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Of bubbles and foams: Umwelt counterpoints in symbiosis

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Without plans, that is, without the sovereign ordinances of nature, there would be no order in nature, only chaos. Every crystal is the product of a plan of nature, and when physicists present Bohr's beautiful atom models, they exemplify the plans of inanimate nature which they seek. The sovereignty of nature's living plans is expressed most clearly in the study of Umwelten. (Jakob von Uexküll 1992: 356)

Abstract. In recent years, our aim has been to expand the concept of 'umwelt' towards its evolutionary aspects. In this contribution, we argue that since the different lineages of life share their origins, they also share, at least to some extent, the (informational) norms and interpretative practices (deeply established rules in addition to memory and experience) that apply in their particular umwelten. If so, some "dialects" of such norms may be understandable to umwelten across different forms of life that inhabit the same space and time. Such "umwelt overlaps" then facilitate a mutual understanding of different life forms, leading to coordinated (negotiated) cohabitation. We highlight some of the ways in which such "vertical" and "horizontal" processes can lead to an evolutionary and/or ecological networking of umwelt "bubbles". We believe that the original concept of 'umwelt' should be expanded so as to encompass *all* living beings and their evolutionary memory, experience, and present ecological settings. Our interpretation also leads to abandoning of the concept of an external "composer of symphony" and allows life forms to compose their being in the world according to their "inner contexts", "players available", and evaluation of external factors, mainly biospheric but also physical.

Keywords: umwelt; *Bauplan*; biospheric web; symbioses; gut–brain axis; *Rhizobium*–legume

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1. An overview: Umwelten and the harmonizing nature

Our group (see e.g. Markoš *et al.* 2009; Švorcová *et al.* 2017; Markoš, Švorcová 2019; Švorcová 2024; see also a survey organized by Tønnessen *et al.* 2016) has been interested in the concept of 'umwelt' for well over a decade. The overall trend of our efforts was to go beyond the mainly animal-centric, static character of the original model formulated by Jakob von Uexküll in the early decades of the 20th century. He initially introduced the concept of 'umwelt' in his *Umwelt und Innenwelt der Tiere* in 1909 (English translation 1985). In his later publications, such as *Streifzüge durch die Umwelten von Tieren und Menschen* from 1934 (English 1992) and *Die Bedeutungslehre* 1940 (English 2010), he developed the concept further.

Uexküll was interested in how animals perceive the world and what aspects of the world are within their reach. He formulated the concept of 'umwelt' as tightly associated with the physiological functioning of organisms, their 'functional circles' (*Funktionskreis*), which include not only various reciprocal relationships between sensory and operational organs but also the overall body structure (*Bauplan*). Once objects from the umwelt are incorporated, the *Bauplan*, which links the organs in an animal's body, forms a cohesive entity. Sensory organs establish connections with the nervous system via perception and action. The structure of the brain is thus adjusted to accommodate the configuration of sensory organs – and, conversely, sensory organs are adapted to the brain structure (Ovčáčková, Švorcová 2024). As a result, the complexity of animals is reflected in the complexity of their organs and *Baupl*äne. In higher animals, the umwelt of their sensory organs expands beyond the umwelt of the "working" organs, that is, those commonly found in lower animals. There emerges a close relationship between the sensory organs and external objects. Uniform impressions (*einheitliche Eindrücke*) aligned with objects in the umwelt can arise in the brain. In short, Uexküll recognized a progression from simple animals with basic umwelten to more complex animal bodies with diverse and elaborate umwelten (Uexküll 1992). Although in his later work Uexküll attributed *Baupl*ä*ne*, autonomy and subjectivity even to individual cells within a multicellular body (Uexküll 1931; Kull 2004), he did not say explicitly that individual cells have umwelten. His umwelt model was originally conceived so as to fit mostly animals equipped with brains and perception.

In the following, we want to build mostly on Uexküll's later ideas about cellular subjectivity. If Uexküll is to be considered a "proto-semiotician", the founding father of biosemiotics (as claimed in Kull 2010), the umwelt model should be applicable to *all* forms of life – and allow for their evolution. Semiosis, after all, had emerged with the first cells (Hoffmeyer 1996). Above all, though, the model should not only incorporate the innerness of living beings but allow it to be the principal precondition for the operation of semiosis. We suspect that Uexküll regretted the loss of harmony that used to reign supreme in biological theories: that harmony was lost with the arrival of Darwinism. He regretted this, although, like Darwin, he also emphasized the pivotal role of a lawful external world or 'nature' (note that living beings are viewed as living as if "outside" nature):

> [T]he countless Umwelten represent the keyboard upon which nature plays its symphony of meaning, which is not constrained by space and time. In our lifetime and in our Umwelt, we are given the task of constructing a key in nature's keyboard, over which an invisible hand glides. (Uexküll 2010[1940]: 114)

