

Morten Tønnessen

The study of past Umwelten

Abstract: *The study of past Umwelten*

In this article I detail how past Umwelten can be studied by applying Jakob von Uexküll's Umwelt theory and informed by contemporary science. I argue that the methodological challenges raised by the lack of present organisms available for real-time observations and whole-body physiological studies can be partly overcome by making qualified assumptions drawn from relevant knowledge and reconstructing likely Umwelt relations. As groundwork for such studies, I outline some basic assumptions in studies of past, current and future Umwelten, consider methodological issues related to the study of past Umwelten in particular, and present a few empirical assumptions that are informative with regard to the study of past Umwelten in different historical periods. I also discuss the relevance of such studies for current conservation work, specifically contemporary discussions about de-extinction, and for economics conceived of as a branch of ecology in the fashion of ecological economics.

Keywords: Umwelt theory, History, De-extinction, Lifeworld, Phenomenology.

1. Introduction

Umwelt theory is usually thought of as a biological theory that is applicable in the study of the lifeworlds of currently existing species. I have earlier argued that it is also feasible to study future Umwelten, by making *Umwelt predictions* and developing *Umwelt scenarios*, as part of a broadly informed *Umwelt futurology* (Tønnessen 2019). In this article I make the case that it is furthermore theoretically and methodologically meaningful to study past Umwelten.

Von Uexküll was aware that Umwelten are changing over time, in the long run of history. 'The Umwelten were certainly less complicated at the outset of the world drama than later', he acknowledges (von Uexküll 1982, 69-70), commenting that each new Umwelt represented 'an advance', and emphasizing that 'Meaning ruled them all. Meaning tied changing organs to a changing medium.' While Umwelt theory is most often applied in studies of momentary action and perception, von Uexküll conceptualized and theorized about what we could call different *Umwelt temporalities*, ranging from moments, to the duration of a succinct action, to action patterns over

time, life stages, a lifetime, and time perspectives spanning over several generations. The latter perspective overlaps with evolutionary time.

Due to his expressed opposition to some of Darwin's ideas about evolution, von Uexküll is sometimes regarded as being in opposition to the idea of evolution as such, but this is not the case (Kull 2004). What von Uexküll dismissed, was first of all the idea that evolution is blind, mechanistic or determined by the physical environment alone (see Brentari 2015, 129-132). In his own perspective, physiological, ethological and ecological developments over time must be seen as interlinked, and evolution therefore involves changes in meaningful relations between organisms that have the appearance of being 'planned' or, as one might just as well say, logical or functional. From the perspective of von Uexküll's "subjective biology", all such changes must make sense from the perspective of the organism itself.

Different scientific fields are concerned with studies of the past. In the human realm, a distinction can be drawn between *history*, which typically studies history considered as the time period when humans have used written language, and *archaeology*, whose time perspective is longer and based on recovery and analysis of material culture. In this context, any time-period predating written languages is referred to as pre-history. This stresses how central textual analysis and language is to history as a field of study. In biology, *paleontology* is devoted to the study of past life via fossil remains, whereas the more specialized branch *paleobiology* is concerned with the biology of fossil organisms. Moreover, *evolutionary theory* has a natural historical orientation, and the same can to some extent be said about *geology*, in so far as it involves *Earth history* after the advent of life. The study of past Umwelten is relevant for all these various fields.

Both due to his application of philosophical ideas in the development of his theoretical biology, and the inspiration philosophers have found in von Uexküll's work over the last century, there is a clear affinity between Uexküll's Umwelt theory and philosophy (Buchanan 2008, Michelini and Köchy (eds.) 2020). In our time, biosemioticians and zoosemioticians are at the forefront of advancing Umwelt theory, thus showing the relevance of semiotics for philosophy. Tønnessen et al. (2018) make clear that Umwelt theory demonstrate that there are phenomena beyond human experience, and that Umwelt theory is therefore highly relevant for phenomenology, which should be reconceptualized so as to be able to account for animal experience and phenomena as well.

As Kalevi Kull expresses in his article with the telling title "Zoosemiotics is the study of animal forms of knowing" (2014, 47), semiotics in general can be conceived of as 'approaches to the study of various forms of knowing [...] considering that knowing is possible only due to semiosis' (i.e., sign exchange), and 'Zoosemiotics is focused on the animal type of knowing'. A first observation to be made drawing on these statements is that semiotic studies

are relevant for epistemology, a second is that zoosemiotics can work as an auxiliary science in philosophical studies related to the nature of animal minds and lifeworlds. Given the intimate connections between knowing, learning and acting (see Kull 2014) that become visible in Umwelt theory, we can further state that zoosemiotics can help improve our understanding not only of what animals know, but also of how animals come to be, and why animals behave as they do. Contemporary developments of Umwelt theory with a philosophical inclination arguably have the potential of contributing to what Thom van Dooren (2017, 60) calls “field philosophy”, understood ‘as an effort to interrogate the structures of meaning, valuing, and knowing that shape our worlds – often in unacknowledged but profoundly consequential ways’, partaking in the larger endeavor of “Multispecies Studies”.

