recognition (identification) of the object by an organism involved (these, i.e., are sign relations). These relations are *ecologically inheritable*. (2) *Umwelt* (the term introduced by Jakob von Uexküll around 1909) can be defined as a set of relations an organism has in an ecosystem (as in a semiosphere). The formation of an umwelt is dependent on the modelling system of the organism. (3) *Biophony* (the term introduced by Bernie Krause around 2000) denotes the coordination of inter- and intra-species relations in a soundscape of a biological community. This can be seen as a special case of *Komposition* as defined by Jakob and Thure von Uexküll. (4) *Ecological code* (as introduced, e.g. by Alexander Levich around 1977) can be defined as the set of (sign) relations (regular irreducible correspondences) characteristic to an entire ecosystem. We also mention the concepts of *ecomones* and *coactones* (introduced by Marcel Florkin in 1965) as the substances which are responsible for mediation of ecological inter-individual relations. All the relations as sign-relations evidently imply both a static or structuralist description (in terms of codes), and a processual description (in terms of semiosis carried on by interpretation). We conclude that all the above mentioned concepts can be viewed as conceptually connected and are suitable for semiotic description of biological communities.

Keywords Ecosystem structure · Ecological codes · Ecological inheritance · Ecomones · Sign relations · Consortium · Umwelt

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Introduction

What preserves the structure of ecological communities? What makes particular species eat certain species, certain insect species pollinate certain plant species, certain species live in or on the bodies of particular host species, etc.?

The problem I attempt to describe here concerns the major mechanisms that form—design and develop—the biocoenoses, and thus ecosystems. The hypothesis that will be discussed states that this mechanism is communication, or more precisely—semiosis. In this case an ecosystem should be seen not as consisting of populations of separate species, as for instance in the individualistic approaches that follow the tradition of Henry Gleason. Neither can it be described as a holistic and entirely organismic entity regulated by element cycles, as it has been well described by the tradition of Frederic Clements and the Odum brothers.[1] The semiotic approach, instead, would focus on relations—which are neither individual nor total, but partial.

Organisms are not separate; they are linked. They are linked by their own relations—sign relations. These relations themselves should be our objects if we want to understand the life process of living communities, life as it happens in ecosystems. From a semiotic point of view, ecological communities are not sets of organisms (or species) as elements; instead, a community is a composition of *relations* between the organisms or species.[2]

At least those organisms that can actively move, can also find what they may recognise.[3] Therefore, they can form communities on the basis of sign relations.

Obviously, each species prefers (has a habit to prefer) certain other species with its features, which it recognises and remembers. The existence of these species in an ecosystem renders it possible to inherit these relations, on the basis of memory, which directs their recognition and action capacity. This means that there is ecological inheritance.

Ecological relationships can be described using different languages of description. In case of physical descriptions, we could pay attention to the dynamic processes of chemical exchange between individuals. In case of semiotic descriptions, we would focus on the relations that the organisms (individually or group-wise) retain.[4] This paper focuses on the latter, i.e. on the semiotic principles of the organisation of ecosystems.

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 make coincidentally, and may then re-establish and transmit (epigenetically, genetically, socially, culturally) via semiosis.[5] These relations—if regular—can be described as

[1] This opposition, as initiated by the seminal works of Gleason (1926) and Clements (1928), has been central in vegetation science and in the study of ecological balance for almost a century (see Kull and Zobel 1994).

[2] It should be added that these relations of mutual recognition between organisms can themselves be responsible for the categorization of organisms into the species-like categories.

[3] Active movement is possible for many unicellular organisms; thus, it is a characteristic of both vegetative and animal levels. Different from the Aristotelian tradition, that points to movement when distinguishing the vegetative and animal, we would point to the crucial difference in the processes of interpretation and learning (see Kull 2009b)—animal learning is parallel, making new associations (indexes), whereas vegetative learning is sequential (exclusively iconic).

[4] These two approaches were compared as phi-scientific (physical) and sigma-scientific (semiotic) descriptions in Kull (2009a).

[5] Relations are both functions and signs (sign processes). Everything that life does can thus be described on the basis of relational processes.

codes, or *habits*, or *rules* (as different from physical laws). There are several concepts in biology that have been used to describe these sets of regular semiosic relations.

The semiotic view, or in other words, the understanding of the relational nature of living systems, would require the usage of concepts and models that point to the relations themselves—the concepts that characterise the primacy of relations in comparison to the elements.[6] The aim of the current paper is to gather and review some of the relational concepts that are in use in ecology, and to demonstrate their relevance in a semiotic approach.

