



# Vivoscapes: an Ecosemiotic Contribution to the Ecological Theory

Almo Farina<sup>1</sup>  · Philip James<sup>2</sup>

Received: 16 November 2020 / Accepted: 3 March 2021 / Published online: 15 March 2021  
© The Author(s) 2021

## Abstract

Vivoscope, from Latin ‘vivo’ (living) and the English ‘scape’ (shape and form of a place) is presented as a new ecosemiotic agency that integrates the interactions between biological and ecological components of a taxon with the environment. According to this model, the interactions between species and the environment are fused into a new functional unity driven by external and internal events (vivoevents). Sensorial and relational channels are used by a taxon to sense external energy gradients, matter, information and to return actions and proactions in an external operational environment. The eco-field model is suggested as the functional ecosemiotic mechanism associated with each vivoevent.

**Keywords** Ecosemiotics · Vivoscope · Vivoevent · Ecological species · Eco-field

## Introduction

The separation between the human and natural worlds has dominated debate in both academic and cultural domains for centuries, for example, the Greek idea of rationalism (Abram, 2012), Judaeo-Christian concepts which differentiate these domains (White, 1967) and the ongoing scientific and humanities debate (e.g., Jenkins, 2002). Yet this separation is not seen in the real world. All forms of life modify their environment (White, 1967), and the growing human intrusion into natural ecosystems (Pimm et al., 2014) is producing unprecedented world-wide modifications to the composition, structure and functioning of natural populations, communities and habitats and of communication mechanisms (Beniston & Stephenson, 2004; Haberl et al., 2007). Humans and the natural world are clearly linked and part of the same system. Cultural development

---

✉ Almo Farina  
almo.farina@uniurb.it

<sup>1</sup> Department of Pure and Applied Sciences, Urbino University, Urbino, Italy

<sup>2</sup> School of Science, Engineering and Environment, University of Salford, Salford, UK

associated with the human quality of life expectations has a growing impact on ecological paradigms that in turn influence human decisions (Fish et al., 2016). Changes in human lifestyle aggravate the environmental uncertainty experienced by individuals and species and are associated with an increased risk of local and global extinction (Maxwell et al., 2020).

Models that have been considered as pillars of ecological knowledge (e.g., metabolic theory, niche theory, ecological succession, food web, etc.) (Brown et al., 2004; Fretwell, 1987; Marquet et al., 2014; Scheiner & Willig, 2008) today seem inadequate to assure an appropriate level of knowledge applicable to address the increased complexity and difficulty in maintaining efficient complex relationships between human societies and natural environments. Such relationships are largely affected by technological energy-demanding advances and rarely regulated by ecological feedback systems. As a result, the scientific community has requested that an effort should be made to accumulate new knowledge to inform solutions addressing these challenges (Seymour, 2016; Smith & Varzi, 1999), especially in the energy-demanding human habitats such as metropolitan cities, suburbs and rural areas in dry or in cold climates (Milner-Gulland, 2012). This requires concepts to be revisited to ensure that they can be integrated in a way that allows the new environmental conditions to be navigated successfully.

Scholars such as Forman and Godron (1986); Naveh and Lieberman (1984); Wu (2017) recognized the role of spatial considerations in biological, ecological, socio-political, economic and cultural phenomena, disclosing new perspectives on the application of ecology to the design and management of land and territories. They also connected ecological processes to the spatial dimension and to consequential emergent properties (Tilman & Kareiva, 1997). These functional, spatial and temporal relationships can be conceptualized as pillars of eco-complexity observed inside coupled human-natural systems (Pickett et al., 2005) and defined by Michener et al. (2001) ‘as properties emerging from the interplay of behavioral, biological, chemical, physical, and social interactions that affect, sustain, or are modified by living organisms, including humans’. However, after decades of producing models, empirical evidence and applications, today this conceptualization requires some refreshment to maintain an alignment with the advances in many philosophical, environmental, ecosemiotics, cognitive and socio-economic disciplines (e.g., Maran, 2020; Maran & Kull, 2014; Smith & Varzi, 1999, 2002).

Although the systems approach in ecology has illuminated several previously hidden processes, contributing to a better understanding of the emergent properties of the environment (Dale, 1970; Evans, 2012; Grace, 2015), we believe that moving down the complexity scale will return further useful information to address the environmental challenges we currently face. In pursuance of this goal, we suggest exploring the ecological domain from an *individual-based perspective*. From such a perspective we can see that there is potentially perceptible sensory information distributed irregularly in the space around individuals and this forces every individual to scan around them within a four-dimensional space (including time as, for example scent marking leaves information about what has happened (another individual, say, of the same species or of a predator species has been in that place and, if the scent is still strong, may return to the potential detriment of the individual detecting the scent). This continuous scanning centred around an individual returns information that depends on the radius of

sensitivity of the sensors (ears, eyes, etc.) and on the medium in which the organism is embedded (air, soil or water). Where there are topographical or other obstructions, the scanned area will be less than where no such obstructions exist.

The individual-based model in ecology is an efficient approach to complete ecological theory (DeAngelis & Grimm, 2014), especially with regard to the spatial realm (Patten, 1978, 1982). Moreover, the ecosemiotic relationship between individual species and their environment represents a fundamental agency of species adaptation that has long been neglected and under-developed in ecological research and sometimes perceived as subordinate to other ecological approaches (Maran & Kull, 2014). To address this requires the development of new concepts, theories and models that illuminate the interdisciplinary frontier between the phenomenological dimensions in which species interact with their environment (Prosser et al., 2007; Scheiner & Willig, 2008).

