Article

A New Look at the Concept of Ecosystem

Jaime Gómez-Márquez

Department of Biochemistry and Molecular Biology, Faculty of Biology – CIBUS, University of Santiago de Compostela, 15782 Santiago de Compostela, Galicia, Spain
* Correspondence: jaime.gomez.marquez@usc.es

Abstract: The ecosystem is an essential biological concept linking the living and the inanimate and represents the main structural and functional unit of nature. The biodiversity that exists on our planet can be organized into closely interconnected living worlds: acellular (viruses and capsidless genetic elements), prokaryotic (bacteria and archaea), and eukaryotic (all nucleated organisms). I want to highlight the presence of viruses as components of biodiversity because they are often overlooked in many studies despite their essential ecological and evolutionary role. Furthermore, I propose seven distinctive hallmarks that are inherent to any ecosystem: biodiversity, physical environment, hierarchy, interactivity, openness, "homecostasis", and evolutionary. From the interaction and coupling of these living worlds with the environment (the environmental world),I define the ecosystem as a specific and dynamic ensemble of living and non-living worlds that functions as an open, hierarchical, and evolving system. This complex web of interactions that we call ecosystem can be graphically represented as a triangle reflecting the dynamic equilibrium between all the worlds. Finally, I propose a new way of graphically relating the ecosystem to biodiversity by taking the ecosystem as the nucleus from which all living worlds emerge.

Keywords: ecosystem concept; ecosystem hallmarks; ecosystem representation; living worlds

1. The concept of the ecosystem

An ecosystem is a geographical area or a specific place in which certain living organisms interact with each other and with the environment they inhabit. Since the concept of the ecosystem was introduced almost a century ago (Tansley 1935), not much has changed because whatever it is, it must always include the interrelationships of species with their environment. The ecosystem has served as the central organizing concept of ecology and the study of ecosystems has become an important applied science for the analysis of global change and human environmental impacts (Currie 2011).

Analysis of the ecosystem concept among specialists does not contradict the common usage of the term, but many of the underlying assumptions have been questioned (Golley 1993; O'Neill 2001; Mayer and Rietkerk 2004; Currie 2011). Some ecologists even claim that there may not be a single correct definition for the term ecosystem and that there may be several definitions depending on different circumstances (Jax 2007). Other specialists did propose a formal description of the concepts and relations linked to the ecosystem definition as an ontology that can serve as a basis for future discussion, modelling and conceptual work (Gignoux et al. 2011).

It is worth noting that some ecologists have introduced the concept of "novel ecosystem" to describe ecosystems that have been altered by humans (Chapin and Starfield 1997). It has been proposed that a novel ecosystem can be identified by its origins rooted in the human activity, the ecological thresholds it has crossed, the alteration of the original biodiversity, and a capacity to sustain itself (Morse et al. 2014). Certainly, we are living in the Anthropocene and human activity is increasingly influencing the evolution of ecosystems. To understand how humans change ecosystem dynamics, we need to integrate research into all components of each ecosystem and, perhaps, change the standard paradigm of the ecosystem concept.

In this paper, to define the concept of ecosystem, I used a strategy based first on the identification of the elements that characterize it. Once these components were defined, I elaborated an alternative definition to the classical concept of ecosystem (not necessarily better, but with a different approach), as well as a novel and very clear way of representing it that implicitly includes all the multiple interrelationships that exist in such a natural or human-altered space.

2. The hallmarks of the ecosystem

What are the elements that characterize any ecosystem? Reflecting on this question and considering what is said in the ecological literature (I am obviously referring only to the bibliography that I have been able to consult, although I am aware that there are many, many more references on such a broad topic as the ecosystem concept and characteristics that define it), I concluded that there are seven general elements, which I call the hallmarks of the ecosystem, that serve to specifically characterize any ecosystem.

The first two hallmarks are the biodiversity and the physical environment; both are structural because they define the elements that make up and distinguish each ecosystem. Both hallmarks represent the most obvious features of any ecosystem, the ones that always appear in any definition of an ecosystem. But an ecosystem is much more than a static representation of its biotic and abiotic components, it is an interactive and dynamic entity. Metaphorically, we could say that the ecosystem is more like a video than a portrait. This ability of species to interrelate with each other and with their environment, to adapt to new circumstances resulting from genetic changes or environmental alterations, is reflected in two new hallmarks: interactivity and evolutionary. These hallmarks define the functioning of an ecosystem because they include the multiple interactions (biotic-biotic, biotic-abiotic, abiotic-abiotic) that take place in the ecosystem, as well as its capacity to evolve. Finally, there are three more hallmarks that have both a structural and functional character. I refer to hierarchy, openness, and "homecostasis". These hallmarks are related to hierarchical processes such as trophic chains (hierarchy), to the constant exchange of matter and energy (openness), to the relationship with other ecosystems and to the resistance and resilience mechanisms necessary to maintain ecosystem homeostasis (homecostasis).

3. First hallmark: biodiversity

The importance of biodiversity in an ecosystem is not only the large number of species living in it, but also the multiple interrelationships between all organisms. To fully understand how an ecosystem is structured and how it functions, we must consider all organisms and the networks behind them.

How can we organize all the biodiversity that lives in an ecosystem? The three-domain system divides all organisms with cellular structure into three groups: archaea, bacteria and eukarya (Woese et al. 1990); However, this organization of biodiversity excludes viruses because they are not considered living things as they do not have a cellular structure, and this is, in my opinion, a serious biological problem. I think viruses deserve to be included in the tree of life because they have played an important role in the evolution of species (Harris and Hill, 2021) and because there are strong biological arguments to support their consideration as living things (Raoult and Forterre 2008; Dupré and O'Malley 2009; Gómez-Márquez 2021). In addition to the *woesian* tree of life, there are other phylogenetic variants of the tree of life that depend on the characters used to construct it (Williams et al. 2020; Choi and Kim 2020). In any case, the tree of life is a metaphorical construct that cannot be experimentally validated (Choi and Kim 2020).