Semiosic Bonds

In contrast with the relationships based on physico-chemical affinity, there are others that require work in order to be maintained and repeatedly formed. The work that organisms perform is utilized *inter alia* in keeping the relations, i.e. the semiosic relations (sign relations), persistent.

Semiosis, or interpretation *sensu lato*, is a process that is permanently changing, and in fact unique at every instant. But just as much as change, habit-making is its fundamental feature, since semiosis cannot make a step without memory being involved. Habits and codes consist of repeated relations.

Particular instances (occurrences) of semiosis, such as functional cycles, can be seen as relations in process, and each of these makes a connection—as a relation always does.[7] These semiosic connections can be interpreted as ecological bonds.

The development of semiosic bonds is dependent on the distinctions the organisms can make. Detailed distinctions imply narrow recognition window and small differences that may count for an organism when establishing a particular bond. Exact distinctions mean narrow recognition window, the approximate distinction a wide recognition window. A further consequence: the narrower the recognition window, the higher the diversity.

Consortium

Consortium is a term introduced by Johannes Reinke[8] in 1872 (Reinke 1872a)[9] to denote the mutual relation between the organisms which turns them into a unity. Reinke used this term particularly in the cases when the body of an organism consists of two species (Reinke 1872a, 1872b, 1873b, 1901: 484). Unlike August

[6] Cf. Bains 2006.

[7] In addition to Uexküll's *Funktionskreis*, I refer here to the concept of *Gestaltkreis* of Victor von Weizsäcker, as referred to in connection with biosemiotics by Rothschild (1994). See also Harries-Jones 2002; Berthos and Christen 2009; Chang 2009; Fagot-Largeault 2009.

[8] Reinke (1872a) mentions that he had heard the term first in a conversation with August Grisebach, who used it for the description of the relations between the algae and fungi in lichens.

[9] Another work—Reinke 1873a—which is sometimes referred to in the literature as the source for the term 'consortium', does not actually include this term in the text (Sööt 2009).

Grisebach, who described the relations of algae and fungi in lichens as parasitic, Reinke emphasised the stability of the relation and a dual control without domination, thus excluding unilateral benefit (see Frank 1877; Hejný 1972; Ainsworth 1976; Sapp et al. 2002).[10] In the first decades of its usage, the concept was mainly applied in lichenology (Strasburger et al. 1912: 417); but e.g. Church (1920) had a broader sense in mind.[11]

Since the 1950s, the concept of consortium has come into use in general biocoenology, first by way of Beklemishev (1951) and Ramensky (1952), and later Rabotnov (1972; 1973) and Masing (1976, 1981). The concept itself has become considerably richer. The component species of the consortium is termed a *consort* (Masing 1981), or a *consorting* organism or unit (Gaino et al. 2004). The species in relation to which the consortium is described is called *edificator* (by Beklemishev 1951) or *determinant* (by Masing 1981) or *inconsort* (Belomesyatseva 2002). Masing (1981) gave classifications of consortia based on the systemic level of its major components (individual, clonal, populational, regional, species, synusial), and their functional relationships (mero-consortia, holo-consortia, sapro-consortia). In addition to the local consortia, according to Rabotnov (1972), vicarious consortia occur as well, in the case of introduction of alien species. Consorts can be either *trophoconsorts* or *topoconsorts* (Masing 1981). Consorts can belong to the first, or second, or higher *concentre* of a particular determinant.

Besides its usage in some biocoenological studies (e.g. Belomesyatseva 2002; Gaino et al. 2004; Matafonov et al. 2005; Gómez 2007; Porras-Alfaro et al. 2008), the concept of consortium has a slightly more specific contemporary usage in soil microbiology, where it marks the groups of functionally related species. Popa (2004: 210) defines it this way: “consortium: in microbiology, an association of micro-organisms from different species living in metabolic interdependence”. In this case, a consortium can be a group of microorganisms that work together in fulfilling a certain biochemical transformation of the substrate (Caron 2000; Brenner et al. 2007). According to another description, a consortium is a “spatial grouping of bacterial cells within a biofilm in which different species are physiologically coordinated with each other, often to produce phenomenally efficient chemical transformations” (Elvers and Lappin-Scott 2004: 161). In our view, these occurrences can be seen as special cases of the same concept.