With regard to our understanding of time, Riin Magnus (2011a, 139; emphasis added) notes that von Uexküll’s limited influence on the philosophies about time of philosophers of his time can likely be explained by ‘the small attention paid by him to time perceptions *in man*, the philosophical object par excellence’. Both Heidegger and later Maurice Merleau-Ponty discussed von Uexküll’s Umwelt notion (Heidegger 1995, Merleau-Ponty 2003), but in their main works, they both had an exclusive focus on ‘*human* cognition and consciousness of time’ (Magnus 2011a, 139; emphasis added).

This is made particularly clear in Heidegger’s work. As van Dooren narrates (2014, 279), with reference to Buchanan (2008), according to Martin Heidegger, ‘the animal cannot ‘die’ in a proper sense, no matter how true it is that their lives come to an end just as our human lives do, since ‘for Heidegger humans are unique in our relationship with that ending, in our ability to be consciously oriented towards our deaths, in his terms, to ‘die’ ([Heidegger] 1996).’ Along with other ideas about what animals lack compared to humans, including Heidegger’s assertion, in his discussion of von Uexküll’s Umwelt notion, that animals have Umwelten but are “poor in world” (Heidegger 1995), this builds a picture ‘of humans as thoroughly and essentially different to the rest of the animal kingdom’ (van Dooren 2014, 279).

A central premise for the whole Umwelt theory is that it is applicable to both humans and animals. From von Uexküll’s side, however, Umwelt theory is underdeveloped in its capacity to be applied in the human realm (see Magnus and Kull 2012, 653) – which might not be much of a surprise, since he was after all a biologist, not a social scientist or humanities scholar. This calls for further development of his theory, aiming to make it more applicable in studies of human Umwelten. Given the ecological crisis of our time, which is caused by humans, and affects most living creatures, the study of human Umwelten is not a narrow field or special interest, but broadly relevant, as it involves theoretical and empirical studies that are urgently needed to understand the past and future development of human ecology with all its ecological ramifications.

Umwelt theory can arguably contribute to conservation biology. As van Dyck (2012, 144) suggests, ‘the Umwelt-concept [...] needs to be integrated in the way we think about habitat and habitat selection’, as this ‘may offer new opportunities for conservation and may help avoid failures with habitat restoration.’ Applying Umwelt theory in conservation biology implies ‘that we should be more sensitive to the environmental “carriers of significance” that differ among species and individuals’ (2012, 146), and acknowledge that humans ‘are interfering [...] with the use of environmental cues by wild organisms to a much larger extent than is often realized’ (2012, 145).

One reason why we should study *past* Umwelten, as well as the Umwelten of current fauna, is that due to extinction risks and ongoing marginalization of wildlife in many parts of the world, several currently extant species may soon be *past* species either globally or locally.¹ Another reason is that studies of past Umwelten can in some cases facilitate rewilding schemes or other conservation schemes today or in the near future by solidifying our understanding of what it takes for a species to be viable. An Umwelt perspective can also be informative when considering the feasibility of recent proposals of “de-extinction”.

I will discuss the Umwelt theory’s relevance for conservation issues – specifically, the debate about “de-extinction” – as well as the Umwelt theory’s relevance for economics in general and ecological economics in particular, towards the end of this article. I will start out, however, by outlining the concept of Umwelt, presenting some basic assumptions for studies of past, current and future Umwelten, making some methodological considerations for the study of past Umwelten in particular, and presenting a few empirical assumptions that are informative with regard to the study of past Umwelten in different historical periods. The article as a whole is intended to serve as groundwork for the study of past Umwelten.

2. *The concept of the Umwelt*

As Kull (2009, 44) narrates, von Uexküll’s Umwelt notion was first used, along with his notion of ‘subjective biology’, in an article with the telling title “Die Umrisse einer kommenden Weltanschauung”, meaning the outline of a coming world view (von Uexküll 1907). Its subsequent development is visible in von Uexküll’s major works (1921, 1928, 2010 [1934/1940], see also Brentari 2015, Tønnesen et al. 2016). For sentient organisms, the Umwelt can be divided into a *Merkwelt* (perceptual world, related to sense organs) and a *Wirkwelt* (operational world, related to muscles and movements),

¹ As for the human Umwelt, a reason to study past Umwelten is that 93% of all human beings that have ever lived, lived in the past (Kaneda and Haub 2022).

which are connected by the nervous system. In some contexts, the Umwelt notion is also applied to simpler organisms.

Kull (2009, 43) stresses the modelling aspect of the Umwelt, with a description of an organism's Umwelt serving to demonstrate 'how the organism (via its *Innenwelt*) maps the world, and what, for that organism, the meanings of the objects are within it' (see von Uexküll 1921). The Umwelt concept is thereby a fundamental term in ethology, the study of animal behaviour – although, as Allen (2014, 137), notes, 'the concept of Umwelt has played more of a heuristic role than a well-defined theoretical role' in ethology to date. Given that von Uexküll underlined the importance of understanding and describing 'the multispecies community of organisms on the basis of *relations* between Umwelten of different species of organisms' (Kull 2009, 44; emphasis added), it is also a key term in ecology. Kull (2010) underlines the importance of semiotic relations and complexes of different kinds, with Umwelten being constituent parts of nature's relation-based complexity.