It is quite obvious from Uexküll's terminology (*Bauplan*, *Entstehungsplan*, *Planmäßigkeit,*[3] God–nature, 'mysterious plan') that he assumes the existence of a teleological principle, a plan, behind all development in living nature (Ovčáčková, Švorcová 2024). One can detect here a clear inspiration by Immanuel Kant, whose works Uexküll read as a young scholar, but also by Johann Friedrich Blumenbach, who was first to use the term '*Bauplan*' (Brentari 2015). Anchored in modified Kantianism (Jaroš, Brentari 2022), Uexküll's 'Nature' is understood as a goal-directed natural factor which arranges the umwelten of all living beings so as to facilitate their effective interaction. From our current perspective, though, there is a certain tension in Uexküllian thinking in that it seems to express both mechanistic and antimechanistic views. Although Uexküll does not want to reduce biology to mere physics and chemistry (Uexküll 1905; Brentari 2015) and his view on nature is holistic, he is convinced that living entities can be interpreted in mechanistic terms: only beyond the realm of the living do we find an extra-material force (imagined by Man in the Kantian sense) that has a harmonizing influence on all natural entities. Yet Uexküll also admits that organisms are endowed with faculties that machines do not have, such as morphogenesis or regeneration (Brentari 2015).

Similarly, in many instances, Uexküll refers to the predetermined *Bauplan* that dictates the actions of both individual cells within organs and of entire organs.

[3] Uexküll also discusses a dual sense of purposefulness in case of animals: "[...] firstly, the organism is purpose-built and secondly, the organism is purpose-fitted into its environment" ("[...] *einmal ist der Organismus zweckmäßig gebaut und zweitens ist der Organismus zweckmäßig in seine Umgebung eingepasst.*", Uexküll 1912: 100). By 'functioning according to plan' (*Planmässigkeit*) he implies that "[...] the parts are arranged according to a ground plan or a plan in such a way that together they form a uniformly functioning whole" ("[...] *daß die Teile entsprechend einem Grundriße oder einem Plane derart angeordnet sind, daß sie gemeinsam ein einheitlich funktionierendes Ganzes bilden.*"; Uexküll 1912: 100). Inspiration by Immanuel Kant is evident here. [Translation by Lenka Ovčáčková (Ovčáčková, Švorcová 2024: 351)].

This *Bauplan* is closely connected to mechanistic functioning: with increasingly more elaborately regulated *Baupläne* (i.e. fixed organization), living entities become increasingly more mechanistic. In the case of an amoeba that constantly changes its structure, Uexküll can say that "an amoeba is less of a machine than a horse" (Uexküll 1985: 26; Brentari 2015: 70). On the other hand, he uses the metaphor of a melody to emphasize the harmony and holistic nature of organismic processes, with individual cells sounding their individual self-tones and jointly forming a living carillon. Self-tones combine into melodies that require no mechanical interrelation of the cell bodies to have an effect on each other (Uexküll 1992). Analogically, organ components have their own unique meaning tone (*Bedeutungston*). As in Aristotle, Nature knows what is best for each living being[4] and imposes its pressure on a keyboard that is, once again, constructed by itself. "Nothing is left to chance in nature," writes Uexküll (2010a: 100). Yet even Nature itself does not know everything: it is ruled by a positive law, an immutable juridical corpus (established by whom?).

2. Harmonizing nature from today's perspective

Uexküll as if confirms some older views of Emanuel Rádl,[5] who at the beginning of the 20th century observed that, with respect to the old schools in biology, Darwinism took away what was dearest to them, namely the belief in the intelligibility of nature. Rádl's contemporary Jakob von Uexküll was a late offshoot of these "old schools" of German and continental science in general, and a fierce opponent of Darwinism. Words such as 'chance' or 'contingency' irritated both him and many of his predecessors and contemporaries, such as for example Neolamarckians: in their view, Darwinian evolution by natural selection was like a Russian roulette where survival was decided by inherited genes and chance. The individual could do nothing to mitigate bad heredity. Lamarckism, on the other hand, allowed the individual to choose a new habit when faced with an environmental challenge and thus shape the entire future course of its own evolution (Bowler 1983).

As noted above, Uexküll's texts are full of depictions of natural events presented as a well-played counterpoint, harmony, meaning. Meaning? When a butterfly

4 For illustration, two quotations from Aristotle: "Nature does nothing in vain but always what is best from among the possibilities for the substance of each kind of animal, which is why if it is best in a certain way, it is also in this way according to nature" (*De incessu animalium* 2, 704b15-18); "Nature does everything either because it is (conditionally) necessary or because it is better" (*Generatio animalium* I, 4, 717a15-6). (Translation quoted after Aristotle 1984–1985.)