The traditional set of concepts used to characterise interspecific relationships include symbiosis or mutualism (+,+), amensalism (−,0), commensalism (+,0), prey-predator and parasitism (+,−), competition (−,−) and neutralism (0,0). These relationships, when defined for pairs, are often characterised on the basis of the measurable effects on organisms (or, on the population growth rate). This means that the common distinction between these relationships is not based on the identification of the mechanism of the relationship, but just on the effect which one species has

[10] Another early use of the term ‘consortium’ in a similar sense belongs to Andrei Famintsyn. See, e.g., Ryan (2002: 52).

[11] Albert Bernhard Frank (1877) introduced the term *homobium* to denote the system in which the partner organisms form a new organism (and lose their separate independence), thus leaving the term consortium for a broader meaning (see also Höxtermann and Mollenhauer 2007).

upon the other, either increasing (+), decreasing (−), or not causing a change (0) in the population of other species. Since these influences can be entirely indirect or even not presuppose any communication between the organisms, we cannot use these concepts automatically for a semiotic approach. However, in some cases these relationships can be based on the perceptual recognition between the organisms, i.e. on true sign relations. The criterion for the acceptance of a particular relationship as semiotic could thus be the existence of consortial relations.[12]

The consortial system can be characterised by Hoffmeyer's words: "The situation, in other words, has a matrix-like structure with multiple interdependent relationships binding populations of many different species into a shared interpretive universe or motif" (Hoffmeyer 2008: 195).

Consortium can therefore be defined as a *group of organisms connected via (sign) relations*. Accordingly, consortia are the true elementary components of ecosystems,[13] because the relations consortia involve are decisive in turning a set of populations that occur in the same territory into a system that is not just a set but maintains coherence. The relations involved in a consortium are both *trophic* and *topic*—in any case, these relations imply recognition (identification) of an object by an organism involved (which means these are sign relations). Accordingly, consortia are groups of semiosic links in biocoenosis, related to a particular species or function.[14] These links (relations) are *ecologically inheritable*.

Ecological Inheritance

Consortia (as complexes of sign relations) are *ecologically* inheritable—in order to become inherited (conveyed from one generation to the next), a relation requires all of its relata; one is not enough.

Inheritance is the process that keeps relations alive; it both regenerates and generates relations. Relations are local rules, based on recognition-and-action circles. What keeps the relations alive is, of course, these recognition-action circles themselves, or more precisely—semiosis, which is, in other words, interpretation. This means that inheritance is itself an interpretation-type process—an interpretation that has turned into a habit, in a Peircean sense. This is the case for any sort of inheritance, including genetic and ecological.

Any living system can be seen as a process on inheritable relations (or the process of inheriting relations *per se*). This process reshapes the relationships in many ways—spatially, temporally, chemically. It makes things move differently—intentionally, and therefore unpredictably from the point of view of physics. This is because the relations themselves are the rules that are established by life.

What is inherited are the codes, or relations. Codes and relations are processes that work as restricted correspondences. Since ecological codes can be defined as

[12] See also Kull 1999.

[13] E.g. according to Matafonov et al. (2005: 490), a consortium can be seen as an "elementary biocenosis that includes interacting populations of the edificator and consort species".

[14] Matafonov et al. (2005) find it possible to speak about the *key consortia* as the ones that may be of particular importance in terms of the stability of a biocoenosis.

(relatively stable) consortial relations, ecological inheritance primarily passes consortial relations.

The idea that genetic inheritance is only one inheritance type among several that characterise living systems has been repeatedly described by Eva Jablonka. She has written (Jablonka 2001: 100):

> [The] replicator-centered, gene-derived view of heredity is, however, not only severely limited, but also severely misleading. There are multiple inheritance systems, with several modes of transmission for each system, that have different properties and interact with each other. They include the genetic inheritance system, cellular or epigenetic inheritance systems, the systems underlying the transmission of behaviour patterns in animal societies through social learning, and the communication system employing symbolical languages. These systems all carry information, which I shall define here as the *transmissible organization of an actual or potential state of a system*. [...] Inheritance systems with replicator-like properties are very unusual, and certainly do not represent or sum up the many ways in which heritable variations are transmitted across generations. I use 'transmission' in a general way, to denote all the processes leading to the regeneration of the same type of organization-states across generations. This includes the direct transfer of resources, as well as the activities that lead to the reconstruction of ancestral phenotypes.