An alternative way of organizing biodiversity is by grouping all living things in the Acellular World (AW), the Prokaryotic World (PW) and the Eukaryotic World (EW); these living worlds are themselves immersed in the environmental world (EnW). The PW comprises all prokaryotes grouped in the Bacteria and Archaea networks. These networks form complex ecological interactions, including win-win relationships such as mutual

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 17 February 2022 doi:10.20944/preprints202202.0202.v1

cross-feeding and cooperation interactions, win-lose relationships such as predator-prey and host-parasite interactions, and loss-loss relationship such as competitive exclusion interactions (Faust and Raes 2012; Lv et al. 2019). The EW includes all organisms with a true nucleus and is subdivided into photosynthetic (autotrophic) and non-photosynthetic (heterotrophic) organisms. Considering plants as the main eukaryotic organisms capable of photosynthesis, however there are some exceptions to this such as non-photosynthetic mycorrhizal plants (Bidartondo 2005), although we cannot make the exception the main thing. The AW is mainly composed of viruses, but also includes genetic elements such as viroids, plasmids, and transposons, although these elements, unlike viruses, should not be considered as living beings.

I want to pay a little more attention to viruses because many studies of biodiversity and ecosystem evolution have ignored viruses because they are not considered living, and this exclusion is a major shortcoming in understanding the full complexity of ecosystems. Viruses should not be ignored if we are to understand how an ecosystem works because they participate in food webs, in horizontal gene transmission or in biogeochemical cycles (Rower et al. 2009; O'Malley 2016; Gilbert and Cordaux 2017). The high abundance and diversity of viruses in nature, often in the apparent absence of disease, suggests that they are embedded into global ecosystems at all ecological scales (French and Holmes 2020). As Barabási (2016) said: "we will never understand complex systems unless we develop a deep understanding of the networks behind them".

A final consideration on biodiversity: conserving biodiversity is essential because it means maintaining a biological richness that is the fruit of millions of years of evolution and because we rarely know a priori which species are critical to current functioning or provide resilience and resistance (see below) to environmental changes (Stuart Chapin III et al. 2000). Humans are destroying ecosystems on a massive scale through increased pollution, deforestation, climate change and other man-made factors and this will have irreparable consequences on biodiversity and, ultimately, on the well-being of the entire planet (Goudie 2018).

4. Second hallmark: physical environment

Life on Earth is made possible above all by solar radiation as a primary source of energy, by water, an essential solvent for biochemical reactions to occur, and by temperature, which favours the interactions that allow living things to thrive. These and other characteristics form part of the physical environment and are the substrate on which the life process takes place. This abiotic component of the ecosystem can affect an organism in multiple ways, causing molecular, cellular, physiological, or behavioural changes, in a transient or permanent way.

The physical environment has four main components which determine the survival of the species (Monteith and Unsworth 2014). First, it is a source of radiant energy that is harnessed in photosynthesis to synthesize organic matter from inorganic molecules. Second, the environment is a source of the water and all chemical elements needed to form the components of living cells. Thirdly, factors such as temperature, gravity or daylength provide stimuli for, for example, the growth and development of plants, or the onset of reproductive cycles in many plant and animal organisms. Fourth, the physical environment determines the spatial and temporal distribution of species and the viability of pathogens and parasites which attack living organisms, and the susceptibility of organisms to attack.

When we define an ecosystem, we are delimiting a physical space and environmental conditions (Odum and Barret 2005). The physical component of environment includes air, water, soil, sunlight, temperature, climate, minerals, etc. The habitat is the physical environment where an organism, a population, a community lives or thrives (Kearney 2006). Habitats can be an open geographical area (e.g., a forest) or a specific location (*e.g.,* a tree), and their boundaries can differ in origin, spatial structure, and dynamics, having a profound importance for the conceptualization of an ecosystem (Strayer et al. 2003; Post et al.

2007). Like habitat, niche is determined by biotic and abiotic factors, but it is a functional concept as it describes the functional role of a species within the ecosystem as well as its interactions (Polechová and Storch 2019). In a simple way we could say that the habitat is *where* and the niche is *how*, and in this sense, the concept of niche should fit better into the next two ecosystem hallmarks.

Ecosystems are not isolated spaces, independent of the environment which in turn is formed by one or more other ecosystems. In fact, it is not always easy to define the boundaries of an ecosystem and in these places there are interactions with other ecosystems creating an interdependence between different ecosystems (Strayer et al. 2003). Several authors have examined ecotones or ecological boundaries using a hierarchical approach to provide a general criterion for identifying ecological entities (Yarrow and Salthe 2008; Kolasa 2014). Overall, as Schulze et al. (2019) say "the limits of an ecosystem must extend so far that the relevant fractions of all substance flux rates per ground area (e. g. carbon assimilation, nitrogen mineralization, and formation of groundwater) of this particular ecosystem are taken into account".

5. Third hallmark: hierarchy

The third hallmark, hierarchy, refers to the hierarchical structure and organization of ecosystems (O´Neill et al. 1986). Ecosystems are complex and organized networks in which each species unconsciously plays a role whose purpose is, in addition to the survival and perpetuation of the species, to contribute to maintaining the dynamic equilibrium necessary for the stability of the whole. From an organizational perspective, we can perceive an ecosystem as a complex system organized at different nested hierarchical levels (Reuter et al. 2010; Landl et al. 2018). Each level in the hierarchy represents an increase in complexity and this hierarchization is important for at least three reasons: i) the emergence of emergent properties (Nielsen and Müller 2000; Ponge 2007); ii) hierarchical structures are more stable (Simon 1969); iii) the packing of the maximum amount of complexity into the same container (Miller III 2008).