5 We refer here to an abridged English translation (Rádl 1930); the German original dates from 1906 and 1909.

scares away a bird by spreading its wings, "the butterfly does not know that the sparrow flees at the sight of a cat's eyes. However, *that which brings* this umwelt-composition into being exhibits an awareness of these facts." (Uexküll 2010a: 102; our emphasis, A. M., J. Š) The 'that which brings' is not specified in any way: is it nature, as in Aristotle, is it God, or is it Latour's OWWAAB?[6] Everything happens like a massive, well-rehearsed symphony (or a glockenspiel) of nature, and the task of biology is to discover the score by which it is played. We do find in Uexküll the notion of mutual tuning of the "players", but we prefer the concept of 'negotiation', as presented in Kauffman 2000. Uexküll's approach understandably provoked controversy: it was criticized by Darwinians but also by his peers – after all, biologists of his time already lived in a radically different scientific paradigm and believed in evolution (as well as in "progress"). Uexküll then argued that in *every* period of evolution, this mighty symphony is played, albeit understandably differently, with different musicians and instruments. Life has a "meaning score" such that, for example, spiders build their webs because they are "fly-sensitive" (*fliegehaft*) and have a "feeling" of counterpoint that needs to be played relative to the fly. But do they really have a "feeling" or are they simply adjusted so by "nature"?

If we take Uexküll's previous quote given above (p. 440), we find the invisible hand as in Darwin, again belonging to nature but in a different way. It is because he evoked the meaning that dominates all life, a source of inspiration that led to the extension of semiotics to non-human animals and eventually all living things. With the advent of Darwinism, he regretted the loss of the neat, lucid world of scientific laws, so drastically inflicted by Darwin's intrusion.

One more thought to ponder about: we saw above that the "conductor" of the biospheric symphony is "nature", but we did not learn much about the amount of freedom the "musicians" themselves have. Are they assembled in advance (and if so, by whom?) like parts of a clockwork? It would seem not, since Uexküll constantly rails against "mechanicism". Nevertheless, at one point he suggests by the way of an example that an expert, after examining a clock's music roller, can determine what melody the clock would produce (could we perhaps view the roller as analogical to the DNA script?). In another place, as mentioned above, he re-states that the task of biology is to discover the score of the "symphony" that is being played. It thus seems that while living things (animals or cells)[7] do recognize meanings and behave accordingly, they only recognize what they are attuned to, and their reactions are more or less predictable and determined. It is also unclear

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6 To please everyone, Latour (2017) uses the awkward acronym OWWAAB (Out-of-Which-We-All-Are-Born).

7 The cell also has its own "personal tone" that matches the tones of other cells in the organism. It is aware of the meaning of what is being played (see, e.g. 'cellular music' in Uexküll 1937)

how the "orchestra" copes with disruptions, such as the collapse of a flutist or even the conductor, the existence of fake "players" who "deliberately" spoil it, or sudden disasters, such as fall of a chandelier in the "hall". Moreover, 'predictable' does not mean 'hardwired' but rather 'within a certain statistical distribution': for example, we all know that a tower glockenspiel can sound off tune in certain outdoor temperatures. Moreover, it is not assumed that the "players" draw on the vast deposits of the memory and experience of their lineage because they do not govern themselves: it is "nature" that moves them like puppets. Sometimes the reader gets the impression that Uexküll was two generations ahead of his time and had he lived today, he would have been content with the analogy of "digital" music players and the discoveries of molecular biology. So, was he really a proto-biosemiotician?

Let us introduce a different view of lawful behaviour. Zdeněk Neubauer understands natural laws rather as a genuine corpus created by the evolution of nature itself. He argues:

> In the spirit of the liberal tradition, Darwin meant the expression *Laws of Nature* (*Leges Naturae*) as the genitive *subiecti* – not *obiecti*, as it has been understood until now and as Darwin was and still is interpreted. It is therefore not laws *determined by* nature, but laws naturally established by nature itself. Nature has thus been elevated for the first time to the subject of legislation in the natural sense, where 'laws' arise of their own accord – with tradition. And they change with application and with interpretation, the two – interpretation and decree – falling into one. Moreover, natural laws are also natural in the sense that they do not exist supernaturally as if valid *in abstracto* but are applied *in concreto* to the here-and-now of each individual, in individual cases of procreation and survival, just as in society laws exist only in their application in legal cases and legal decrees/decisions. (Neubauer 2010: 292)

Perhaps, but there is also the opposite view formulated by David Depew and Bruce Weber (1996), who depict Darwin as a hardcore Newtonian; what Neubauer praises may perhaps hold for some interpretations of Darwinism but Uexküll is certainly right concerning the mainstream Darwinian paradigm.

3. Umwelt revisited: The *norm* and the game

In Markoš and Švorcová 2019, we suggest a scenario of life's origin according to which certain *norm*s were, in the very beginning, established for both intracellular and intercellular proceedings. The rest is a game based on these rules:

> Once the rules are established for the game (whether ice hockey, opera, courtroom, or ...), what is important is that the *performance* takes place within the framework of some [...] ring (chessboard, playground). With this in mind, we invite the reader to compare two approaches. J. von Uexküll prods us to uncover – behind the tangled web of life – the scoring of the symphony of nature, which he sees as the very task of biology. In contrast, we argue that the ringing in the biosphere is not only the performing of symphony, but before all else, a genuine, endless jam session! [...] The statement does not suggest that the opposite does not exist – frozen communities do stick piously to the norm (sects, living fossils, etc.). They provide us a stable background for the jamming of others. (Markoš, Švorcová 2019: 2)

Our basic presuppositions can thus be summarized as follows:

(1) We expand the concept of 'umwelt' as a repository of memory and experience of one or more individuals, communities, or species that move within the spacetime of their umwelten. 'Umwelt' can be thus taken to mean the realm of subjective experiences of an organism, but memory of the lineage is not discussed by Uexküll. Moreover, he does not address the issue of how new experiences are incorporated in an umwelt: our interpretation of the umwelt is more plastic and less static.