Moving from speculation to the phenomenological real world, we can assign biological species the status of a component of a broader category, that is to say of an ‘ecological species’ (Andersson, 1990; Mayden, 1997). Van Valen (1976) defines any species using an ecological perspective as ‘a lineage (or a closely related set of lineages) which occupies an adaptive zone minimally different from that of any other lineage in its range and which evolves separately from all lineages outside its range’. The relationship with this operational environment is guided by genetically and culturally (*sensu lato*) transmitted mechanisms. We can assume that a portion of environmental functionality depends on the genome of the species; every taxon is responsible for and exerts influence on a portion of the environment, and this portion of the environment is associated with the two-way interaction between the environment and other individuals and species present. This creates a new holistic entity, the ecological species, which has a distinct and unitarian position in biological and ecological theories. These assumptions are concordant with Gause’s universally accepted principle of competitive exclusion (Gause et al., 1934) that states that every organism reduces competition with all other species living in the same region, differentiating the use of resources. On one hand, individuals try to reduce competition with other individuals and species, by resource repartition (MacArthur & Levins, 1967; Rosenzweig, 1981), however, inadvertently acquired information may offer some advantages when species intercept and decode the ‘sensoriality’ of other species living in the surroundings (Lewanzik et al., 2019).

Organisms produce environmental modifications – a phenomenon well formalized by the niche construction principle (Odling-Smee et al., 2013) – that may persist over time (ecological inheritance) (Odling-Smee & Laland, 2011) and that have consequences for a multitude of other species according to eco-evolutionary dynamics (Mullon & Lehmann, 2018). Each species is an agent (the engineer) of the environment, and genes control the quality of the ‘operational environment’, defined as a class of phenomena that has a strict relationship with species (Mason & Langenheim, 1957). When a biological species becomes locally or globally extinct, the ‘ecological species’ follows the same fate and environmental consequences follow (Janzen, 1974; Memmott et al., 2007). For this reason, preserving biological species implicitly means the portion of the environment (ecological interactions) associated with that species is maintained. If an individual species is eradicated, voluntarily or involuntarily, from an area, environmental interactions are suppressed, and the causalities (effects)

associated with that species are changed or absent. The fewer species present in an area, the fewer ecological interactions function, and those that do are less complex and differently driven. For instance, an agricultural field usually is sown with one variety of crop at a time and during the growing season the diversity of invertebrate fauna is lower than that encountered in natural grassland which is richer in grasses and forbs (Riggins et al., 2009). The suppression of a species, for example, a pollinator or flowering plant (e.g., Schiestl & Johnson, 2013; Willmer, 2011), is not simply a matter of the physical elimination of a genomic expression but the loss of species-specific relationships/links is transmitted, via a cascade reaction effect, to other environmental components (Lawton, 1997).

Often, the importance of a species is attributed based only on a cultural evaluation of associated symbolism (Schirpke et al., 2018) neglecting the effective role that a species has in the ecosystem. The term taxon is ordinarily used as a proxy for biological diversity without appreciating that the contribution made by a species to ecological complexity is the fundament guarantor of environmental resilience and that much of this resilience (Holling, 1973) is dependent on the efficient transmission of signals between individuals and the environment. That said, we aim to describe a new ecological model in which the interactions between biological and environmental components of an ecosystem become a tangible emergent property with several important implications for other ecological theories and properties of the ecological systems. To do this, we introduce the concept of ‘vivoscape’, from the Latin ‘vivo’, meaning living and the English ‘scape’, a suffix used to form nouns referring to the shape and form of a place. The concept of the scape is appropriate for the spatial competencies around an individual’s ‘function-circle’ (Von Uexküll, 1926).

## The Vivoscape as an Eco-Functioning Unit of Life

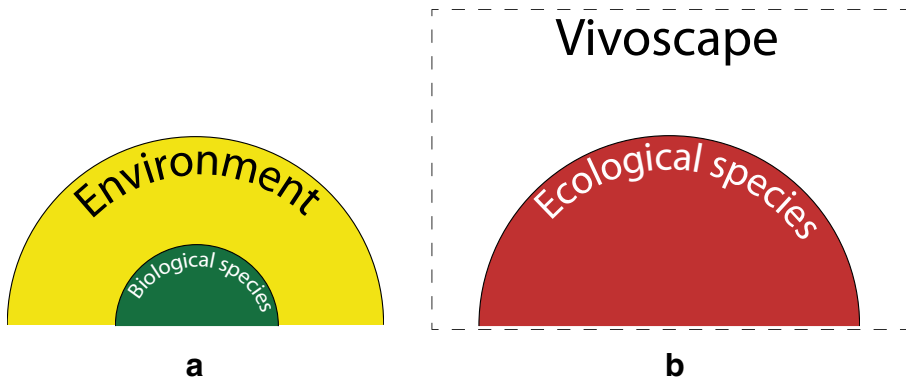
By adopting the term ‘vivo’, we intend the relationships between an agent (organism) and an environmental biotic or abiotic agency. The association of ‘vivo’ with ‘scape’ creates a composite word that means the environmental (spatial) dimension of relationships that is coincident with the ideas formulated by Smith and Varzi (2002). A vivoscape is, used in this way, an eco-taxonomic unit, in which biological and ecological information are actively exchanged with the environment through sensory and interpretive mechanisms. Defined in this way, a vivoscape describes the emergent organismic-oriented mechanism where the capacity of a living being to intercept signals from its surroundings is also strictly connected to the result of its internal elaboration. Vivoscape is, therefore, the ontological unit associated with the interaction between individual taxa and the elements, both biotic and abiotic of the environment with which they are in direct contact at any one time. Sensory channels are activated by receptors that are located in the external part of the animal body (eyes, ears, taste buds, skin and whisker tactile receptors, etc.) or internally (e.g., thirst, hunger, the drive to find a mate) that transmit to the central nervous system electrical signals that will be elaborated in specific areas of the “brain” according to the level of neural complexity of the taxon. The vivoscape represents a collection of different vivoevents related to distinct and discrete life functions: feeding, predator avoidance, finding a mate and so on. To be

successful an individual needs to be aware of both internal and external factors: hunger (internal) sensing a food source (external), being receptive to mating (internal) locating and finding a mate (external) and so on.