There are several hierarchical levels within an ecosystem (Miller 2008). There is a biological hierarchy of structural complexity from viruses, single cells (prokaryotes and eukaryotes) and multicellular organisms to populations and communities. The novelty in this classical ecological hierarchy is the presence of viruses, which, as mentioned above, is justified by their evolutionary relevance, their involvement in processes such as biogeochemical cycles and their control of microbial populations. A level above this hierarchy in the complexity of living things is the ecosystem, which integrates the biotic component, representing the biological hierarchy, and the abiotic component, which incorporates the environmental hierarchy. Above the ecosystem are (in this order) the landscape, which represents a set of different interacting ecosystems, the biome and the ecosphere, which includes all living species on Earth (Odum and Barret 2005).

There is a functional hierarchy that has to do with the role each species plays in the ecosystem and the ecosystem processes are being increasingly viewed as the elements in a hierarchy (Currie 2011). From a general perspective there are autotrophs or the producers of organic matter from inorganic compounds, and heterotrophs, consumers and decomposers, that obtain their energy and organic matter from other organisms (Garvey and Whiles 2017). I would add a new category: "virotrophs" (viruses), which are neither producers nor consumers nor decomposers, but are constantly renewing themselves and therefore recycle organic matter to a large extent. Altogether, autotrophs, heterotrophs and "virotrophs", form the trophic levels, which are organized hierarchically, generating the food web (Duffy et al. 2007). Within the food web there is a unidirectional flow of energy and an increase of the entropy according to the laws of thermodynamics. Energy is what drives the ecosystem and while all matter is conserved (it is recycled), energy enters all ecosystems as sunlight and is gradually lost as heat.

6. Fourth hallmark: interactivity

An ecosystem is defined by the interactions that take place within it. Interactivity means that each ecosystem represents a complex and specific network of interactions between living organisms and with their environment (Jordano 2016). These interactions are part of the framework that forms the complexity of ecological communities (Lang and Benbow 2013), and result in a flow of energy from the abiotic component (primarily the sun) to life, from autotrophs, making organic matter through photosynthesis, to heterotrophs and back to the environment, increasing the entropy of the universe.

In the ecosystem, there are many kinds of interplay between living worlds (Pascual and Dunne, 2006) following what I named as the "cooperating thrust" (Gómez-Márquez 2020). There are trophic interactions (feeding), mutualistic interactions (positive-positive) such as the symbiosis between intestinal bacteria and human beings or between the nitrogen fixation bacteria and the legumes, and competitive interactions (interference for common resources). We can also see positive-negative interactions in which one organism benefits while the other is negatively affected (parasitism). The life cycle of any virus is an example of interaction between the acellular world and the prokaryotic or eukaryotic worlds, involving parasitic relationships but also being an example of horizontal transmission of genetic information and biological warfare between virus and host that drives the evolution and adaptation of both species. In this sense, we could say that an infectious disease is an example of the fight between organisms and this biological war can help to evolve both species or to extinct one of them. On the other hand, we can also see many examples of interactions between living beings and their environment, such as the interaction of birds with the aerial environment or fish with water.

Two extraordinary examples of global interactions within the ecosystem are the food web, which represents the feeding relationships among organisms or the trophic levels, and the biogeochemical cycles which are the interactions of living beings with chemical processes in nature (Thompson et al. 2012; Zak et al. 2006). It is worth noting that from these multiple ecosystem interactions, emergent properties arise, i.e., new properties or processes that appear in the ecosystem that were not present in each of the individual ecosystem components (Ponge 2005; Gilbert and Henry 2015; Schulze et al. 2019). Emergent properties help living beings to better adapt to their environment and thus increase their chances of survival.

Today, human activities are having an increasing impact on ecosystems because they are causing multiple alterations in the interactions between species and the environment. We are transforming the earth, species composition, biogeochemical cycles, etc. and all this stress is gradually leading to the destruction of natural spaces (Goudie 2018). For this reason, the analysis of the interactions among ecosystem stressors is fundamental for the conservation of the ecological systems (Côté et al. 2016).

7. Fifth hallmark: openness

An ecosystem is an open system. Openness means that ecosystems are thermodynamically open systems, where both matter and energy are exchanged in a constant process of transformation and recycling (Chapman et al. 2016). We know that in the ecosystems, energy is conserved, and matter can neither be created or destroyed, it can only be transformed. Thus, energy enters in the ecosystem ultimately from sunlight and leave in the form of heat, carbon enters as CO_2 and is converted into organic matter through photosynthesis while respiration returns CO_2 to the atmosphere generating ATP and heat (we can say that respiration is pumping out "disorder"), and water enters through rainfall and leave through evaporation or stream flow.

The simplest way to demonstrate the flow of energy in the ecosystem is through the analysis of a food chain, from primary producers to consumers (Begon and Townsend 2021). In the food chain, the transfer of energy is unidirectional in contrast to the cyclical behaviour of matter and not all the energy generated or consumed at one trophic level will be available to organisms at the next higher trophic level. Moreover, the study of food webs has revealed different patterns of energy flow and biomass partitioning depending on the type of ecosystem (Shurin et al. 2006).