(2) No living entity has the capacity to withdraw from the totality of its umwelt, but it can change its coordinates within it: during ontogeny, pushed by external conditions, by contingence, or even by "inventing" new links to the external world (which mostly represents other, closely interconnected umwelten).

(3) Thanks to shared ancestry and shared *norms*, all umwelten partially overlap, which facilitates mutual communication and "getting along" with others. In this way, the manifold of mutually interconnected umwelt "bubbles" forms a "foam" of ever-changing biosphere. There is a *norm* that encompasses the basic informational processing shared conservatively across the biosphere: the basic sets of nucleotides and amino acids, the rules of the genetic code, metabolic or signal transduction pathways, receptors, structural elements such as membranes or cytoskeletons, and the list could go on. Naturally, this norm is never shared absolutely and there are exceptions, but evolution does use a certain defined toolkit that enables understanding even among distantly related taxa.

The view of evolution as changes, in time, of entirely "isolated" lineages (perhaps best articulated in the ideal trees of cladistics) has recently shifted towards a reticulate scheme of entities engaged in mutual interactions: via symbiotic interactions, hybridization events, or horizontal gene (or even genome) transfer. Moreover, vesicle traffic across lineages can contribute to such exchanges by carrying structures, viruses, plasmids, etc. On the one hand, this reflects the holistic view of nature that Uexküll would have agreed with. On the other hand, he could not have known about the extensive mutual interdependence between distant species. Can this be integrated into the umwelt theory?

In our interpretation of Uexküll's original definition, umwelt is an imaginary "bubble" in which a living being is enclosed and knows only what it needs to know of the world to fit well into the counterpoint of nature. For our own purposes (Švorcová *et al.* 2017) we have tried to interpret the idea of the umwelt as follows.

Let us start with a "bubble". It represents the part of the world which the living thing can access. Its perceptions depend on its coordinates in the bubble, i.e. among other things, on the perspective from which (within the confines of the umwelt) these perceptions come and how strong they are. The umwelt therefore must (in its different coordinates) satisfy *all* of the living entity's survival requirements at different ontogenetic stages (egg, embryo, larva, pupa, imago, male or female), seasons, times of day, etc. During ontogeny, a living being must often switch between the "desks" of the orchestra that plays the "philharmonic of nature". An adult male moth, for example, is at midday at point **A** of the multidimensional umwelt, at an intersection of perceptions of sharp light and potential danger in the form of birds. Therefore, it remains motionless on the bark of a tree although it may perceive nearby females. The harsh light is evaluated as 'stay still, danger (birds)', and this outweighs the tempting scents. At night, the butterfly is at point **B**: there is much less light and the mating urge thus prevails despite the danger of bats. A female moth also stays at point **A** during the day, but at night her role is different. Aside from mating, she must make sure to choose the right tree and the right time to lay her eggs: her umwelt is at coordinate **C**. Other points could represent the demands of the developmental stages or places occupied only seldom, for instance during severe weather or epidemics. The moth behaviour as described up to now could basically be programmed by any elementary school pupil; so why do we mention the whole model of umwelt, although extended by us? Let us proceed.

There are also places in the umwelt – and perhaps this applies to the majority of places it encompasses – that are not visited at all *in the present world*. They represent the past memory and experience of a lineage or biome. They can be visited at critical moments or by chance embodied in atavisms or cryptic variability (such as a change of phenotype in the Waddingtonian sense or a heavy metal band discovering a lute). Not every aspect of a *potential* umwelt needs to be addressed. An *actual* umwelt always depends on factors such as those outlined above: momentary interpretation of the norm, environmental conditions, what experience is remembered and what forgotten, or what other creatures are present in the umwelt of a specific organism. Each point of the umwelt overlaps with umwelten of other creatures. In short, an umwelt cannot be conceived of in isolation, and, within the overlapping areas, participants to some extent understand each other and know, at least approximately, the norms of others and their use. A flying moth can pick up some of the echolocation sounds of a bat; it responds by folding its wings and dropping to the ground but the bat flies under it – and waits for it to drop.

Let us return to the concept of 'counterpoint': it allows Uexküll to explain relationships between living organisms by drawing parallels with the rules that guide the interaction of various tones produced by different musical instruments in a composition. Just as each instrument has a distinct set of tones, each animal has at its disposal a specific array of tones which interact in a contrapuntal harmony with those of other animals (Uexküll 2010). A perfect counterpoint is in the slight overlap of two umwelten. Both the female moth and the caterpillar must also somehow "harmonize" with their host trees, although each stage notices different tree characteristics; similarly, the overlap with the woodpecker's umwelt is quite different for the moth's different developmental stages.