Relations between organisms endowed with an Umwelt can fruitfully be understood in light of the functionality of Umwelten, with the functional cycle (von Uexküll 1928) illustrating how perceptions and actions form a coherent whole, and how one organism's behaviour affects other organisms in a common ecology. The specificity of functional cycles is decisive both with regard to describing ecological relations, and with regard to describing the species-specific characteristics of each Umwelt. By organizing the most common functional cycles in the topical categories of medium, food, enemy, and sex, von Uexküll (1982, 33) provided a common scheme for animal lifeworlds, and simultaneously indicated major categories of ecological relations and functionality.

Magnus (2011b) stresses the emphasis von Uexküll placed on the temporal constitution and "time-plans" of living beings, which are important elements in the species-specific configurations of space and time as subjectively experienced that different Umwelten can be understood as involving (this is described in detail in von Uexküll 1928). As Magnus observes (2011b, 39), von Uexküll prioritized research on the perceptual time and developmental time of organisms over research on evolutionary time, and considered these two temporal perspectives as theoretical cornerstones for the subjective time of organisms. In short, these relate to the momentary experience of organisms (perceptual time), and the timing of their development in terms of different life stages (developmental time), respectively.

Facets of human Umwelten are explored by Magnus and Kull (2012) and Linask et al. (2015). As Magnus and Kull (2012, 653) note, while von Uexküll's own application of Umwelt theory to humans was fragmentary and not systematically developed, his 'writings on the umwelt concept have served as an impetus for later philosophers and representatives of other humanities to delve on the issue of its applicability to human beings.' In the

context of human culture, Magnus and Kull suggest that we could ‘say that culture is continuously created via human umwelt making’ (2012, 650). They also propose that culture could in an Uexküllian perspective be seen as ‘an extension of the same vital need to cope with the environment’ as we can observe in other organisms’ biological adaptations and specialization, but met by other means (2012, 658). Linask et al. (2015,192) argue that three stages of human ontogeny can be derived from von Uexküll’s work, namely a ‘pre-representational *Umwelt* stage of meaning factors’ during embryonic development, a ‘stage of *Umwelt* of meaning carriers or objects, which relate the subject to its environment’ (as the typical mature animal *Umwelt*), and ‘the stage of the observer with an *Umwelt* of neutral objects’. The latter of these correspond to the mature, self-reflective human *Umwelt* which encompasses a potentially scientific understanding of other *Umwelten*.

While free will has in philosophy traditionally been understood as a human prerogative, Brembs (2011) and Kull (2022) both argue for developing more comprehensive notions of freedom and free will with a more general application, and recognizing that decision-making is carried out by nonhuman organisms too. This aligns well with a modern conception of *Umwelten* and animals. Observing that free will is basically a biological trait that comes in degrees, Brembs argues that traditional, now dubious metaphysical accounts of free will should be replaced by a scientific account applied to all sentient animals. He rejects determinism, arguing that sentient animals are capable of behaving variably by making choices and acting spontaneously, even when facing identical circumstances. In a somewhat similar manner, Kull (2022), lamenting that ‘free will is seldom seen as a biological problem to be studied and solved by biologists’ (2022, 3), calls for development of a ‘non-anthropomorphic understanding of free choice’, and argues that ‘freedom is an attribute of life’ (2022, 1). In Kull’s view (2022, 7), ‘the *momentary umwelt* as defined by Uexküll’s is suitable for describing the different options animals typically face simultaneously – which is the starting point for making choices. According to Kull, ‘the conditions for free choice emerge together with *umwelt*’ (2022, 1) – and on this basis, we can assume ‘that the existence of choice is coextensive with subjective time and space – i.e. *umwelt*’ – in other words, ‘all organisms who can make a choice have an *umwelt*’, and ‘precisely those who have *umwelt* can choose’ (2022, 5).

3. Basic assumptions in studies of past, current and future *Umwelten*

Some basic assumptions can be made regardless of whether we study past, current or future *Umwelten*. For instance, the idea of a “minimal *Umwelt*” (depicted in Figure 1) is telling of the fundamental features of most if not all *Umwelten*. The minimal *Umwelt* can be regarded as a sort of blueprint or

template for Umwelten, and will tentatively apply to any historical period. Being based on what are the most common functional cycles according to Jakob von Uexküll (1982, 33), the minimal Umwelt incorporates the relational aspects of Umwelten and their significance for ecological roles and functions. Given the relational, ecological orientation of any Umwelt, this implies that any specific past Umwelt should be studied in context with other, related Umwelten. On a similar note, Maran and Kull (2014, 44) observe that ‘Changing signs can change the existing order of things. Living organisms change their environment on the basis of their own images of that environment’, demonstrating that ‘semiosis itself is a major source of environmental change’ (2014, 44).