Vivoscape differs from other concepts such as the Umwelt – the surrounding as sensed and interpreted by individual species (Von Uexküll, 1982, 1992) –, ecoscape – the organizational shape or layout of an ecosystem (Backhaus & Muringi, 2006) and lifescape – the landscape and the people who live in it due to the inclusion of the internal environment of the individual and the individual's response (Gasteyer & Butler Flora, 2000, Convery et al., 2008). Consider the case of a common kingfisher (*Alcedo atthis*) which having caught a fish and returned to its perch drops the fish as it tries to manipulate it so that it can be swallowed. The common kingfisher is driven by hunger to seek to retrieve the fish but is aware of the danger posed by predators once it is on the ground. Internal and external sensory channels drive different behaviours. The bird may fly down momentarily to retrieve the fish. If it cannot be retrieved quickly will give up and return to catching a new fish, leaving the first fish to change the environmental clues by giving off odors that will attract other animals that will eat it. In a second example, it is emerging that the fear of humans has a great influence on the distribution and behaviour of large and medium predators at the landscape scale (Suraci et al., 2019). This process has been termed the “landscape of fear” (Gaynor et al., 2018) but it is evident that this is a case of a “fear event” that is a component of a vivoscape where the fear of humans as apex predators modifies the perception of the surroundings and several consequent actions (Gallagher et al., 2017; Laundré et al., 2014).

The entire vivoscape mechanism is driven by the primarily individual need to track the indispensable resources required to stay alive and to perpetuate life (Farina, 2012). In this definition, the concept can be adapted to every individual as the holistic semiotic agency that connects biological to ecological processes by specific events in an organism-environment functional-circle (Von Uexküll, 1926). To develop a vivoscape narrative, we pragmatically assume a conceptual model that considers life as the ensemble of physiological discrete events finalized to maintain a gradient between the internal parts of an organism and the external environment by input/output of resources (energy and matter) (Muller, 1966). We intend that the term vivoscape should embrace the entire set of processes that connect the inside world of an organism with the surrounding world, based on distinct sensorial process of species-specific sensory organs and the transfer of matter and energy from the external to the internal world of a taxon and vice versa. The vivoscape is the field of existence or domain of an ecological species representing the totality of biological, ecological and semiotical interactions between an organism and its operational environment (Fig. 1). These interactions are represented by cybernetic loops in which energy, matter, and information are exchanged between the external environment and the internal part of an organism (Korzeniewski, 2001). The vivoscape can also be considered the functional application of the ecological niche concept (Patten & Auble, 1981).

The sensorial capacity of an individual allows it to detect differences in some fundamental signals that are voluntarily or involuntary broadcast by the abiotic and biotic components of its vivoscape. The signals that a species can intercept from the surroundings have a common origin in the physical characters of matter (e.g., colour) and the perceived gradient of energy (e.g., sound, heat). Changes in the status of matter



**Fig. 1** In a traditional ecological perspective, biological species enter in relation/contact with a distinct/separate environment. According to the vivoscape model biological species and environment become a unique functional unit: the ecological species

are produced independently of the cognitive activity of organisms and represent an energy-gradient process. In summary, physical signals are the result of the amount of energy that impacts and flows across a biotic or abiotic entity and are sensed by organisms. For instance, visual signals are the result of the different reflection of the sunlight capacity of objects: the black colour is typical of materials that absorb all the spectral frequency of the light, in contrast to the white colour that is the result of the reflection of all the wavelengths. The different colours are the complementary results of substances that absorb a specific electromagnetic wavelength subtracting from the full spectrum of visible component of the light (which varies according to the taxon). At the same time, acoustic signals are the result of the vibration of a medium (e.g., air and water) (Shambaugh, 1930; Sturm et al., 2019), and olfactory signals are the interception of chemical molecules released by liquid, solid and gaseous substances (e.g., Page et al., 2011).

The combination of different perceptions allows many species to enter into better contact with the external elements of their vivoscape and in several cases by partitioning the environmental information and reducing predatory risk and interspecific competition for resources (Hebblewhite & Merrill, 2009), although the opposite is also possible. The interspecific convergence of some signals may have semiotic benefits, reducing the energy spent by individual species in scanning the environment searching for resources (Laiolo, 2012; Tobias & Seddon, 2009). Such cooperation can expose species to some unexpected competitive conditions. It is evident that every sensorial capacity describes a perceived feature of the organisms internal or external environment in a specific way and produces an appropriate reaction. Every organism interacts with the surroundings using a set of sensory organs that produce a perceptual world, or “creaon” (Patten, 1978; Von Uexküll, 1926). This creaon allows an individual organism to select the most suitable habitat in which to track the resources (material and/or immaterial) necessary to accomplish its physiological needs that in turn control every vital function of the organism (Farina, 2012). The ecosemiotic mechanisms utilized by organisms to intercept resources are described by Farina and Belgrano with the eco-field model (Farina, 2021b; Farina & Belgrano, 2004, 2006).