In the ecosystem, the order and organization of complex living structures that make up the biomass is maintained by the catabolic activity, primarily cellular respiration, which continuously "pumps out disorder". Consequently, we can consider ecosystems as being open thermodynamic systems in disequilibrium (equilibrium is incompatible with life) that continuously exchange energy and matter with the environment to decrease internal entropy (to maintain the vital order) but increase external entropy thus satisfying the laws of thermodynamics (Gómez-Márquez 2020; Nielsen et al. 2020).

In ecosystem ecology, the principle of maximum power and the principle of maximum entropy production (MEP), which is an extension of the second law of thermodynamics in non-equilibrium systems, have been applied to provide a mechanistic explanation of how systems develop and organize in the context of energy uptake and use for ecosystem maintenance (Meysman and Bruers 2010; Sciubba 2011). The MEP states that thermodynamic processes far from equilibrium will adapt to steady states at which they dissipate energy and produce entropy at the maximum possible rate (Kleidon et al. 2010). Therefore, according to the MEP principle, ecosystems evolve until they reach a dynamic equilibrium in which the entropy increases as the result of the functioning of the ecosystem. In this situation of steady state, the evolutionary process should slow down because the system has reached a level of dynamic stability that runs counter to the need to evolve. The openness of the ecosystem favours its development and evolution, and serves to cover its energy needs, preventing its degradation and disappearance.

8. Sixth hallmark: homecostasis

Homeostasis is the term used to describe any process of self-regulation whereby biological systems tend to maintain equilibrium by adjusting to conditions that are optimal for survival. It denotes dynamic equilibrium and is considered a general property of ecosystems (Trojan 1984; Morgan and Brown 2001). Indeed, all ecosystems are continuously adjusting biogeochemical cycles and ecophysiological processes as well as changes in species composition to reach steady state (Schulze et al. 2019). At this point, I want to propose a new term, homecostasis, derived from the homeostasis, which refers specifically to the processes and mechanisms needed to maintain stable the ecosystems.

Gradual changes in environmental factors such as temperature might have little effect on the steady state of the ecosystem. However, the dynamic equilibrium of an ecosystem could be strongly altered by extraordinary or catastrophic physical and geological agents such as volcanoes or climate change, and with a lesser impact by forest fires, severe floods, or periods of drought. When this happens, the ecosystem reaches an alternative stable state (Beisner et al. 2003; Scheffer and Carpenter 2003).

Resistance and resilience are two fundamental components involved in the maintenance of ecosystem homeostasis. Ecological resilience was defined as the amount of disturbance that an ecosystem could withstand without changing self-organized processes and structures (Gunderson 2000) and resistance as the ability for an ecosystem to remain unchanged when being subjected to a disturbance or disturbances (Nimmo et al. 2015). The resilience and resistance of an ecosystem is a measure of its robustness, its ability to recover whether due to natural causes or human intervention (Falk et al. 2019). If disturbances are tolerable for the ecosystem, it will return to its pre-disturbance state, either because it is resilient to change or because it is resistant to internal or external disturbances (Gunderson 2000). When the resilience limit of the ecosystem is exceeded, new pattern-process relationships are created in complex systems, thus creating the basis for innovation (Allen and Holling 2010; Baho et al. 2017).

Understanding the mechanisms of homecostasis, or how ecosystems withstand environmental perturbations, is basic for predicting the consequences of environmental changes on ecosystem functioning (Wang and Loreau 2014), and so it is critical to address the global changes resulting from human activity and population growth, which is eroding natural resources and causing the extinction of many species (Capdevila et al. 2020).

9. Seventh hallmark: evolutionary

As ecosystems are made up of living things that can evolve to better adapt to their physical environment, which also evolves over time, it is an imperative of nature that the ecosystem must also evolve towards new stable states and it is the evolutionary process that ultimately shapes the biodiversity that populates the ecosystem (Pennel and O`Connor 2017; Weber et al. 2017). We know that ecosystems are dynamic in nature and their characteristics can vary over time. In fact, the structure of ecological networks reflects the evolutionary history of the ecosystem because the community dynamics is strongly driven by eco-evolutionary processes and environmental changes (Segar et al. 2020).

Throughout the history of life, the evolution of biodiversity has transformed the environment, such as the concentration of oxygen in the atmosphere or the composition of soils, while major changes in the environment have modulated the variety of species living there, such as glaciations or changes caused by plate tectonics (Zektser et al. 2006). It is well known that ecological factors influence adaptive radiation and that adaptive radiation, even in the short term, can have profound effects on ecosystems (Mathews et al. 2011). The idea of organism-environment interaction in the evolutionary process was clearly stated by R. Lewontin (1978) when he wrote: "There is a constant interplay of the organism and the environment, so that although natural selection may be adapting the organism to a particular set of environmental circumstances, the evolution of the organism itself changes those circumstances”.

A complex set of interactions within an ecosystem can maintain overall biodiversity relatively constant over long periods of time as long as environmental conditions are stable. If there is a modest disturbance to the ecosystem, it can return to its original state due to homecostasis mechanisms, rather than becoming a different ecosystem (Arnoldi et al. 2018). However, ecosystems must evolve in response to strong natural (e.g., intense volcanic activity or climate change) or anthropogenic disturbances to adapt to new circumstances. Ecological succession is a good example of how communities readjust to adapt to the changing environment (Chang and Turner 2019).

Despite the conceptual understanding that evolution and species interactions are inextricably linked, it remains a challenge to study ecological and evolutionary dynamics together over long time scales (Weber et al. 2017). There is no definite ecological theory about the mechanism for ecosystem evolution (Matthews et al. 2011; Lu, 2014) but as it was written elsewhere, “Ecology and evolution are tightly linked through the reciprocal causal relationships connecting organisms to both biotic and abiotic components of their local environment” (Barker and Odling-Smee 2014).