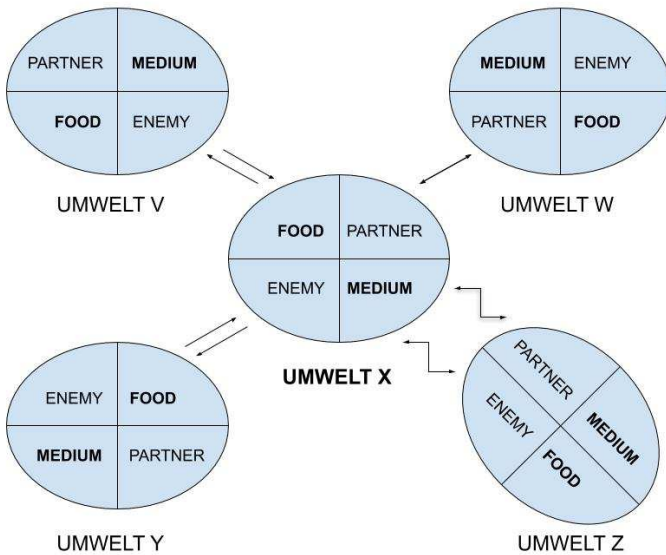


Figure 1. The minimal Umwelt.² Bold font indicates universal functions in Umwelten, with their related perceptions and actions. Parallel straight arrows pointing in opposite directions indicate a contrapuntal relation (food-enemy relation, typically a predator-prey relation). Straight arrows pointing in opposite directions indicate a mutual relation (partner-partner relation, typically a sexual relation). Elbow connectors indicate possible relations between Umwelt creature X and Umwelt creature Z where Umwelt creature Z is the medium of Umwelt creature X and Umwelt creature X might (in a wide, functional sense) be an enemy or a partner to Umwelt creature Z.

²From Tønnessen 2019, 415 (Figure 2).

Further insights can be gained by outlining how changes in the *Innenwelt* (in which the organism relates to itself) are correlated with changes in the *Umwelt* (in which the organism relates to its exterior) and the *Umgebung* (the physical environment) – see the three-dimensional interactive semiotic model of environmental change presented in Tønnessen (2019) and further developed in Tønnessen (2021). Such correlated changes in inner experience, experience of the exterior, and changes in the physical environment, can be mapped onto past, current and future time scales, and is applicable both to human and animal lifeworlds.

One of the *Umwelt* temporalities von Uexküll introduced himself is the *Umwelt-tunnel* in which an organism spends its lifetime, and which encapsulates all its experience and actions (von Uexküll 1928). As Magnus (2011b, 49) remarks, the subjective time of any organism endowed with an *Umwelt* is organized in line with ‘its perceptual properties and abilities as well as species-specific developmental constraints and possibilities’. This implies that each species ‘possesses a specific timing for different life activities as well as for the length of life itself’ (2011b, 50). In extension of this notion, we can envisage a series of *Umwelt* tunnels in evolutionary time, together making up *Umwelt trajectories* (Tønnessen 2014), or paths in time taken by the *Umwelt* of e.g. a species as they continue to develop. On different time scales, organisms endowed with an *Umwelt* further go through various *Umwelt transitions* (Tønnessen 2009), which can be regular (e.g. occurring in the development of any organism as it grows and matures) or irregular (e.g. historical events in personal, cultural or ecological history).

4. Methodological considerations for the study of past *Umwelten* in particular

A key limitation of any study of past *Umwelten* is the lack, in the data for the study, of present organisms available for real-time observations and whole-body physiological studies, which was the methodological starting point for von Uexküll’s *Umwelt* research. This limitation can be partly overcome by making qualified assumptions drawn from relevant knowledge and by reconstructing likely *Umwelt* relations. Studies of past *umwelten* can draw on general *Umwelt* theory as outlined in the introduction of this article as well as in the section ‘The concept of the *Umwelt*’, and on the observations made and concepts presented in the section ‘Basic assumptions in studies of past, current and future *Umwelten*’. As an example, the notions of the minimal *Umwelt* and *Umwelt* transitions can, in combination, serve to guide reconstructions of past *Umwelten* and how they might have developed over time, given our current knowledge and the ways we can tentatively “fill in the blanks” by making qualified assumptions. In this manner, we can attempt to reconstruct past *Umwelten* whether the knowledge we do

have to build on concerns indications of physiological features, ethology or ecology, or related animals and similar cultures.

Both in the case of studies of past Umwelten, and in studies of future Umwelten, the lack of living bodies available for scientific real-time observations or whole-body physiological studies entails that there must always be elements of reconstruction and qualified assumptions in the studies of such Umwelten. Strictly speaking, any model of reality – such as the Umwelt, as a scientific model of an organism's subjective world – is a simplification. The difference between the reliability of a scientifically reconstructed model of a *past* lifeworld, and the reliability of a scientifically reconstructed model of a *present* lifeworld, is arguably a difference of degrees rather than a difference between kinds, at least if the data used for reconstructing the past lifeworld is plentiful enough (and to some extent the same holds true for future lifeworlds). On the other hand, the reliability of a model of a past lifeworld will admittedly be lower the scantier the data used to reconstruct it is.

For various reasons, classical Umwelt theory has some limitations. As Brentari (2015, 132) notes, Uexküll did 'not have the theoretical tools available to deal with those themes which are closely related to the idea of the contingency of evolution – such as the problem of the extinction of species, which is in his works never dealt with in a systematic manner'. Generally, we can state that von Uexküll's classical version of the Umwelt theory neglected themes of historical environmental change and overemphasized stability in nature (Tønnesen 2009). This points to a need for updating and further developing Umwelt theory, to make it applicable in our own time. Relatedly, there is also a need for theory and methodology development in several adjacent fields of study.

Despite the fact that human-environment relations in the deep past 'are, in the absence of written records, only accessible archeologically', there has been little theoretical or methodological integration between the environmental humanities as it has developed over the last couple of decades, and archaeology (Hussain and Riede 2020, 1). The cultural taxonomies of the Paleolithic, or the Old Stone Age, are said to be 'in crisis' (Riede et al. 2020, 49), and in need of updating.