## The Structure of the Vivoscope

The vivoscope represents an individual, the portion of the environment (operational environment) and the interactions between these components. The vivoscope narrative sets an individual both at the centre and, at the same time, as part of the vivoscope. The reality is a more complex whereby different taxa are connected by relationships that can be trophic (transfer of material resources) or semiotic (transfer of information) at different levels of importance, and these processes lead, by extension, to the concept of a meta-vivoscope. Extending the concept from a single to an ensemble of interacting vivoscapes, it is reasonable to expect that the relationship between different vivoscapes may create emerging properties in a system. Like in every ecological web the vivoscapes are not isolated agencies but share some characters and functions with other surrounding vivoscapes. From this, the idea of a meta-vivoscope describes the relationships between different species either trophically (e.g., producers and primary consumers, or prey-predator), or semiotically (e.g., emitter and receiver during an “acoustic” semiosis) aspects that are well referenced in the ecological community and the ecological guilds models.

## The Physiology of the Vivoscope

There are at least two types of relationships (channels) between the internal world of a taxon and the external world: the first is represented by the inputs/outputs from the sensory organs, and the second by the elaboration of the information to track further information from the external world. We call these two channels sensorial and relational respectively, because these are the ways species take decisions to gain resources, that means in general to satisfy internal needs (Fig. 2). Every sensorial channel has access to the “world-as-sensed” (sensu Von Uexküll, 1926) and the relational channel to the ‘world-of-action’, (sensu Von Uexküll, 1926). The relational channels are the result of a process of sensorial elaboration that may involve many sensorial channels at the same time. A sensorial channel is activated before the relational channel, although a relational channel can be activated in turn by some sensorial channels to complete the environmental screening (Fig. 3).

Every sensory capacity is taxon-specific. For example, bats (Chiroptera) communicate and activate their bio-radars using ultrasound (>20 kHz), a frequency range that cannot be perceived by many other vertebrates, and inside this taxon exists a further partitioning of frequencies to reduce interspecific competition, such as in Rhinolophoid bats (Heller & Helversen, 1989). The extent of sensory capacity varies with each species and each individual; some individuals in a population have impaired or enhanced sensory perception in one or more of their senses. The link between sensorial channels and relational channels may be sense-specific, but in general relational channels receive input from different sensorial channels. The relation channels, in which information, meaning and semiosis circulate, are created by individual needs and assume the form of events (vivoevents) (Fig. 4). Living process can be simplified and approximated as a sequence of individual events that are guided by internal physiological needs, powered by autopoietic and teleonomic mechanisms (Maturana & Varela, 1991; Monod, 1974; Monod & Jacob, 1961) and achieved by the eco-field

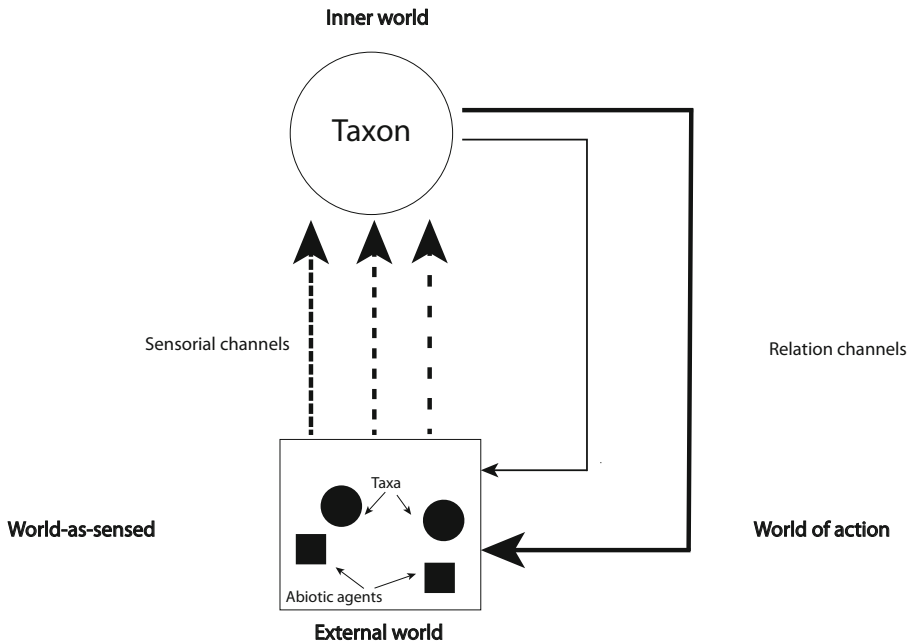


Fig. 2 Vivoscape model that operates between an inner world and an external world (world-as-sensed and world of action) through sensorial and relation channels

mechanisms (Farina & Belgrano, 2004, 2006) that assure a physical or physiological reaction largely driven by procedures fixed in the genome of the ‘ecological species’ (Van Valen, 1976) and by external stimuli. In synthesis, there are different vivoevents (e.g., foraging event, mating event, fear event, spawning event, etc.) for each organism according to the required resources and the