In our understanding, empty space in the bubble represents the *possibilities* prepared for *a particular individual* by the course of its life and its experience (a view similar to that of Tønnessen 2014). On top of that, there are also areas of deeper experience, which encompass the historical (evolutionary) memory and experience of the whole lineage of ancestors that has led to that particular moth. Such areas can become accessible by chance (mutations, epimutations, atavisms), via environmental influences (e.g. various long unseen and suddenly reappearing stimuli), or as a result of extreme changes in external conditions (onset of a glacial period, being transplanted to another part of the world, and the like). Naturally, such "resurrected" experience is *interpreted* by a being that already lives under those changed conditions. The meaning which the living being assigns to it may be quite different from the original one and may even contribute to a loosening of the boundaries of the umwelt towards new evolutionary outbursts. Moreover, the individual enters into a "counterpoint" with the current – not former – players in the biosphere, which can affect its *fitness* for better or for worse.[8]

Finally, a bubble can also "burst" into the outside world by appropriation (perhaps under selection pressure) of something new, hitherto absent in the bubble. A new player or instrument is added to the "orchestra" of skills.

Let us now climb up to a larger scale and consider the umwelt of a species. The space of the bubble includes all possible forms – past, but also many potential, though as yet unrealized ones – that characterize the species, its lineage, and possibly its close symbionts. Other species, too, carry their versions of certain

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8 How would a tyrannosaurus or a woolly mammoth "musically" perform if they were resurrected into our biosphere?

traits inherited from a common ancestor so that, once again, when they meet or establish symbiosis with species that have such traits, they "get along" thanks to the partial overlap of their umwelten. Prolonged cohabitation may even lead to a single common interpretation of such traits or to the development of new shared interpretation of the world. One could climb even higher and consider a bubble representing an entire genus or a yet higher taxon. Different forms of a species may emerge from this "generic" field of possibilities only to disappear later, but the genus persists (Flegr 2015).

4. Umwelt's counterpoints

Let us now shift our attention to comprehension, collaboration, and reciprocal influence. The significance of communities has often been undervalued: traditionally, priority has been given to individuals or their genes. We believe that individual understanding is possible thanks to the abovementioned *norm*, which forms the basis for the overlapping of umwelten, i.e. the counterpoints of organisms. These concepts are not implicit in the original Darwinian paradigm, although competition (the struggle for survival) is the focal point of the theory of evolution, and this competitive aspect could easily include cooperative behaviours as well. Overlapping umwelten probably played a role even in the symbiotic emergence of three types of cells (i.e. archaea, bacteria, and eukaryotes) and cell organelles, such as mitochondria and plastids. It most likely took place during the era of the Last Universal Common Ancestor (LUCA), because with greater distance from the beginning of life it became much less common for two entities to fully fuse into one. With the divergence of basic lineages of life, the likelihood of mutual understanding over time decreased in a process somewhat akin to the evolution – and diversification – of human cultures and languages (Markoš, Švorcová 2019).

But to return to Uexküll: the Darwinian concept of 'adaptation' (or '*Anpassung*' in German) according to Uexküll fails to capture fully the dynamic interplay between organisms and their environment. Organisms do not simply conform to the physical attributes of the world: they interact with the world of signs. Uexküll favours the term '*Einpassung*' (Uexküll 1927), which encompasses not only the fitting of organs and their components to their functions and the matching of organisms to their environments, as noted above, but also *the alignment of umwelten with one another* (Uexküll 1927; Kull 2004). This is highly isomorphic to how one can view symbiotic (and even symbiogenetic) relationships, where the host or symbiotic partner becomes in effect the environment (or a better-constructed niche) for other organisms.

There is a vast number of examples of symbiotic relationships throughout the biosphere. In fact, once one starts noticing them, one finds them everywhere. They range from parasitism and commensalism all the way to mutualism. In fact, few (if any) relationships in nature are consistently neutral toward each other. Typical examples are fungus–plant relationships (mycorrhiza) or lichens as composites of algae, fungi, and even yeasts. There is also a wide range of cases of animal–bacterium symbiosis in the gut or skin microbiome of many animals, from insects to humans (for instance, the spotted salamander *Ambystoma maculatum* develops in the presence of algae that live around the salamander's eggs and nowhere else) or intracellular symbioses, where we would find an endless variety of examples across all lineages, from protists to corals or insects. In order fully to embrace the cooperative nature of the biosphere, scholars have introduced the term 'holobiont' (for the history of this term, see Rosenberg, Zilber-Rosenberg 2013), which denotes the complete living entity comprised of not only the host organism but also all of its symbiotic partners. Some scientists regard a holobiont as a full-fledged biological individual. Below, we give examples of holobionts concerning (1) the ecosystem of human body and (2) bacterium-plant symbiosis.