In an article about the work of Estonian geologist Ivar Puura (1961-2012), Maran (2013) mentions the field of *paleosemiotics* which Puura envisioned (2013, 146). This would include, as a central notion, "semicide", understood as 'a situation in which signs and stories that are significant for someone are destroyed because of someone else's malevolence or carelessness, thereby stealing a part of the former's identity' (Puura 2013, 152). As Maran remarks (2013, 147-148) distinguishing between intentional and unintentional semicide is called for in studies of historical cases of semicide, which may concern cultural as well as natural diversity.

Much needed theory and methodology development could in some cases take place by connecting other fields of study with Umwelt theory and methodology. As Tønnessen et al. (2016, 146) remark, ‘each scientific field that has incorporated’ the Umwelt notion ‘to its conceptual toolbox has stressed some (discipline-specific) novel aspects of the term while connecting it with the existing terminological corpus of the discipline.’ Tønnessen et al. further note that it is ‘conceivable that discipline-specific Umwelt models may be developed in specialized fields such as conservation biology and human ecology, and in general disciplines devoted to studying human behavior such as sociology, history, and psychology.’

In astrobiology, the prospective study of extraterrestrial life, a “biosignature” is a term signifying a sign of life, or evidence of life, of extraterrestrial origin. Since all solid current knowledge about life is based on studies of life on Earth, astrobiology has to rely on what we know about life on Earth, including in the distant past. In the words of Grenfell (2017, 1), due to ‘the paucity of data in Earth-like planetary atmospheres a common approach is to extrapolate knowledge from the Solar System and Early Earth to Earth-like exoplanets.’ In effect, this implies that the study of *spatially distant* life overlaps methodologically with the study of *temporally distant* life. In extension of this fact, we may see the approaches of astrobiology in its search for life beyond Earth as relevant also in the context of our ongoing search for signs of life on Earth in the past. A challenge in the terrestrial context as well as in the extraterrestrial context is to distinguish proper biosignatures – that is, biosignatures of a biological origin – from substances or phenomena that have an abiotic origin.

David Dunér (2018) provides a semiotic framework for the study of biosignatures, dividing them into three categories, namely bioicons, bioindices, and biosymbols, and noting that they each come with their own epistemological challenges. Body fossils, ‘the imprints of the hard parts of animals and plants’, are examples of bioicons, which imply similarity between signifier (the substance or phenomenon that is interpreted as a sign) and signified (the object it is a sign of – in this context, a biological process or activity) (2018, 52). For bioindices, which imply connection by contiguity, ‘atmospheric, chemical biosignatures that refer to biological processes, such as the metabolism of living organisms’ constitute examples (2018, 54). Lastly, biosymbols imply an arbitrary relation between the signifier and the signified. As Dunér points out, symbols are ‘detached representations and, as such, dependent on cultural and social interactions’ (2018, 58), and ‘most attempts at interstellar message constructions’ to date ‘violate this basic semiotic understanding of signs that distinguishes between expression and content’. In the same way as ‘a potential information transfer containing a symbolic message from an alien civilization would be constrained by’ any ‘bio-cultural coevolution’ we may have gone through with ‘the extraterrestrial intelligence that coded

it' (2018, 58), our possibilities for understanding biosymbols originating from past Earth history are contingent on our bio-cultural coevolution, if any, with the creatures that made them.

5. *Empirical assumptions in the study of past Umwelten*

Throughout the history of life on Earth, biodiversity including species diversity has tended to increase over time. Many of the major phyla that make up most of today's diversity in animal lifeforms have their origin in the Cambrian explosion some 540 million years ago (Leakey and Lewin 1996). In the context of this article, 'the Cambrian explosion represents a unique historical event which involved a vast expansion of complexity and variation in Umwelten', with its 'rapid evolution of senses, and thus sense-saturated Umwelten', although 'the Umwelt as such, in simpler forms, emerged much earlier' (Tønnessen 2022, 453). Since the Cambrian explosion – if not even before – the overall trend towards growing diversity has several times been interrupted by episodes of mass extinction (Leakey and Lewin 1996).

According to demographers, the about 8 billion human beings who live today make out about 7% of the around 117 billion human beings that have ever lived (Kaneda and Haub 2022). These estimates imply that there were about 2.5 million people on Earth in the Upper Paleolithic (ca. 50,000 B.C.E. to 8000 B.C.E.). By the time the agricultural revolution started, about 9 billion people had lived, as hunter-gatherers. 8,000 years later, at 1 C.E., the world population had reached about 300 million people, and about 55 billion people had lived, with the majority having lived while agriculture provided sustenance. Around the start of the industrial revolution, the population of humans had reached about 795 million, and about 98 billion people had lived. By 1950, world population had increased 3-fold in only 200 years, with about 2.5 billion people living and 108 billion having lived. Since then, world population has increased more than 3-fold yet again, in only around 70 years, representing the fastest population growth in human history. Of the 117 billion human beings that have ever lived, around 8% have lived as hunter-gatherers, while around 16% (about 19 billion people) have lived after the industrial revolution. The vast majority, around 76% (about 89 billion people), have lived in agricultural societies before the industrial revolution.