The term 'ecological inheritance' became more widely used in biology in connection with the concept of niche construction and its consequences for the understanding of evolution. Laland et al. (2001: 119) give the following definition: "We define as ecological inheritance any case in which an organism experiences a modified functional relationship between itself and its environment as a consequence of the niche-constructive activities of either its genetic or ecological ancestors". It is important that ecological inheritance encompasses not only modification of the ancestral environments that are bequeathed onto the next generation. It primarily concerns the relation, as should be the case in any type of inheritance.

The mechanisms that establish a new, or modify an existing relation, can in principle be one and the same for interspecific (ecological) and intraspecific inheritance. One such mechanism may be imprinting, as it has been fittingly described by Hess (1973: 351):

> Not long ago (Hess 1962) we defined imprinting as 'the primary formation of social bonds in infant animals.' Now, however, we no longer regard imprinting as simply primary socialization. Rather, we see imprinting as a particular type of learning process—that is, a tool (in the same sense as eating or breathing are tools), which may be used by a species for the formation of a filial-maternal bond, pair formation, environment attachment, food preferences, and perhaps other cases involving some sort of object-response relationship. It is, furthermore, a genetically programmed learning, with some species-specific constraints upon the kind of object that may be learned and upon the time of learning. In other words imprinting is a genotype-dependent ontogenetic process.

Umwelt

Umwelt is a concept which was introduced by Jakob von Uexküll around 1909; though it took more than 10 years before he defined it properly. Certain differences (and developments) can be noticed also in the definition of this term among the followers of Uexküll. A quite usual definition says that umwelt is the personal world of an organism, or a self-centred world, “the world as known or modelled” (Cobley 2010: 348). This definition is correct by itself, but it does not emphasise the relational aspect enough. Therefore we would prefer here a different wording, and we define umwelt as *a set of relations an organism has in an ecosystem* (as in a semiosphere). The formation of an umwelt is dependent on the *Innenwelt* as the primary modelling system of the organism. This definition corresponds to the view of Jakob von Uexküll as expressed in his *Bedeutungslehre* (Uexküll 1940 [1982: 64, 69]):

> Meaning in nature’s score serves as a connecting link, or rather as a bridge, and takes the place of harmony in a musical score; it joins two of nature’s factors. [...] Each meaning-carrier was always confronted with a meaning-receiver, even in [...] earlier umwelten. Meaning ruled them all. Meaning tied changing organs to a changing medium. Meaning connected food and the destroyer of food, enemy and prey, and above all, male and female in astonishing variations.

Thus, if umwelt is made of relations, of semiosic bonds, we can conclude that organisms are derivates of (sign) relations, not vice versa. Umwelt (as relational, i.e. a meaningful world) exists prior to its representations, since life can often do without representations. Conversely, of course, there cannot be an umwelt without life. Life is centred on organisms, in their agency; therefore, umwelten are also individual and individualised.

Biophony

Biophony is a concept that was introduced by Bernie Krause around 2000 to describe both inter- and intra-species relations in the soundscape of a biological community. “Animal symphony,” as he writes, “the unique manner in which creatures vocalize in a symbiotic relationship to one another in any given healthy habitat, is what I call biophony” (Krause 2002: 24). Here is a longer description:[15]

> Through my field work, I discovered that in undisturbed natural environments, creatures vocalize in relationship to one another very much like instruments in an orchestra. On land, in particular, this delicate acoustic fabric is almost as well-defined as the notes on a page of music when examined graphically in the form of what we sometimes call *voice prints*. For instance, in healthy habitats, certain insects occupy one sonic zone of the creature bandwidth, while birds, mammals, and amphibians occupy others not yet taken and where there is no competition. This system has evolved in a manner so that each voice can be

[15] From a speech B. Krause made to the San Francisco World Affairs Council, titled “Loss of national soundscape: Global implication of its effect on humans and other creatures”, on January 31, 2001.

> heard distinctly and each creature can thrive as much through *its* iteration as any other aspect of its being. The same type of event also generally occurs within marine environments. This biophony, or creature choir, serves as a vital gauge of a habitat's health. But it also conveys data about its age, its level of stress, and can provide us with an abundance of other valuable new information such as why and how creatures in both the human and non-human worlds have learned to dance and sing.

This can be seen as a special case of *Komposition* as defined by Jakob and Thure von Uexküll (Uexküll 1980).