4.1 Ecosystem of the human body

(1) *The gut–microbiome–brain*[9] axis has attracted unprecedented attention in the past two decades, and the number of studies mapping this axis has boomed. Our

[9] The concept of gut–microbiome–brain axis is nowadays used to refer to a bidirectional communication pathway that connects the central nervous system (including the brain and spinal cord) to the enteric nervous system of the digestive tract. Human intestines are innervated and contain about 500 billion neurons and enteric glia, which collectively form the enteric nervous system (ENS). The ENS comprises two types of plexuses: the myenteric plexus, which controls peristalsis (the rhythmic contraction and relaxation of intestinal wall), and the submucosal plexus, which regulates enzyme secretion, absorption, and overall chemical conditions in the intestines. The enteric nervous system can communicate bidirectionally with the central nervous system via the vagus nerve and prevertebral ganglia, which constitute the parasympathetic and sympathetic nervous systems. Together, they form the brain–gut–microbiome axis, which allows signals from the brain (e.g. those induced by stress or fear) to regulate digestion and, conversely, signals from the gut microbiome, including metabolites produced by gut bacteria, can influence human brain function and overall mood (Markoš, Švorcová 2019). These processes are governed by neurotransmitters (acetylcholine, dopamine, serotonin, adrenaline, noradrenaline, etc.), both those found in the brain and gut of the host and those produced by the bacteria themselves. Also, the ENS maturation in mice is bacteria-dependent (De Vadder *et al.* 2018), including the degree of nerve density in the gut (Collins *et al.* 2014) or the abundance of enteric glia in the mucosal layer (Kabouridis *et al.* 2015). On top of that, it is believed that gut bacteria of the infant play an important role in stimulating its postnatal brain development (Frerichs *et al.* 2024).

digestive tract, which spans from the stomach through the colon to the anus, hosts a vast array of different types of organisms. This ecosystem includes archaea, protists, animal commensals and parasites, fungi, viruses, and, most notably, up to 1,500 species of bacteria. Their signalling influences various systems in our body, including the endocrine, immunological, and neuronal systems. Metabolites and signalling substances have a far-reaching impact on host metabolism: they facilitate the breakdown of fibre and polysaccharides, synthesize essential nutrients such as vitamin K or short-chain fatty acids, metabolize the bile acids, confer tolerance to food antigens, regulate the development of nervous systems, and much else. Our microbiome is a facet of our phenotype that is not fully determined by our genes but is nonetheless crucial for sustaining optimal health (Markoš, Švorcová 2019).

The epithelial cells that line intestinal walls in our gut are joined together by tight junctions, which form a barrier that prevents bacteria in the lumen (the inner space of the intestine) from triggering an immune response. Moreover, commensal bacteria inhabiting the mucus covering the epithelium also form a barrier against pathogenic bacteria. This bacterial barrier is physiological (when the gut is colonized by commensal bacteria, pathogens cannot spread), chemical (bacteria produce a variety of substances), and immunological (bacteria stimulate the development and functioning of the immune system). The mucous membrane secretes mucinous material, which nourishes the resident bacteria and is continuously replenished by epithelial cells (with a turnover rate of about seven hours). Dendritic cells monitor the presence of pathogenic bacteria in the lumen from behind the epithelial wall. When they detect some, they initiate an immune response involving T cells. Additionally, commensal bacteria produce molecules which regulate the activity of immunosuppressive regulatory T cells, thus contributing to the maintenance of a balanced and healthy immune system (Eisenstein 2018).

Human gut colonization by bacteria based on counterpointed communication is established from the very first moments of our lives, as can be demonstrated on contemporary ways of giving birth. The microbial composition of the gut in newborn infants varies depending on whether the birth was natural or by emergency (eventually elective) caesarean section. In babies born by caesarean section, one can observe a delayed colonization of the intestine by bacterial genera that would otherwise have been acquired along the newborn's journey through the mother's birth canal, bacteria which constitute healthy microbiota populations in the gut. We will not go into details here, but the relationships between the mother, the infant, and his/her gut are one of the most telling examples of coevolutive umwelt overlapping: mother's milk contains a number of nutritional substances such as proteins, fats, or carbohydrates, but also substances such as immunoglobulin A, cytokines, and active enzymes, including lysozymes or lactoferrin, which modulate the immune system of the newborn, help with digestion, and contribute to its defence against pathogens. Lactoferrin, for instance, can inhibit the growth or even kill pathogenic bacteria. Milk also contains physiologically active bacteria, which consequently occupy the infant's gut. Certain complex sugars present in breast milk cannot be digested by newborns but are intended for bacterial symbionts such as the *Bifidobacteria*. The genome of *Bifidobacterium longum* subspecies *infantis* contains a specific region with genes responsible for metabolizing these complex sugars. Interestingly, these genes are absent in related *Bifidobacteria* which are not found in the human gut: this indicates a coevolutionary relationship between *Bifidobacteria* and their hosts (Roger *et al.* 2010). The absence of these genes in other *Bifidobacteria* further underlines the coevolution between *B. longum infantis* and its host (Underwood *et al.* 2015).