## Vivoscape

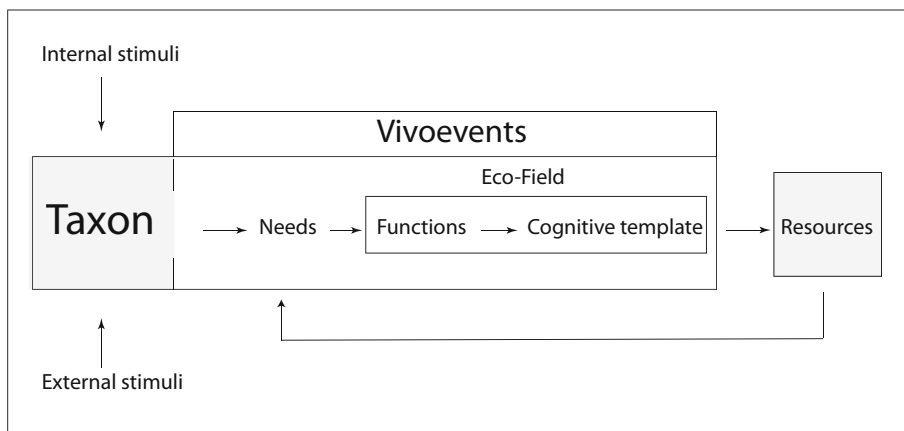


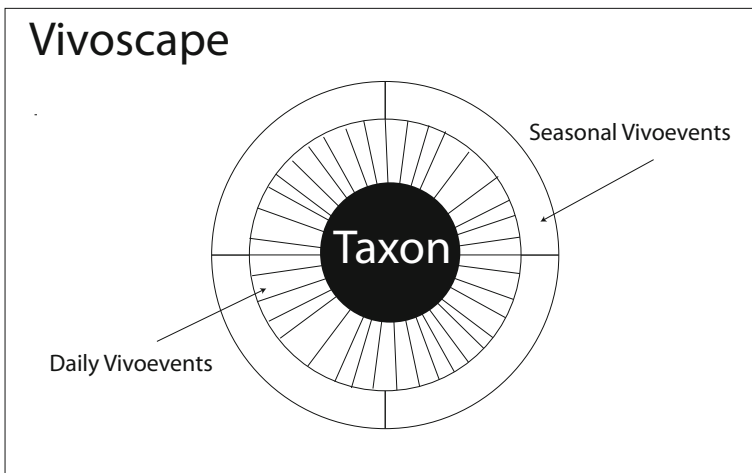
Fig. 3 General schema with which vivoevents utilize eco-field mechanisms inside the vivoscape to gain resources



reactions to external stimuli. Vivoevents have different temporal recurrence and impact on the ecological species according to their origin, the entire collection of vivoevents composes every taxon-specific vivoscape (Fig. 4). Each vivoevent is realized by a specific eco-field process: a function-specific ecosemiotic template requested to intercept a spatial configuration carrier of meaning (Farina & Belgrano, 2004, 2006).

### Vivoscape as Common Agency Shared by Humans and Animals to Track Resources

The General Theory of Resources states that every organismic-based performance is motivated by an internal deficit of specific resources (Farina, 2012) and is an important theoretical candidate to allow a reconnection between the human and natural domains, by-passing cultural belief. In fact, the necessity to track resources is common to all (auto-trophic and hetero-trophic) living organisms. From these premises, the vivoscape concept has a central role as a functional context utilized by organisms to explore the external world looking for resources. All living organisms require consumption of energy and a consequent depletion of stocks. However, humans additionally require spiritual, cultural and technological resources, and every day discover/invent new needs and consequently require new resources (blog, chat, etc.). Furthermore, humans seem not to place limits on resource use or, put another way, have lost the individual and social mechanisms of self-control in resource use, triggering unsustainable mechanisms that cause resource depletion.



**Fig. 4** A vivoscape is the result of a collection of vivoevents that are originated by internal needs (e.g., feeding) and by external occurrences (e.g., threat from predation). Some events have a regular temporal occurrence, for example the dawn and dusk choruses in birds at a daily scale, the egg deposition in frogs occurs at a seasonal scale. Seasonal vivoevents include migration and hibernation and all the associated processes including the modification of the internal physiology and behaviour

## Concluding Remarks

We are aware that many of the ideas encapsulated within the vivoscope model have similarities with those especially utilized in biosemiotics (Hoffmeyer, 2008: the semi-otic niche) and in the landscape ecology (Farina, 2021a: interpreted landscape). However, the semiotic niche considers the entire set of signs utilized by an organism to interact with the environment and the “interpreted landscape” is the representation of the surroundings created by the use of species-specific set of filters that attribute a meaning to a sensed environment.

The vivoscope paradigm describes a world in which biological and ecological processes are integrated into a unique entity. Utilizing the metaphora of checkers the pieces are the taxa and the board is the physical background on which organisms exist, insist and interact. The rules of this game have been fixed into the evolutionary realm and are modified by the natural selection mechanisms. Organisms and background are the ingredients that concur to create the vivoscope. Definitively the vivoscope is the environmental unit of reference comprising and individual and its biotic and abiotic environment mediated by interacting processes.

The local extinction of a species is not simply the disappearance of a taxon but is also the disappearance of all the interactions between that species and other species and the physical background. If, like after a severe deforestation in the tropics, all the species are extinct, the environment disappears and only bare mineral soil persists. The vivoscope, thanks to the unitarian vision, can contribute to guide actions to protect the environment and enhance its resilience, to restore degraded habitats, and to select the best actions to assure the wellbeing of human and non-human organisms.

**Acknowledgements** The authors wish to thank Flora McTavish-McDonald for her help with copy editing the original version of this article.

**Funding** Open access funding provided by Università degli Studi di Urbino Carlo Bo within the CRUI-CARE Agreement.

**Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

## References

- Abram, D. (2012). *The spell of the sensuous: Perception and language in a more-than-human world*. Vintage.
- Andersson, L. (1990). The driving force: Species concepts and ecology. *Taxon*, 39(3), 375–382. <https://doi.org/10.2307/1223084>.
- Backhaus, G. (2006). An introduction to the conceptual formation of ecoscapes. In: G. Backhaus & J. Muringi (eds.), *Ecoscapes*, (pp. XIII-XXXII). Lanham, MD: Lexington Books, Rowman & Littlefield Publishers, Inc.