Ecological Code

Ecological codes (as introduced, e.g. by Alexander Levich around 1977, see Levich 1983) can be defined as the sets of (sign) relations (regular irreducible correspondences) characteristic of an entire ecosystem, including the interspecies relations in particular. It should be obvious that if we can identify consortia that maintain themselves throughout the changes of generations, i.e. which are ecologically inheritable, then it has to be possible to describe the correspondences within this set of consortial relations—correspondences that fulfil all the requirements of a code. In other words, the existence of consortia (as defined above) logically implies the existence of ecological codes.

A general characteristic of codes is the existence of certain mediators that may not have any other role than ensuring the identity of the code, which is often described as its informational function. In case of ecological codes, such a role can be played by what Marcel Florkin has called *ecomones*.

According to Florkin (1965),[16] "in an ecosystem, besides the contribution of the trophic chains in supplying molecules endowed with nutritive functions and ensuring the flux of matter and of energy one may describe non trophic molecules active in insuring a flux of information as well as the constitution and maintenance of the community (*ecomones*)". Florkin has defined ecomones as "The molecular factors, specific or non-specific, exercising an action on the constitution and the persistence of a biotical community".[17] Among the ecomones, Florkin identifies *coactones*: "Some ecomones are recognized as being specifically active in the process of the coaction of organisms upon each other. Such specific substances or *coactones* are determinant in the relationship between the coactor (active and directing organism) and the coactee (passive and receiving organism)".

Conclusion

From a biological point of view, in order to understand what keeps the interspecific communities together—a phenomenon without which there would be no stable

[16] Also in Favareau (2010: 454). See also Ikeshoji 1977.
[17] See also Gauthier and Aubert (1981: 226).

ecosystems—we need to look at the nature of bonds between the species. Since these are communicational relations, based on the ontogenetic and phylogenetic experience of the organisms, these are sign relations. As Hoffmeyer (2008: 195) has said, "I believe that *semiotic mutualism* involving a delicate balance of interactions between many species is widespread". Of the existing concepts that specifically focus on these types of relationships in ecosystems, we find the concept of consortium well fitted for semiotic approaches to ecology.

From a more technical point of view, it is evident that relations that are sign-relations require both a static or structuralist description (in terms of codes), and a processual or dynamic or semiosic description (in terms of semiosis performed by interpretation).

Thus we may conclude that all the above mentioned concepts—consortium, ecological inheritance, umwelt, biophony, ecological code—are conceptually connected. They can form an inherently connected system of concepts, and can be used in a semiotic description of biological communities.

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References

Ainsworth, G. C. (1976). *Introduction to the history of mycology*. Cambridge: Cambridge University Press.

Bains, P. (2006). *The primacy of semiosis: An ontology of relations*. Toronto: University of Toronto Press.

Beklemishev, V. N. (1951) Беклемишев, В. Н. (1951). О классификации биоценологических (симфизиологических) связей. *Бюллетень Московского общества испытателей природы 56* (5), 3–30.

Belomesyatseva, D. B. (2002). The fungi in the consortium of common juniper in Belarus. *Mycena, 2*(1), 4–16.

Berthos, A., & Christen, Y. (Eds.). (2009). *Neurobiology of "Umwelt": How living beings perceive the world*. Berlin: Springer-Verlag.

Brenner, K., Karig, D. K., Weiss, R., & Arnold, F. H. (2007). Engineered bidirectional communication mediates a consensus in a microbial biofilm consortium. *Proceedings of the National Academy of Sciences of the United States of America, 104*(44), 17300–17304.

Caron, D. A. (2000). Symbiosis and mixotrophy among pelagic microorganisms. In D. L. Kirchman (Ed.), *Microbial ecology of the oceans* (pp. 495–523). New York: Wiley-Liss.

Chang, R. S. (Ed.). (2009). *Relating to environments: A new look at Umwelt*. Charlotte: Information Age.

Church, A. H. (1920). The lichen symbiosis. *Journal of Botany, British and Foreign, 58*, 213–219. 262–267.

Clements, F. E. (1928). *Plant succession and indicators*. New York: H. W. Wilson.

Cobley, P. (Ed.). (2010). *The Routledge companion to semiotics*. London: Routledge.

Elvers, K. T., & Lappin-Scott, H. M. (2004). Biofilms and biofoulding. In M. Schaechter (Ed.), *The desk encyclopedia of microbiology* (pp. 161–167). Amsterdam: Elsevier Academic.