Another example of an elegant reciprocal connection is the colonization of the gut by *Bacteriodes fragilis*, a bacterium that plays a fundamental role in modulating human immunity and gut development but is also associated with cancerous and inflammatory diseases as an opportunistic pathogen. In fact, this commensal/pathogen relationship duality is observed with numerous species of bacteria, showing that categorization of these complex dynamics is far from straightforward. Gregory Donaldson and colleagues (Donaldson *et al.* 2018) have described the communication between *Bacteroides fragilis* and the host (infant) immune system: the bacterium can alter its surface so as to facilitate the binding of host immunoglobulin A (IgA). This adaptation makes it easier for the bacterium to adhere to the intestinal mucosa and to be recognized by the host immune system, which thus enhances gut colonization. IgA can be gained from the mother's milk or by activating specific cells in the gut, and it serves as a sign mediating these two overlapping umwelten. Such a sign perspective enables the study of holobionts as model organisms.[10]

The story does not end here, however: *B. fragilis* (together with *Bacillus subtilis*) also promotes the development of mammalian gut-associated lymphoid tissue (GALT) (Bouskra *et al.* 2008) by producing polysaccharide A. In general, when bacteria are absent in the gut of germ-free rabbits or mice, GALT structures such as Peyer's patches or isolated lymphoid follicles which are necessary for the immune response of the host, do not develop properly. Also, the immunoglobulin production in the host cells can be reduced. When *B. subtilis* and *B. fragilis* are introduced together into germ-free rabbits, healthy GALT is formed (Rhee *et al.* 2004). Other combinations of bacterial species introduced did not lead to the formation of GALT. Also, polysaccharide A produced by *B. fragilis* is known to protect the

[10] We thank the anonymous reviewer for this remark.

gut from *Helicobacter hepaticus* infection, which usually leads to inflammation. This protective ability of *B. fragilis* is mediated by its production of polysaccharide A, which promotes subsequent production of anti-inflammatory interleukin IL-10 by the immune system of the host (in comparison with a situation when polysaccharide A is not produced due to a laboratorial induction of mutation in the bacteria). In general, *B. fragilis* modulates the host immune system and its development (Troy, Kasper 2010) and there are already many known examples how gut microbiota regulate the differentiation and function of intestinal cell types, intestine or nervous systems development and gut-brain communication in general (for more information, see e.g. the review by Ye, Rawls 2021).

In principle, one can thus say that through mutual counterpoints of the umwelten in the form of different substances, such as IgA or polysaccharide A (and these are but a fraction of molecules through which the two species communicate with each other), *umwelten not only overlap but construct or modify each other.*

4.2. Bacterium-plant symbiosis

Interdependence between *Rhizobium* bacteria and the roots of leguminous plants is another well-described example of umwelt overlap of two evolutionarily distinct lineages. Plants lack the ability to fix nitrogen from the air on their own. To acquire nitrogen, they need a symbiotic relationship with bacteria. Different species of legumes cooperate with different species of *Rhizobium*. Thanks to this relationship, atmospheric nitrogen (N_2 gas) undergoes conversion into ammonium, which facilitates its deployment in processes such as the synthesis of amino acids.

This partnership starts by the production of flavonoids by legume roots. These are recognized by a compatible species of *Rhizobium* (Oldroyd *et al.* 2011; Hawkins, Oresnik 2022). Interestingly, there are thousands of different flavonoids known so far and, in most cases, they are produced as part of defence against pathogens. Nevertheless, isoflavonoids, a highly specific group of flavonoids, are found only in legumes (Hirsch *et al.* 2001). These compounds signal to the *Rhizobium* bacteria the presence of a compatible host: it thus seems that, in the course of evolution, the presence of isoflavonoids (i.e. a sign of stress) came to be interpreted as an invitation to establish a mutualistic relationship. In an umwelt counterpoint, a *normative sign* can acquire a new meaning. Subsequently, the root extends towards the bacteria, thus facilitating colonization. In response, and after recognizing the isoflavonoids, the bacteria start to produce a lipo-chito-oligosaccharide called the Nod factor, which mediates suppression of the plant's immune system and triggers a calcium spike in the cortex. That results in cell division and the formation of nodules. Osmotic stress, low oxygen content and other factors in the environment also play a role (Hawkins, Oresnik 2022): in these nodules, the bacteria produce nitrogenase enzymes, which can capture atmospheric nitrogen, bind it with hydrogen, and thus produce ammonium. The plant then uses ammonium in the synthesis of amino and nucleic acids.

Bacteria are also capable of forming haem groups which, when combined with a globin protein of legume origin, yields leghaemoglobin (Beringer *et al.* 1979), which helps supply the bacteria with oxygen without disrupting the ammonium pathway (because nitrogenase activity is inhibited by oxygen). Consequently, the bacterium undergoes a transformation: it sheds its cell wall, increases in size, and activates genes crucial for nitrogen fixation (Miller, Oldroyd 2012; Van Zeijl *et al.* 2015).