The term "human being" is somewhat ambiguous in evolutionary terms. The biological name for our own kind is *Homo sapiens sapiens*, which can be regarded as the only extant (i.e., surviving) subspecies of the species *Homo sapiens*, which in turn stands for 'modern humans'. In a slightly wider sense, the genus *homo* encompasses various human species, of which *Homo sapiens* is the only surviving species. These evolutionary facts imply that there have,

in the past, been several human *Umwelten* beyond that of our own kind. In the early history of the human genus – characterized by being ‘large-brained, stone tool-making, meat-eaters that traveled far and wide’ – there were three known human species, namely *Homo habilis*, *Homo rudolfensis*, and *Homo erectus* (Dunsworth 2010, 363). Of these, *Homo habilis* appears to have evolved first, and to be the ‘first stone tool makers’, while *Homo erectus* was the first human species to disperse beyond Africa (2010, 363).

There is no consensus on the exact number of human species that have existed. Modern humans (*Homo sapiens*) emerged some 200,000 years ago. This new human species ‘had skeletons very similar to those of present-day people’, and over time acquired behaviors that in many ways resemble those of present-day humans (Pääbo 2014, 216). Apparently, these novel behaviors ‘were never acquired, even over hundreds of thousands of years, by the other, so-called archaic humans who were eventually replaced by the modern humans’ (2014, 216).

As for co-existence, according to Dunsworth (2010, 361) there are at least two confirmed instances where two or more human species have ‘overlapped in space and time’ – namely, the co-existence of Neanderthals (*Homo neanderthalensis* or *Homo sapiens neanderthalensis*) and *Homo sapiens* in Europe, and the co-existence of *Homo floresiensis* and *Homo sapiens* in Indonesia (cf. also Hussain and Riede 2020, 8).

After the advent of modern humans, several animals and other lifeforms have declined as measured by biomass (reflecting population decline, but not necessarily species loss). This must be seen in context with our species’ higher kill rates than comparable species (Darimont et al. 2015). Bar-On et al. (2018) estimate that there were 6 times as many wild mammals 100,000 BP as there are today.³ While wild terrestrial mammals are marginalized in modern and contemporary times, humans and livestock have grown significantly in numbers and now dominate mammalian biomass – and domesticated poultry outnumber wild birds by a factor of 3 to 1 (by biomass). Wild fish stocks, too, have seen some decline, albeit more modestly compared to pre-human levels.

As for animals overall, it is noteworthy that there are – and have been – more animals in the oceans than on land, given the predominance of marine arthropods and fish in the animal realm (2018, 6507). In terms of species diversity, insects (the largest group of terrestrial arthropods) are the most abundant animal lifeform, but in terms of individual organisms, arthropods are narrowly outnumbered by nematodes, i.e., roundworms, which is the most abundant animal lifeform by this measure (2018).⁴

As Fricke et al. (2022a) discuss, the extinction of megafauna after the emergence of the human species has had a significant impact on wild seed dispersal,

³ Supplementary Information Appendix, p. 88 (Fig. S5).

⁴ Supplementary Information Appendix, p. 85 (Fig. S2).

given that about half of all plant species rely on seed dispersal by animals, and that large-bodied animals play an important role in this context. Fricke et al. (2022b) investigated terrestrial mammal food webs over the past ~130,000 years and found that these typically ‘underwent steep regional declines in complexity through loss of food web links after the arrival and expansion of human populations’ (2022b, 1008). The decline in complexity is lowest in Africa and Eurasia, where hominins and other mammals have a longer history of co-evolution. Fricke et al. observe that human-induced extinction of species ‘has contributed to mammal food web collapse’ (2022b, 1009), even though ‘only ~6% of terrestrial mammal species have gone extinct since the Late Pleistocene’ (2022b, 1010). Their analysis shows that species extinction ‘that occurred centuries to millennia ago’ and ‘range contractions in surviving species’ have contributed in equal measure to the disappearance of ‘more than half of mammal food web links’ compared to pre-human levels (2022b, 1010).

Human history and interaction with the environment can be seen in context with the globalization of the human species in different senses – in terms of our expanding geographical range historically, in terms of the expanding range of our affiliated species as well as parasites and “blind passengers”, and in terms of the expanding range of our administrative and economic capabilities as a species (Tønnessen 2010a). Relatedly, “the Anthropocene” denotes the historical epoch in which human beings collectively have acted as a decisive or dominant geological force (Steffen et al. 2011). There is currently considerable disagreement on about when the Anthropocene started, with many favoring a time perspective covering the time since the industrial revolution, and some arguing for a shorter – or much longer – time perspective.

Drawing on studies in archaeology, comparative psychology, evolutionary theory and cognitive science, Mendoza-Collazos et al. (2022) suggest a stage-based model for the evolution of design capabilities in humans and some animals which is informative with regard to the development of complex cognition over time. They apply a framework in cognitive semiotics that overlaps with that of biosemiotics and incorporates the Umwelt notion (2022, 163). According to Mendoza-Collazos et al., nonhuman apes first developed capabilities for proto-design, involving tool-making based on e.g. bending, shaping and combining materials, around 20 million years ago. About 3 million years ago, hominins acquired simple design capabilities, which were further developed in species of humans (*Homo*), which made use of mimesis in design processes. Starting some 200.000 years ago, *Homo sapiens*’ use of speech made planned conception of tools, such as hand axes, possible. Around 10.000 years ago, drawing appeared as a significant semiotic resource, making early craftsmen capable of designing tools with decoration and indications of identity – a first instance of complex design. Craft guilds then developed, making use of polysemiotic resources (integrated communicative

systems with several semiotic resources combined), and further refining styles and introducing brand identity. Over the last 300 years or so, starting with the first industrial revolution in the 18th century, polysemiotic resources have become more and more complex, enabling designers to develop advanced design characterized by branding and product identity.