- Beniston, M., & Stephenson, D. B. (2004). Extreme climatic events and their evolution under changing climatic conditions. *Global and Planetary Change*, 44(1–4), 1–9. <https://doi.org/10.1016/j.gloplacha.2004.06.001>.
- Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, 85(7), 1771–1789. <https://doi.org/10.1890/03-9000>.
- Convery, I., Mort, M., Baxter, J., & Bailey, C. (2008). Exploring the lifescape. In: I. Convery, M. Mort, J. Baxter, & C. Bailey. *Animal Disease and Human Trauma* (pp. 132–150). London: Palgrave Macmillan.
- Dale, M. B. (1970). Systems analysis and ecology. *Ecology*, 51(1), 2–16. <https://doi.org/10.2307/1933596>.
- DeAngelis, D. L., & Grimm, V. (2014). Individual-based models in ecology after four decades. *F1000prime reports*, 6:39. <https://doi.org/10.12703/P6-39>.
- Evans, M. R. (2012). Modelling ecological systems in a changing world. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1586), 181–190. <https://doi.org/10.1098/rstb.2011.0172>.
- Farina, A. (2012). A biosemiotic perspective of the resource criterion: Toward a general theory of resources. *Biosemiotics*, 5(1), 17–32. <https://doi.org/10.1007/s12304-011-9119-z>.
- Farina, A. (2021a). *Landscape ecology: Theories, methodologies and applications. An agenda for the Second Millennium*. Springer.
- Farina, A. (2021b). *Ecosemiotic landscape. A novel perspective for the toolbox of environmental humanities*. Cambridge University Press.
- Farina, A., & Belgrano, A. (2004). The eco-field: A new paradigm for landscape ecology. *Ecological Research*, 19(1), 107–110. <https://doi.org/10.1111/j.1440-1703.2003.00613.x>.
- Farina, A., & Belgrano, A. (2006). The eco-field hypothesis: Toward a cognitive landscape. *Landscape Ecology*, 21(1), 5–17. <https://doi.org/10.1007/s10980-005-7755-x>.
- Fish, R., Church, A., & Winter, M. (2016). Conceptualising cultural ecosystem services: A novel framework for research and critical engagement. *Ecosystem Services*, 21, 208–217. <https://doi.org/10.1016/j.ecoser.2016.09.002>.
- Forman, R. T., & Godron, M. (1986). *Landscape ecology*. John Wiley.
- Fretwell, S. D. (1987). Food chain dynamics: The central theory of ecology? *Oikos*, 50(3), 291–301. <https://doi.org/10.2307/3565489>.
- Gallagher, A. J., Creel, S., Wilson, R. P., & Cooke, S. J. (2017). Energy landscapes and the landscape of fear. *Trends in Ecology & Evolution*, 32(2), 88–96. <https://doi.org/10.1016/j.tree.2016.10.010>.
- Gasteyer, S. P., & Butler Flora, C. (2000). Modernizing the savage: Colonization and perceptions of landscape and lifescape. *Sociologia Ruralis*, 40(1), 128–149. <https://doi.org/10.1111/1467-9523.00135>.
- Gause, G. F., Nastukova, O. K., & Alpatov, W. W. (1934). The influence of biologically conditioned media on the growth of a mixed population of *Paramecium caudatum* and *P. aureliax*. *Journal of Animal Ecology*, 3(2), 222–230. <https://www.jstor.org/stable/i201553>.
- Gaynor, K. M., Hohnowski, C. E., Carter, N. H., & Brashares, J. S. (2018). The influence of human disturbance on wildlife nocturnality. *Science*, 360(6394), 1232–1235. <https://doi.org/10.1126/science.aar7121>.
- Grace, J. B. (2015). Taking a systems approach to ecological systems. *Journal of Vegetation Science*, 26(6), 1025–1027. <https://doi.org/10.1111/jvs.12340>.
- Haberl, H., Erb, K. H., Krausmann, F., Gaube, V., Bondeau, A., Plutzer, C., Gingrich, S., Lucht, W., & Fischer-Kowalski, M. (2007). Quantifying and mapping the human appropriation of net primary production in earth's terrestrial ecosystems. *Proceedings of the National Academy of Sciences*, 104(31), 12942–12947. <https://doi.org/10.1073/pnas.0704243104>.
- Hebblewhite, M., & Merrill, E. H. (2009). Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. *Ecology*, 90(12), 3445–3454. <https://doi.org/10.1890/08-2090.1>.
- Heller, K. G., & Helversen, O. V. (1989). Resource partitioning of sonar frequency bands in rhinolophoid bats. *Oecologia*, 80(2), 178–186. <https://doi.org/10.1007/BF00380148>.
- Hoffmeyer, J. (2008). The semiotic niche. *Journal of Mediterranean Ecology*, 9, 5–30.
- Holling, C. S. (1973). Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics*, 4(1), 123.
- Janzen, D. H. (1974). The deflowering of Central America. *Natural History*, 83, 48–53.
- Jenkins, R. (2002). The human world and the natural world. In R. Jenkins (Ed.), *Foundations of sociology* (pp. 111–138). Palgrave.
- Korzeniewski, B. (2001). Cybernetic formulation of the definition of life. *Journal of Theoretical Biology*, 209(3), 275–286. <https://doi.org/10.1006/jtbi.2001.2262>.
- Laiolo, P. (2012). Interspecific interactions drive cultural co-evolution and acoustic convergence in syntopic species. *Journal of Animal Ecology*, 81(3), 594–604. <https://doi.org/10.1111/j.1365-2656.2011.01946.x>.