10. An alternative definition and representation of the ecosystem

First, I would like to stress that I do not disagree with the classical definition of ecosystem because there is nothing wrong with it. In this work, I propose a different definition based on the seven hallmarks common to all ecosystems, an alternative view of this concept as an open interacting life system. Consequently, I define the ecosystem as a specific and dynamic ensemble of living and non-living worlds that functions as an open, hierarchical, and evolving system. Every ecosystem has its own set of interconnected worlds that makes it different from other ecosystems.

How could we graphically represent this concept of ecosystem? From the definition proposed above, we can imagine the ecosystem as an ensemble of interconnected worlds (the worlds as an ensemble) that functions as an open interacting life system constantly exchanging matter and energy with its environment. As shown in Figure 1, the ecosystem is graphically represented as a triangle (it could also be a tetrahedron) in which the four worlds permanently interact with each other and with the other worlds in a dynamic equilibrium. The entire ecosystem is primarily powered by the energy from the sun. Ecosystem activity generates heat and waste, from metabolic activity and the degradation and decomposition of organic matter that will be largely recycled, leading to an overall increase in the entropy of the universe according to the universal laws of thermodynamics. The dynamic equilibrium of the ecosystem is maintained by "homecostatic" mechanisms but can be profoundly altered by extraordinary physical and geological agents such as volcanoes or climate change, and with less impact by forest fires, severe floods, or periods of drought. It should be noted that the graphical representation of the ecosystem is essentially unchanged if we use the three *woesian* domains (Archaea, Bacteria and Eukarya) instead of living worlds. The main difference between the two representations is whether viruses are included in this web of multiple biotic and abiotic interactions. On the other hand, this representation also reflects the series of cycles that take place in nature.

The biosphere, also known as the ecosphere, is made up of the parts of Earth (atmosphere, hydrosphere, and lithosphere) where life exists. The biosphere is a living system characterized by the continuous cycling of matter and an accompanying flow of solar energy. We can consider the planet Earth as a big, interconnected global ecosystem. Then, how could we represent the gigantic ecosystem that is the biosphere? Figure 2 shows the global planetary ecosystem, the biosphere, as a sum of ecosystems that interact with each other across physical boundaries, because no ecosystem is completely isolated from the rest and therefore its autonomy, its dynamic equilibrium, can be affected by what happens in other ecosystems near or far away. One ecosystem encroaches into another along areas called ecotones, where there is a mixing of species from the two ecosystems.

Finally, how can we incorporate this representation of the ecosystem in a new conception of the tree of life? Figure 3 shows the linkage between the graphical representation of the ecosystem and the tree of the living worlds. Although this representation does not reflect the evolutionary history of biodiversity (it is not a phylogenetic tree), it would be possible to do so by showing the interrelationships between organisms and their evolutionary ancestors (manuscript in preparation).

Author Contributions: All work presented in this manuscript was done solely by the author (J G-M).

Acknowledgments: This work is dedicated to my beloved granddaughter Daniela NG.

Conflicts of Interest: The authors declare no conflict of interest.

References

Allen CR, Holling CS (2010) Novelty, adaptive capacity, and resilience. Ecol Soc 15: 24.
Arnoldi J-F, Bideault A, Loreau M, Haegeman B (2018) How ecosystems recover from pulse perturbations: a theory of short- to long-term responses. J Theor Biol 436:79-92.
Baho DL, Allen CR, Garmestani AS, Fried-Petersen HB, Renes SE, Gunderson LH, Angeler DG (2017) A quantitative framework for assessing ecological resilience. Ecol Soc 22:1-17.
Barabási A (2016) Network science. Cambridge University Press.
Barker G, Odling-Smee J (2014) Integrating ecology and evolution: niche construction and ecological engineering. In G. Barker, E. Desjardins, and T. Pearce (eds), Entangled life, History, Philosophy and Theory of the Life Sciences. Springer.
Begon M, Townsend CR (2021) Ecology: from individuals to ecosystems (5 ed). Wiley.
Beisner BE, Haydon DT, Cuddington K (2003) Alternative stable states in ecology. Front Ecol Environ 1:376-382.
Bidartondo MI (2005) The evolutionary ecology of myco-heterotrophy. New Phytol 167:335-352.
Capdevila P, Stott I, Beger M, Salguero-Gómez R (2020) Towards a comparative framework of demographic resilience. Trends Ecol Evol 35:776-786.
Chang CC, Turner BL (2019) Ecological succession in a changing world. J Ecol 107:503 509.
Chapman E, Childers D, Vallino J (2016) How the second law of thermodynamics has informed ecosystem ecology through its history. BioScience 66:27-39.
Choi J, Kim S-H (2020) Whole-proteome tree of life suggests a deep burst of organism diversity. Proc Natl Acad Sci 117:3678-3686.
Côté IM, Darling ES, Brown CJ (2016) Interactions among ecosystem stressors and their importance in conservation. Proc R Soc B 283:20152592.
Currie WS (2011) Units of nature or processes across scales? The ecosystem concept at age 75. New Phytol 190:21-34.
Duffy JE, Cardinale BJ, France KE, McIntyre PB, Thébault E, Loreau M (2007) The functional role of biodiversity in ecosystems: incorporating trophic complexity. Ecol Lett 10:522-538.
Dupré J, O'Malley MA (2009) Varieties of living things: life at the intersection of lineage and metabolism. PTPBio 1:e003.