The nodule, along with the specialized bacteria it harbours, will perish within a few days, but it also contains non-transformed bacteria that thrive on the decomposing nodule. This is as if a form of recompense for the sacrifice made by the specialized, terminally differentiated bacteria. The bacteria retain all the nitrogen transformation genes (a shared norm), which they would not require in a free-living state in the soil, while letting the specialized bacteria perish. Once more, the examples provided above aim to underscore a shared norm of signs among diverse life forms, where their meaning undergoes continual negotiation and reinterpretation throughout evolution, as seen in traits like IgA or flavonoids. This *norm* allows counterpoints at all, as considered by Uexküll.

5. Conclusions

We propose a broadening of the umwelt concept: it should encompass all forms of life. This is in line with our understanding of the emergence of semiosis in the earliest cells and it is consistent with Uexküll's later writings. While Uexküll's model is invaluable for extending the concept of subjectivity beyond humans, certain aspects of his concept of umwelt nowadays seem outdated. Additionally, we point to some contradictions in Uexküll's ideas, particularly between holism and mechanicism. Last but not least, we find it problematic that the *Bauplan* as the foundation of umwelt seems overly predetermined and externally driven.

What we advocate is a concept of a plastic umwelt, where new experiences can be acquired and coordinates adjusted in evolution. Our interpretation, illustrated through two selected examples of symbiotic relationships between evolutionarily distinct taxa, demonstrates how umwelt counterpoints can be formed through specific sign reinterpretation. This concept presupposes shared biospheric norms, enabling mutual overlaps of umwelts. It supports an evolutionary model in which organisms align their umwelts with one another, forming the holistic, interconnected biosphere that Uexküll envisioned.

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O bublinách a pěnách: Kontrapunkty umweltů v symbióze

V posledních letech jsme se snažili rozšířit pojetí umweltu i o jeho evoluční dimenzi. V tomto příspěvku tvrdíme, že vzhledem ke společnému původu různých forem života sdílejí tyto formy, alespoň do určité míry, normy pro přenos informací a způsoby jejich interpretace, které jsou pro ně rovněž společné. Tyto praktiky, včetně hluboce zakořeněných pravidel, paměti a zkušeností, se projevují v jejich umweltech. Pokud to platí, mohou být určité „dialekty" těchto norem srozumitelné i pro jiné formy života, které sdílejí stejný časoprostor. Tyto „překryvy umweltů" pak mohou usnadnit vzájemné porozumění různých organismů a vést ke koordinovaným činnostem a sjednanému spolužití. Upozorňujeme pak na některé způsoby, jak „vertikální" a „horizontální" procesy mohou přispět k evolučnímu nebo ekologickému propojení umweltů, což vytváří dynamiku propojených „bublin". Domníváme se, že původní koncept umweltu by měl zahrnovat všechny živé bytosti včetně jejich evoluční paměti, zkušeností a aktuálního ekologického kontextu. Tato interpretace také opouští myšlenku vnějšího „skladatele symfonie" a místo toho umožňuje formám života komponovat své vlastní bytí ve světě na základě jejich „vnitřních souvislostí", dostupných „nástrojů" v komunitě a zhodnocení vnějších faktorů, zejména biosférických, ale i fyzikálních.

Vahust ja mullidest: omailmakontrapunktid sümbioosis

Viimastel aastatel oleme püüdnud laiendada omailma mõistet selle evolutsiooniliste aspektide suunas. Käesolevas kirjutises väidame, et kuna elu erinevatel arenguliinidel on ühine päritolu, jagavad need ka vähemalt mõnel määral (informatsiooni)norme ning tõlgenduspraktikaid (tugevasti kehtestunud reegleid lisaks mälule ja kogemusele), mis nende konkreetsetes omailmades kehtivad. Kui see on nii, võivad mõned selliste normide „dialektid" olla mõistetavad erinevate ühes ja samas ajas ja ruumis elutsevate eluvormide omailmadele. Sellised „omailmakattuvused" hõlbustavad erinevate eluvormide vastastikkust mõistmist, viies välja koordineeritud (läbi räägitud) kooselule. Toome esile mõned viisid, kuidas sellised „vertikaalsed" ja „horisontaalsed" protsessid võivad välja viia „omailmamullide" evolutsioonilisele ja/või ökoloogilisele ühistoimimisele. Me usume, et algset omailmamõistet tuleks laiendada nii, et see hõlmaks kõiki elusolendeid ning nende evolutsioonilist mälu, kogemust ja praeguseid ökoloogilisi olusid. Meie tõlgendus toob kaasa ka välise „sümfoonia autori" mõistest loobumise ning lubab eluvormidel luua oma viibimist maailmas vastavalt nende „sisemistele kontekstidele ", „olemasolevatele mängijatele" ja peamiselt biosfäärilistele, ent ka füüsikalistele välisteguritele antavatele hinnangutele.