- Laundré, J. W., Hernández, L., Medina, P. L., Campanella, A., López-Portillo, J., González-Romero, A., Grajales-Tam, K. M., Burke, A. M., Gronemeyer, P., & Browning, D. M. (2014). The landscape of fear: The missing link to understand top-down and bottom-up controls of prey abundance? *Ecology*, *95*(5), 1141–1152. <https://doi.org/10.1890/13-1083.1>.
- Lawton, J. H. (1997). The role of species in ecosystems: Aspects of ecological complexity and biological diversity. In T. Abe, S. A. Levin, & M. Higashi (Eds.), *Biodiversity* (pp. 215–228). New York, NY: Springer.
- Lewanzik, D., Sundaramurthy, A. K., & Goerlitz, H. R. (2019). Insectivorous bats integrate social information about species identity, conspecific activity and prey abundance to estimate cost–benefit ratio of interactions. *Journal of Animal Ecology*, *88*(10), 1462–1473. <https://doi.org/10.1111/1365-2656.12989>.
- MacArthur, R., & Levins, R. (1967). The limiting similarity, convergence, and divergence of coexisting species. *The American naturalist*, *101*(921), 377–385. <https://www.jstor.org/stable/2459090>.
- Maran, T. (2020). *Ecosemiotics: The study of signs in changing ecologies*. Cambridge University Press.
- Maran, T., & Kull, K. (2014). Ecosemiotics: Main principles and current developments. *Geografiska Annaler: Series B, Human Geography*, *96*(1), 41–50. <https://doi.org/10.1111/geob.12035>.
- Marquet, P. A., Allen, A. P., Brown, J. H., Dunne, J. A., Enquist, B. J., Gillooly, J. F., Gowaty, P. A., Green, J. L., Harte, J., Hubbell, S. P., O'Dwyer, J., Okie, J. G., Ostling, A., Ritchie, M., Storch, D., & West, G. B. (2014). On theory in ecology. *Bioscience*, *64*(8), 701–710. <https://doi.org/10.1093/biosci/biu098>.
- Mason, H. L., & Langenheim, J. H. (1957). Language analysis and the concept environment. *Ecology*, *38*(2), 325–340. <https://doi.org/10.2307/1931693>.
- Maturana, H. R., & Varela, F. J. (1991). *Autopoiesis and cognition: The realization of the living* (Vol. 42). Springer Science & Business Media.
- Maxwell, S. L., Cazalis, V., Dudley, N., Hoffmann, M., Rodrigues, A. S. L., Stolton, S., Visconti, P., Woodley, S., Kingston, N., Lewis, E., Maron, M., Strassburg, B. B. N., Wenger, A., Jonas, H. D., Venter, O., & Watson, J. E. M. (2020). Area-based conservation in the twenty-first century. *Nature*, *586*(7828), 217–227. <https://doi.org/10.1038/s41586-020-2773-z>.
- Mayden, R. L. (1997). A hierarchy of species concepts: The denouement in the saga of the species problem. *Systematics Association Special Volume*, *54*, 381–424.
- Memmott, J., Gibson, R., Carvalheiro, L. G., Henson, K., Heleno, R. H., Mikel, M. L., & Pearce, S. (2007). The conservation of ecological interactions. In A. J. A. Stewart, T. R. New, & O. T. Lewis (Eds.), *Insect Conservation Biology*, (pp. 226–244). CABI Royal Entomological Society DOI. <https://doi.org/10.1079/9781845932541.0226>.
- Michener, W. K., Baerwald, T. J., Firth, P., Palmer, M. A., Rosenberger, J. L., Sandlin, E. A., & Zimmerman, H. (2001). Defining and unraveling biocomplexity. *BioScience*, *51*(12), 1018–1023. [https://doi.org/10.1641/0006-3568\(2001\)051\[1018:DAUB\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[1018:DAUB]2.0.CO;2).
- Milner-Gulland, E. J. (2012). Interactions between human behaviour and ecological systems. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1586), 270–278. <https://doi.org/10.1098/rstb.2011.0175>.
- Monod, J. (1974). On chance and necessity. In F. J. Ayala & T. Dobzhansky (Eds.), *Studies in the philosophy of biology* (pp. 357–375). Palgrave.
- Monod, J., & Jacob, F. (1961). General conclusions: Teleonomic mechanisms in cellular metabolism, growth, and differentiation. In: *Cold Spring Harbor symposia on quantitative biology* (Vol. 26, pp. 389–401). Cold Spring Harbor Laboratory Press.
- Muller, H. J. (1966). The gene material as the initiator and the organizing basis of life. *The American Naturalist*, *100*(915), 493–517. <https://www.jstor.org/stable/2459205>.
- Mullon, C., & Lehmann, L. (2018). Eco-evolutionary dynamics in Metacommunities: Ecological inheritance, helping within species, and harming between species. *The American Naturalist*, *192*(6), 664–686. <https://doi.org/10.1086/700094>.
- Naveh, Z., & Lieberman, A. S. (1984). *Landscape ecology. Theory and application*. Springer.
- Odling-Smee, J., Erwin, D. H., Palkovacs, E. P., Feldman, M. W., & Laland, K. N. (2013). Niche construction theory: A practical guide for ecologists. *The Quarterly Review of Biology*, *88*(1), 3–28. <https://doi.org/10.1086/669266>.
- Odling-Smee, J., & Laland, K. N. (2011). Ecological inheritance and cultural inheritance: What are they and how do they differ? *Biological Theory*, *6*(3), 220–230. <https://doi.org/10.1007/s13752-012-0030-x>.
- Page, J. L., Dickman, B. D., Webster, D. R., & Weissburg, M. J. (2011). Getting ahead: Context-dependent responses to odorant filaments drive along-stream progress during odor tracking in blue crabs. *Journal of Experimental Biology*, *214*(9), 1498–1512. <https://doi.org/10.1242/jeb.049312>.
- Patten, B. C. (1978). Systems approach to the concept of environment. *The Ohio Journal of Science*, *78*(4), 206–222.