Mendoza-Collazos et al.'s (2022) portrayal of the evolution of design is instructive in terms of understanding what kinds of tools, artefacts and products have appeared as Umwelt objects at different historical stages, and how these have affected cultural development and social relations.

6. Relevance for current conservation work

“De-extinction” denotes the idea that extinct species may soon be resurrected – brought back to life. In a review of the three currently considered main pathways to de-extinction, back-breeding, cloning and genetic engineering, Beth Shapiro (2017, 1000) concludes that none of these approaches ‘will culminate in the birth of an organism that is an identical copy to one that is extinct.’ She argues that de-extinction should be considered ‘as a means to create ecological proxies for extinct species’ (2017, 996), and could ‘benefit ecosystems, for example by restoring critical interactions among species’ (2017, 997). In Shapiro’s judgment, genetic engineering is particularly promising in light of recent technological advances, and can in the case of mammals be combined with cloning via somatic cell nuclear transfer, assuming that an appropriate surrogate maternal host from a sufficiently similar species is available. However, Shapiro cautions that ‘gene–environment interactions’ will ‘necessarily differ from those experienced by the extinct species’ (2017, 1000), that the animal ‘will be raised by a surrogate species, with different behaviours and social structures, which will affect its phenotype’ (2017, 1000-1001, see also Diehm 2015, 137), and that the animal ‘will live in an environment that is different from that which persisted in the past’, with a different diet, and consequently a different microbiome, etc. (2017, 1001). In short, even cloning will not result in an ‘identical copy’ of the extinct animal.

In light of von Uexküll’s Umwelt theory, Shapiro’s cautious remarks make good sense. The extinction of a population or a species must be understood in the context of its ecological relations. As Shapiro seems to be well aware of, when an animal goes extinct, this removes potentials for ecological interactions associated with that animal species. Reversely, we can only envision the re-appearance of an extinct species by envisioning a re-appearance of something resembling the ecology that persisted when that animal thrived. In Uexküllian terminology, any “de-extinction” of a species would presuppose a resurrection of all its significant, species-defining functional cycles, and this would have to include the resurrection of all species-specific perceptions and

behaviors of this animal. In effect, this would require resurrection not only of the extinct animal itself, but also of the relational environment that sustained it. This makes any talk of actually resurrecting – bringing back – extinct species a tall order. If de-extinction is indeed technically feasible, the Umwelten of the animals resulting from conservation efforts would likely be somewhat different from the Umwelten of the extinct animals. This raises some additional questions: Can the Umwelt of an ecological proxy for an extinct species ever be similar enough to the Umwelt of the extinct species to warrant calling it *the same Umwelt*? In other words, can the Umwelt of an extinct species be resurrected? If mammoths were “resurrected” by cloning, using elephants as surrogate maternal hosts, would their Umwelten be the mammoth Umwelt resurrected, or rather a modified version of the elephant Umwelt?

Dolly Jørgensen (2013, 720) has proposed that de-extinction should be seen as ‘a new kind of reintroduction project, rather than as something entirely novel’, thereby allowing for taking advantage of ‘a wealth of prior experiences and established guidelines’ applying to reintroduction schemes. This would imply classifying “resurrected” animals along with other animals that are “extinct in the wild” and currently held in captive breeding, e.g. in zoos. Jørgensen envisages that reintroduction schemes for resurrected species will likely be more contested the longer the animal species has been absent. In support of this, it could be claimed that a factor in considering reintroducing an extinct species should be the joint Umwelt history (human–animal Umwelt relation) shared by humans and a candidate species. In some cases, reintroduction would align with the conservation or recovery of cultural heritage, in others, reintroduction would likely endanger cultural practices and diversity. This underlines that in the context of conservation biology, ecological interactions should be interpreted as including cultural interactions that involve human–animal relations. On the other hand, human interests should not be taken to be of overriding importance compared to the ecocentric values promoted by conservation biology.

Noting that the de-extinction debate should be informed by current experience with reintroduction schemes as well as experience with invasive species, Robert et al. (2017) particularly emphasize the relevance of conservation genetics and evolutionary conservation biology. They note (2017, 1021) that ‘the most important constraints to the short-term viability of any resurrected population are (i) their intrinsically low evolutionary resilience and (ii) their poor eco-evolutionary experience, in relation to the absence of (co)adaption to biotic and abiotic changes in the recipient environment.’ In their view, the chance of success is ‘critically related to the time elapsed between the extinction of the target species and its resurrection’ (2017, 1022). They assert that ‘it is questionable whether de-extinction has the potential to restore the evolutionary values of lost biodiversity’, and only see de-extinction as potentially viable ‘if it constitutes

responses to short-term (at the evolutionary scale) human influence: a few tens or hundreds of generations since the extinction of the target species' (2017, 1028). This could make de-extinction possible e.g. for the passenger pigeon (*Ectopistes migratorius* – extinct for about 15 generations), but be in doubt for the woolly mammoth (*Mammuthus primigenius* – extinct for about 500 generations), and out of reach for the saber-toothed cat (*Smilodon*) (2017, 1024).