Falk DA, Watts AC, Thode AE (2019) Scaling ecological resilience. Front Ecol Evol 7: 275 (1-16).
Faust K, Raes J (2012) Microbial interactions: from networks to models. Nat Rev Microbiol 10:538-550.
French RE, Holmes EC (2020) An ecosystem perspective on virus evolution and emergence. Trends Microbiol 28:165-175.
Garvey JE, Whiles MR (2017) Trophic Ecology. CRC Press.
Gilbert JA, Henry C (2015) Predicting ecosystem emergent properties at multiple scales. Environ Microbiol Rep 7:20-22.
Gilbert C, Cordaux R (2017) Viruses as vectors of horizontal transfer of genetic material in eukaryotes. Curr Opin Virol 25:16-22.
Gignoux J, Davies ID, Flint SR, Zucker JD (2011) The ecosystem in practice: interest and problems of an old definition for constructing ecological models. Ecosystems 14:1039-1054.
Golley FB (1993) A history of the ecosystem concept in ecology. Yale University Press.
Gómez-Márquez J (2020) What are the principles that govern life? Commun Integr Biol 13:97-107.
Gómez-Márquez J (2021) What is life? Mol Biol Rep 48:6223-6230.
Goudie AS (2018) Human impact on the natural environment. John Wiley & Sons.
Gunderson LH (2000). Ecological resilience in theory and application. Annu Rev Ecol Syst 31:425-439.
Harmon L, Matthews B, Des Roches S, Chase JM, Shurin JB, Schulter D (2009) Evolutionary diversification in stickleback affects ecosystem functioning. Nature 458:1167-1170.
Harris HMB, Hill C (2021) A place for viruses on the tree of life. Front Microbiol 11:604048.
Jax K (2007) Can we define ecosystems? On the confusion between definition and description of ecological concepts. Acta Biotheor 55:341-355.
Jordano P (2016) Chasing ecological interactions. PLoS Biol 14:e1002559.
Kearney M (2006) Habitat, environment and niche: what are we modelling? Oikos 115:186-191.
Kleidon A, Malhi Y, Cox PM (2010) Maximum entropy production in environmental and ecological systems. Philos Trans R Soc B 365:1297-1302.
Kolasa J (2014) Ecological boundaries: a derivative of ecological entities. Web Ecol 14:27-37.
Landl P, Minoarivelo H, Brännström A, Hui C, Dieckmann U (2018) Complexity and stability of ecological networks: a review of the theory. Popul Biol 60:319-345.
Lange JM, Benbow ME (2013) Species interaction and competition. Nature Education Knowledge 4(4):8.
Lewontin R (1978) Adaptation. Scientific American 239: 213-230.
Luo J (2014) Loops and autonomy promote evolvability of ecosystems networks. Sci Rep 4:6440.
Lv X, Zhao K, Xue R, Liu Y, Xu J, Ma B (2019) Strengthening insights in microbial networks from theory to applications. mSystems 4:e00124-19.
Matthews B, Narwani A, Hausch S, Nonaka E, Hannes P, Yamamichi M, Sullam K, Bird KC, Thomas MK, Hanley T, Turner CB (2011) Toward an integration of evolutionary biology and ecosystem science. Ecol Lett 14:90-701.
Mayer AL, Rietkerk M (2004) The dynamic regime concept for ecosystem management and restoration. BioScience 54:1013-1020.
Meysman F, Bruers S (2010) Ecosystem functioning and maximum entropy production: a quantitative test of hypotheses. Philos Trans R Soc B 365:1405-1416.
Miller W III (2008) The hierarchical structure of ecosystems: connections to evolution. Evol: Educ Outreach 1:16-24.
Monteith JL, Unsworth MH (2014). Principles of Environmental Physics (4th ed). Elsevier.
Morgan Ernest SK, Brown JH (2001) Homeostasis and compensation: the role of species and resources in ecosystem stability. Ecology 82:2118-2132.
Morse NB, Pellissier PA, Cianciola E, Brereton RL, Sullivan MM, Shonka NK, Wheeler TB, McDowell WH (2014) Novel ecosystems in the Anthropocene: a revision of the novel ecosystem concept for pragmatic applications. Ecol Soc 19:12-21.
Nielsen SN, Müller F (2000) Emergent properties of ecosystems. In Jorgensen SE and Müller F (Eds.), Handbook of ecosystems Theories and Management. Lewis Publishers.
Nielsen SN, Müller F, Marques JC, Bastianoni S, Jorgensen SE (2020) Thermodynamics in Ecology – An introductory review. Entropy 22:820.
Nimmo DG, Nally R, Cunningham S, Haslem A, Bennett AF (2015) Vive la résistance: reviving resistance for 21st century conservation. Trends Ecol Evo 30:516-523.
Odum EP, Barret GW (2005) Fundamentals of Ecology. Thomson Brooks/Cole.
O´Malley MA (2016. The ecological virus. Stud Hist Philos Biol Biomed Sci 59:71-79.
O´Neill RV (2001) Is it time to bury the ecosystem concept? (with full military honours, of course!). Ecology 82:3275-3284.
O'Neill RV, DeAngelis DL, Waide JB, Allen TFH (1986) A hierarchical concept of ecosystems. Princeton University Press.
Pascual M, Dunne JA (eds) (2006). Ecological networks: linking structure to dynamics in food webs. Oxford University Press.
Pennel MW, O'Connor MI (2017) A modest proposal for unifying macroevolution and ecosystem ecology. Am Nat 189:ii-iii.
Polechová J, Storch D (2019) Ecological Niche. In Fath B (ed). Encyclopedia of Ecology (2nd ed). Elsevier.
Ponge J-F (2007) Emergent properties from organisms to ecosystems: towards a realistic approach. Biol Rev 80: 403-411.
Post DM, Doyle MW, Sabo JL, Finlay JC (2007) The problem of boundaries in defining ecosystems: a potential landmine for uniting geomorphology and ecology. Geomorphol 89:111-126.
Raoult D, Forterre P (2008) Redefining viruses: lessons from mimivirus. Nat Rev Microbiol 6:315-319.
Reuter H, Jopp F, Blanco-Moreno JM, Damgaard C, Matsinos Y, DeAngelis DL (2010) Ecological hierarchies and self-organisation – Pattern analysis, modelling and process integration across scales. Basic Appl Ecol 11:572-581.
Rohwer F, Prangishvili D, Lindell D (2009) Roles of viruses in the environment. Environ Microbiol 11:2771-2774.