- Patten, B. C. (1982). Environs: Relativistic elementary particles for ecology. *The American Naturalist*, 119(2), 179–219. <https://www.jstor.org/stable/2461109>.
- Patten, B. C., & Auble, G. T. (1981). System theory of the ecological niche. *The American Naturalist*, 117(6), 893–922. <https://www.jstor.org/stable/2460571>.
- Pickett, S. T. A., Cadenasso, M. L., & Grove, J. M. (2005). Biocomplexity in coupled natural–human systems: A multidimensional framework. *Ecosystems*, 8(3), 225–232. <https://doi.org/10.1007/s10021-004-0098-7>.
- Pimm, S. L., Jenkins, C. N., Abell, R., Brooks, T. M., Gittleman, J. L., Joppa, L. N., Raven, P. H., Roberts, C. M., & Sexton, J. O. (2014). The biodiversity of species and their rates of extinction, distribution, and protection. *Science*, 344(6187), 1246752. <https://doi.org/10.1126/science.1246752>.
- Prosser, J. I., Bohannan, B. J., Curtis, T. P., Ellis, R. J., Firestone, M. K., Freckleton, R. P., Green, J. L., Green, L. E., Killham, K., Lennon, J. L., Osborn, A. M., Solan, M., van der Gast, C. J., & Young, P. W. (2007). The role of ecological theory in microbial ecology. *Nature Reviews Microbiology*, 5(5), 384–392. <https://doi.org/10.1038/nrmicro1643>.
- Riggins, J. J., Davis, C. A., & Hoback, W. W. (2009). Biodiversity of belowground invertebrates as an indicator of wet meadow restoration success (Platte River, Nebraska). *Restoration Ecology*, 17(4), 495–505. <https://doi.org/10.1111/j.1526-100X.2008.00394.x>.
- Rosenzweig, M. L. (1981). A theory of habitat selection. *Ecology*, 62(2), 327–335. <https://doi.org/10.2307/1936707>.
- Scheiner, S. M., & Willig, M. R. (2008). A general theory of ecology. *Theoretical Ecology*, 1(1), 21–28. <https://doi.org/10.1007/s12080-007-0002-0>.
- Schiestl, F. P., & Johnson, S. D. (2013). Pollinator-mediated evolution of floral signals. *Trends in Ecology & Evolution*, 28(5), 307–315. <https://doi.org/10.1016/j.tree.2013.01.019>.
- Schirpke, U., Meisch, C., & Tappeiner, U. (2018). Symbolic species as a cultural ecosystem service in the European Alps: Insights and open issues. *Landscape Ecology*, 33(5), 711–730. <https://doi.org/10.1007/s10980-018-0628-x>.
- Seymour, V. (2016). The human–nature relationship and its impact on health: A critical review. *Frontiers in Public Health*, 4, 260. <https://doi.org/10.3389/fpubh.2016.00260>.
- Shambaugh, G. E. (1930). The theory of sound perception. *The Journal of the Acoustical Society of America*, 1(3A), 295–300.
- Smith, B., & Varzi, A. C. (1999). The niche. *NOUS*, 33(2), 214–238.
- Smith, B., & Varzi, A. C. (2002). Surrounding space. On the ontology of organism–environment relations. *Theory in Bioscience*, 120(2), 139–162.
- Sturm, R., Polajnar, J., & Virant-Doberlet, M. (2019). Practical issues in studying natural Vibroscope and biotic noise. In P. S. Hill, R. Lakes-Harlan, V. Mazzoni, P. M. Narins, M. Virant-Doberlet, & A. Wessel (Eds.), *Biotremology: Studying vibrational behavior (no. 6)* (pp. 125–148). Springer.
- Suraci, J. P., Clinchy, M., Zanette, L. Y., & Wilmers, C. C. (2019). Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. *Ecology Letters*, 22I, 1578–1586. <https://doi.org/10.1111/ele.13344>.
- Tilman, D., & Kareiva, P. (Eds.) (1997). *Spatial ecology: The role of space in population dynamics and interspecific interactions (MPB-30)* (Vol. 89). Princeton University Press.
- Tobias, J. A., & Seddon, N. (2009). Signal design and perception in *Hypocnemis* antbirds: Evidence for convergent evolution via social selection. *Evolution: International Journal of Organic Evolution*, 63(12), 3168–3189. <https://doi.org/10.1111/j.1558-5646.2009.00795.x>.
- Van Valen, L. (1976). Ecological species, multispecies, and oaks. *Taxon*, 25, 233–239. <https://doi.org/10.2307/1219444>.
- Von Uexküll, J. (1926). *Theoretical biology*. Kegan, Paul, Trench, Trubner and Company Ltd..
- Von Uexküll, J., 1982(1940). The theory of meaning. *Semiotica* 42, 25–82.
- Von Uexküll, J., 1992(1934). A stroll through the worlds of animals and men. *Semiotica* 89(4), 702 319–391.
- White Jr, L. (1967). The historical roots of our ecological crisis. *Science*, 155 (3767), 1203–1207. <https://doi.org/10.1126/science.155.3767.1203>.
- Willmer, P. (2011). *Pollination and floral ecology*. Princeton University Press.
- Wu, J. (2017). Thirty years of landscape ecology (1987–2017): Retrospects and prospects. *Landscape Ecology*, 32, 2225–2239. <https://doi.org/10.1007/s10980-017-0594-8>.