Fagot-Largeault, A. (2009). Anthropological physiology: von Uexküll, Portmann, Buytendijk. In A. Berthos & Y. Christen (Eds.), *Neurobiology of "Umwelt": How living beings perceive the world* (pp. 1–5). Berlin: Springer-Verlag.

Favareau, D. (Ed.). (2010). *Essential readings in biosemiotics*. Berlin: Springer.

Florkin, M. (1965). Approches moléculaires de l'intégration écologique: Problèmes de terminologie. *Bulletin de l'Académie Royale de Belgique (Classe des Sciences), 5e série, 51*, 239–248.

Frank, A. B. (1877). Ueber die biologischen Verhältnisse des Thallus einiger Krustenflechten. *Beiträge zur Biologie der Pflanzen, 2*, 123–200.

Gaino, E., Lancioni, T., La Porta, G., & Todini, B. (2004). The consortium of the sponge *Ephydatia fluviatilis* (L.) living on the common reed *Phragmites australis* in Lake Piediluco (central Italy). *Hydrobiologia, 520*, 165–178.

Gauthier, M. J., & Aubert, M. (1981). Chemical telemediators in the marine environment. In E. K. Duursma & R. Dawson (Eds.), *Marine organic chemistry: Evolution, composition, interactions and chemistry of organic matter in seawater* (pp. 225–257). Amsterdam: Elsevier.

Gleason, H. A. (1926). The individualistic concept of plant association. *Bulletin of the Torrey Botanical Club, 53*, 1–20.

Gómez, F. (2007). On the consortium of the tintinnid *Eutintinnus* and the diatom *Chaetoceros* in the Pacific Ocean. *Marine Biology, 151*, 1899–1906.

Harries-Jones, P. (2002). Where bonds become binds: the necessity for Bateson's interactive perspective in biosemiotics. *Sign Systems Studies, 30*(1), 163–181.

Hejný, S. (1972). Editorial note. *Folia Geobotanica, 7*(1), 1.

Hess, E. H. (1962). Imprinting and the critical period concept. In E. L. Bliss (Ed.), *Roots of behavior* (pp. 254–263). New York: Hoeber-Harper.

Hess, E. H. (1973). *Imprinting: Early experience and the developmental psychobiology of attachment*. New York: Van Nostrand Reinhold Company.

Hoffmeyer, J. (2008). *Biosemiotics: An examination into the signs of life and the life of signs*. Scranton: Scranton University Press.

Höxtermann, E., & Mollenhauer, D. (2007). Symbiose und Symbiogenese—Entdeckung und Entwicklung eines biologischen Problems. In A. Geus & E. Höxtermann (Eds.), *Evolution durch Kooperation und Integration: Zur Entstehung der Endosymbiosetheorie in der Zellbiologie* (pp. 227–284). Marburg: Basilisken-Presse.

Ikeshoji, T. (1977). Self-limiting ecomones in the populations of insects and some aquatic animals. *Pesticide Science, 2*, 77–89.

Jablonka, E. (2001). The systems of inheritance. In S. Oyama, P. E. Griffiths, & R. D. Gray (Eds.), *Cycles of contingency: Developmental systems and evolution* (pp. 99–116). Cambridge: A Bradford Book.

Krause, B. (2002). *Wild soundscapes*. Berkeley: Wilderness.

Kull, K. (1999). Symbiosis is semiosis. In E. Wagner, J. Normann, H. Greppin, J. H. P. Hackstein, R. G. Herrmann, K. V. Kowallik, H. E. A. Schenk, & J. Seckbach (Eds.), *From symbiosis to eukaryotism: Endocytobiology VII* (pp. 663–668). Geneva: Geneva University Press.

Kull, K. (2009a). Biosemiotics: to know, what life knows. *Cybernetics and Human Knowing, 16*(3/4), 81–88.

Kull, K. (2009b). Vegetative, animal, and cultural semiosis: the semiotic threshold zones. *Cognitive Semiotics, 4*, 8–27.

Kull, K., & Zobel, M. (1994). Vegetation structure and species coexistence. *Folia Geobotanica et Phytotaxonomica, 29*, 433–437.

Laland, K. N., Odling-Smee, F. J., & Feldman, M. W. (2001). Niche construction, ecological inheritance, and cycles of contingency in evolution. In S. Oyama, P. E. Griffiths, & R. D. Gray (Eds.), *Cycles of contingency: Developmental systems and evolution* (pp. 117–126). Cambridge: A Bradford Book.