Scheffer M, Carpenter SR (2003) Catastrophic regime shifts in ecosystems: linking theory to observation. Trends Ecol Evol 18:648-656.
Schulze E-D, Beck E, Buchmann N, Clemens S, Müller-Hohenstein K, Scherer-Lorenzen M (2019) Plant Ecology. Switzwerland: Springer.
Sciubba E (2011) What did Lotka really say? A critical reassessment of the “maximum power principle”. Ecol Modell 222:1347-1353.
Segar S, Fayle T, Srivastava D, Lewinsohn TM, Lewis OT, Novotny V, Kitching RL, Maunsell SC (2020) The role of evolution in shaping ecological networks. Trends Ecol Evol 35:454-466.
Shurin JB, Borer ET, Seabloom EW, Anderson K, Blanchette CA, Broitman B, Cooper SD, Halpern BS (2002) A cross-ecosystem comparison of the strength of trophic cascades. Ecol Lett 5:785-791.
Simon HA (1969) The Sciences of the Artificial. MIT Press.
Strayer DL, Power ME, Fagan WF, Pickett ST, Belnap J (2003) A classification of ecological boundaries. BioScience 53:723-729.
Stuart Chapin III F, Zavaleta ES, Eviner VT, Naylor RL, Vitousek PM, Reynolds HL, Hooper DU, Lavorel S, Sala OE, Hobbie SE., Mac MC, Díaz S (2000) Consequences of changing biodiversity. Nature 405:234-242.
Tansley AG (1935). The use and abuse of vegetational concepts and terms. Ecology 16: 284-307.
Thompson RM, Brose U, Dunne JA, Hall Jr RO, Hladyz S, Kitching RL, Martínez ND, Rantala H, Romanuk T N, Stouffer DB, Tylianakis JM (2012) Food webs: reconciling the structure and function of biodiversity. Trends Ecol Evol 27:689-697.
Trojan P (1984) Ecosystem Homeostasis. Netherlands: Springer.
Yarrow MM, Salthe SN (2008) Ecological boundaries in the context of hierarchy theory. BioSystems 92:233-244.
Wang S, Loreau M (2014) Ecosystem stability in space: α, β and γ variability. Ecol Lett 17:891-901.
Weber MG, Wagner CE, Best RJ, Harmon LJ, Mathews B (2017) Evolution in a community context: on integrating ecological interactions and macroevolution. Trends Ecol Evol 32:291-304.
Williams TA, Cox CJ, Foster PG, Szöllosi GJ, Embley TM (2020) Phylogenomics provides robust support for a two-domains tree of life. Nat Ecol Evol 4:138–147.
Woese CR, Kandler O, Wheelis ML (1990) Towards a natural system of organisms: proposal for the domains Archaea, Bacteria, and Eukarya. Proc Natl Acad Sci 87:4576-4579.
Zak DR, Blackwood CB, Waldrop MP (2006) A molecular dawn for biogeochemistry. Trends Ecol Evol 21:288-295.
Zektser I, Marker B, Ridgeway J, Rogachevskaya L, Vartanyan G (2006) Geology and Ecosystems. Springer Nature

Figure captions:

Figure 1. Conceptual illustration of the ecosystem. The ecosystem is graphically represented as a triangle in which the four worlds (AW, EW, EnW, PW) are permanently interacting with each other in a dynamic equilibrium. The entire ecosystem is powered primarily by the sunlight and is influenced by the environment which is subject to physical and geological forces. The generation of heat and waste resulting from ecosystem activity produces an overall increase in entropy of the universe. Discontinuous line represents the openness of the ecosystem. Double-headed arrows represent the interactions between different worlds. The curved double-headed arrows represent the interactions that take place within each world.

Figure 2. Representation of the biosphere. We can consider our planet as a gigantic ecosystem made up of the sum of large ecosystems (deserts, seas, forests, etc.), which are in turn made up of smaller ecosystems. All these ecosystems are

 doi:10.20944/preprints202202.0202.v1

not isolated or independent of each other, but their boundaries are permeable to interactions with neighboring ecosystems or with the larger ecosystem.

Figure 3. The tree of ecosystems and worlds. A tree of life is shown in which the ecosystem is the core from which the three living worlds emerge.