Commenting on 'the de-extinction program proposed by Beth Shapiro', philosopher of science Vinciane Despret (2020, 188) observes that although de-extinction cannot bring back species identical with those that went extinct, de-extinction could potentially bring back some of the *traits* of extinct animals which enable certain ecological interactions. While she expresses that she has 'very serious reservations about this type of program', Despret thinks it is interesting to conceive of 'traits as endowing those who carry them with creative powers, and of reading creation as immanent and continuous, where certain traits create the possibility for other beings to come into existence'. She goes on to write (2020, 188):

Jakob von Uexküll's idea that the animal is the creator of worlds then takes on a whole new meaning: traits, as creators of existence, shift the problem of a relationship guided only by perceptions and meanings – each of the worlds of the *Umwelt* ultimately exists only subjectively – to situate this relationship within the ontological and aesthetic regime of the creative powers.

This is a reasonable observation, in that it is compatible with a fair interpretation of von Uexküll's *Umwelt* theory, and with von Uexküll's own views on the dynamics of evolution and the emergence of new *Umwelten*. *Umwelten* should in no way be seen as isolated entities, but as fundamentally relational entities, as seen both from an ecological, and an evolutionary perspective. In terms of temporality, *Umwelten* change *systematically* in a developmental context over the lifetime of an animal, and they always change *dynamically* in response to environmental circumstances. In an evolutionary perspective, *Umwelten* can be said to change *creatively* to the extent that they change over evolutionary time (i.e., several generations) as a result of spontaneous (improvised, explorative) actions in community with other organisms.

Despret's (2020, 188) preference for 'reading creation as immanent and continuous, where certain traits create the possibility for other beings to come into existence' should also serve as a reminder of the moral issue of in how far we human beings should allow ourselves to be the judges of what ought to live, and what ought to die – which is perhaps the most compelling and decisive ethical question facing conservation biology.

In an assessment of the moral arguments for de-extinction, which are mostly focused on restitution, Diehm (2015) concludes that 'the moral ground that de-extinction advocates have tried to claim is less solid than it might first

appear' (2015, 141). He observes that 'the idea of reviving species fits into a contemporary narrative in which getting things straight with other forms of life is not a matter of decreasing human excesses, but of artificially enhancing nature's ability to withstand them' (2015, 142). Technological optimism may lead some to believe 'that we need not a less intrusive manner of engaging with the natural world, but more effective methods of mastering it' (2015, 142). As Diehm remarks, this resonates with a central line of conflict in the Anthropocene discourse. While de-extinction proposals purport to be advocated 'for nature's sake', they in effect 'reflect the same sort of instrumentalizing rationality that fuels so many environmental wrongs in the first place' (2015, 143).

7. Relevance for economics as a branch of ecology

Herman Daly (1968), a pioneer in ecological economics, portrayed the economy as a subsystem of ecology, and indicated that economics could be conceived of as a branch of ecology. Claiming that 'the ultimate subject matter of biology and economics is *one, viz., the life process*', he asserted that economics can be conceived of as 'the part of ecology which studies the outside-skin life process insofar as it is dominated by commodities and their interrelations' (1968, 392). In his view, 'in a very real sense the entire physical environment is capital, since it is only through the agency of air, soil, and water that plant life is able to capture the solar energy upon which the whole hierarchy of life (and value) depends' (1968, 397). Daly thought it was a shame that economics and ecology have become disjointed fields, so that 'ecologists abstract from the human economy and study only natural interdependences, while economists abstract from nature and consider only interdependences among commodities and man' (1968, 398-399). He quotes the biologist Marston Bates (1960, 247), who lamented 'the game of the economists, "let's pretend that nature doesn't exist"', and pointedly stated: 'The economy of nature and ecology of man are inseparable and attempts to separate them are more than misleading, they are dangerous' (quoted in Daly 1968, 399). In reality, as Daly observed (1968, 400), our 'economic cosmos is not one of uniform circular motion of commodities among men but one of elliptical orbits through interdependent ecological sectors.'

In Tønnessen (2010b), I called for the establishment of "semiotic economy", 'a field which task it is to map the human ontological niche insofar as its semiotic relations are of an economic nature' (2010b, 376), elaborating that this incipient field 'studies the semiotics (aka phenomenology) of economic relations' (2010b, 383). This endeavor was presented as the tenth and final step towards developing a "semiotics of being", with an outlook involving human and nonhuman Umwelten and acknowledging the ecological crisis' nature of being an

ontological crisis (2020b, 375). In this perspective, “Umwelt mapping” is a crucial task not only in the realm of biology, but likewise in the realm of economics.

‘Until recently’, as Daly (1968, 399) remarked around the onset of the modern environmental movement, ‘the economy of man was “peanuts” in the total economy of nature’. The issue of humans’ part in the total economy of nature has become progressively more important over time. This calls for a depiction of the role of past Umwelten in economic history, and in the origin story of the Anthropocene, with an emphasis on how economic relations and practices have affected ecological relations and human and nonhuman lifeworlds.

Department of social studies
University of Stavanger

E-mail: _____

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