Levich, A. P. (1983). Semiotic structures in ecology, or does there exist an ecological code? In *Man and biosphere*. 8th issue (pp. 68–77). Moscow: Moscow University Press. (Левич А.П. 1983. Семиотические структуры в экологии, или существует ли экологический код? // Человек и биосфера. М.: Изд-во Моск. университета, 68–77.)

Masing, V. (1976). Мазинг, В. (1976) Проблемы изучения консорций. *Значение консортивных связей в организации биогеоценосов* (под ред. И. А. Селиванов), с. 18–27. Министерство Просвещения РСФСР, Пермский Государственный Педагогический Институт, Пермь.

Masing, V. (1981). Consortia as elements of the functional structure of biocenoses. In L. Laasimer (Ed.), *Anthropogenous changes in the plant cover of Estonia* (pp. 64–76). Tartu: Academy of Sciences of the Estonian SSR, Institute of Zoology and Botany.

Matafonov, D. V., Kuklin, A. P., & Matafonov, P. V. (2005). Consortia in aquatic ecosystems of the Transbaikalia. *Biological Bulletin, 32*(5), 490–495.

Popa, R. (2004). *Between necessity and probability: Searching for the definition and origin of life*. Berlin: Springer.

Porras-Alfaro, A., Herrera, J., Sinsabaugh, R. L., Odenbach, K. J., Lowrey, T., & Natvig, D. O. (2008). Root fungal consortium associated with a dominant desert grass. *Applied and Environmental Microbiology, 74*(9), 2805–2813.

Rabotnov, T. A. (1972). Consortia, the importance of their study for phytocoenology. *Folia Geobotanica, 7*(1), 1–8.

Rabotnov, T. A. (1973). Работнов, Т. А. (1973) Некоторые вопросы изучения консорций. *Журнал общей биологии 34*, 407–416.

Ramensky, L. G. (1952). Раменский, Л. Г. (1952) О некоторых принципиальных положениях современной геоботаники. *Ботанический Журнал*, *37*(2), 181–201.

Reinke, J. (1872a). Ueber die anatomischen Verhältnisse einiger Arten von *Gunnera* L. *Nachrichten von der Königl. Gesellschaft der Wissenschaften und der Georg-Augusts-Universität zu Göttingen, 9*, 100–108.

Reinke, J. (1872b). Über gonidienartige Bildungen in einer dikotylischen Pflanze (*Gunnera*). *Botanischer Zeitung, 30*, 59–61. cit. in Höxtermann 2007.

Reinke, J. (1873a). Zur Kenntniss des Rhizoms von *Corallorhiza* und *Epipogon*. *Flora, 56*, 145–152. 161–167, 177–184, 209–224.

Reinke, J. (1873b). Untersuchungen über die Morphologie der Vegetationsorgane von *Gunnera*. In J. Reinke (Ed.), *Morphologische Abhandlungen* (pp. 45–118). Leipzig: W. Engelmann. cit. in Höxtermann 2007.

Reinke, J. (1901). *Einleitung in die theoretische Biologie*. Berlin: Verlag von Gebrüder Paetel.

Rothschild, F. S. (1994). Parallels to biosemiotics in Viktor von Weizsaecker's writings. In F. S. Rothschild (Eds.) *Creation and evolution: A biosemiotic approach* (pp. 90–95), (Hess, Jozef Ph., trans.). Jerusalem: J. Ph. Hes.

Ryan, F. (2002). *Darwin's blind spot: Evolution beyond natural selection*. New York: Houghton Mifflin Company.

Sapp, J., Carrapiço, F., & Zolotonosov, M. (2002). Symbiogenesis: the hidden face of Constantin Merezhkowsky. *History and Philosophy of the Life Sciences, 24*(3/4), 413–440.

Sööt, T. (2009). *Konsortsiumi mõiste ökoloogias*. (Bakalaureusetöö.) Tartu: Tartu Ülikool. [Manuscript.]

Strasburger, E., Lang, W. H., Karsten, G., Jost, L., & Schenck, H. (1912). *A text-book of botany*. London: Macmillan.

Uexküll, J. von (1980). In T. von Uexküll (Ed.), *Kompositionslehre der Natur: Biologie als undogmatische Naturwisenschaft*. Frankfurt am Main: Ullstein.

Uexküll, J. von (1982[1940]). The theory of meaning. *Semiotica, 42*(1), 25–82.