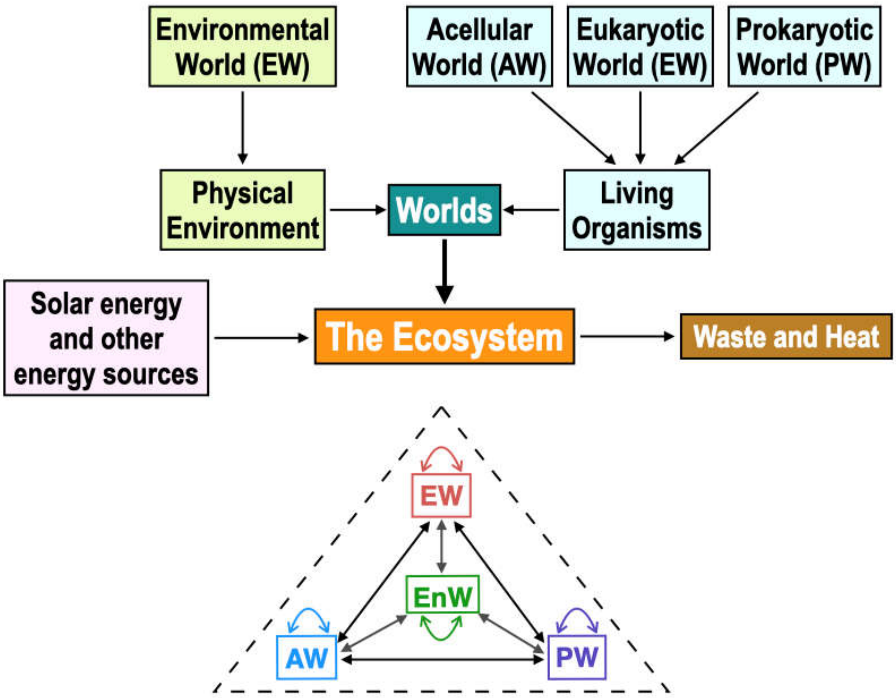

Figure 1.

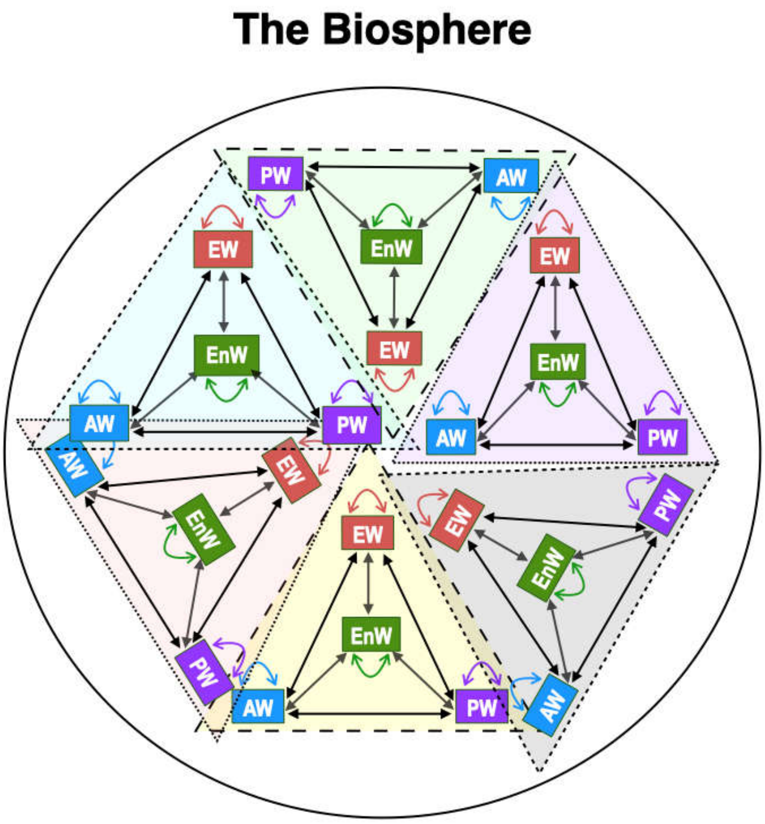

Figure 2.

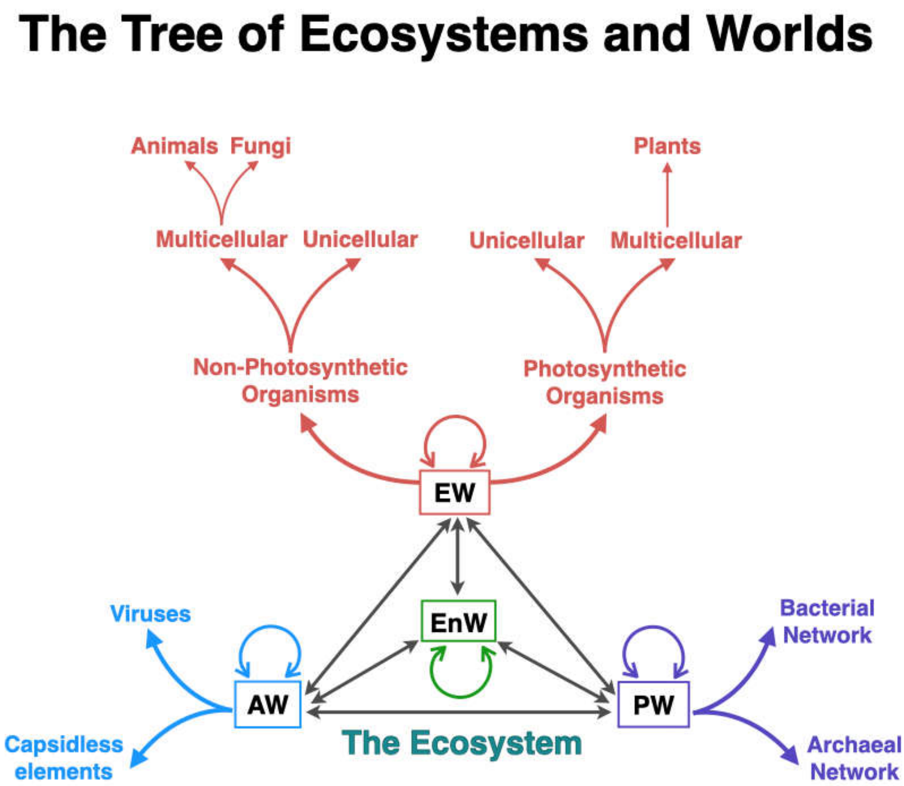

Figure 3. .