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Astroecology: bridging the gap between ecology and astrobiology

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Abstract

Although astrobiology studies how life functions and evolves, ecology is still largely overlooked in astrobiology research. Here we present an argument for astroecology, a merger of ecology and astrobiology, a self-aware scientific endeavour. Ecology is rarely mentioned in influential documents like the NASA Astrobiology Strategy (2015), and terms such as 'niche' can end up being used in a less precise fashion. As ecology deals with sequential levels of organization, we suggest astrobiologically-relevant problems for each of these levels. Organismal ecology provides ecological niche modelling, which can aid in evaluating the probability that Earth-like life would survive in extraterrestrial environments. Population ecology provides a gamut of models on the consequences of dispersal, and if lithopanspermia can be validated as a form of space dispersal for life, then metabiospheres and similar astrobiological models could be developed to understand such complex structure and dynamics. From community ecology, the discussion of habitability should include the concept of true vacant habitats (a misnomer, perhaps better called 'will-dwells') and contributions from the blossoming field of microbial ecology. Understanding ecosystems by focusing on abiotic properties is also key to extrapolating from analogue environments on Earth to extraterrestrial ones. Energy sources and their distribution are relevant for ecological gradients, such as the biodiversity latitudinal gradient – would tropics be species-rich in other inhabited planets? Finally, biosphere ecology deals with integration and feedback between living and non-living systems, which can generate stabilized near-optimal planetary conditions (Gaia); but would this work for other inhabited planets? Are there 'strong' (like Earth) and 'weak' (perhaps like Mars) biospheres? We hope to show ecology can contribute relevant ideas to the interdisciplinary field of astrobiology, helping conceptualize further levels of integration. We encourage new partnerships and for astrobiologists to take ecology into account when studying the origin, evolution and distribution of life in the universe.

Contents

Introduction

'Astrobiology is the study of the origin, evolution, and distribution of life in the universe' – this definition has existed since NASA rebranded its previous 'exobiology' programmes under the umbrella of 'astrobiology' (DeVincenzi, 1984), and it helps us understand that astrobiology is not only limited to the 'science that looks for life on other planets'. Expanding the understanding of how life on Earth functions and evolves is also an important goal of astrobiology that can be harnessed with the help of any area of biology. In that sense, astrobiology draws from various branches of biology, some still full of unrealized potential. We believe that this is the case for ecology, which seems to have been overlooked in astrobiology research so far. Ecology is seemingly restricted to planet Earth, where we have evidence life exists, but it can and should surely go beyond. The extension of traditional ecology into the broader concept of 'astroecology' (as proposed by Mendonça, 2014) represents a great possibility for theoretical advances in both areas it encompasses. In this review, we aim to present an argument for astroecology, a merger of ecology and astrobiology that could be useful and meaningful, as well as a self-aware scientific endeavour.

For defining ecology, we agree with Begon and Townsend (2021) when they state that '*at the heart of ecology lies the relationship between organisms and their environments*', which is a clear recognition of ecology's first definition (Haeckel, 1866). Ecology consists of three main approaches (Krebs, 2014): a descriptive approach, to count and characterize particular aspects of organisms – or groups of organisms – in our world; a functional approach, to understand how complex systems involving life work the way they work; and an evolutionary approach, focusing on studying why the dynamics of life work the way they work through both current and deep time. Each of these can provide insights into the ways that life could originate, occur and thrive in different terrestrial or extraterrestrial environments. The wide range of scales in which ecology can operate includes organisms, populations, communities, ecosystems and the biosphere (Begon, Howarth and Townsend, 2014). At a first glance, we can state that organismal ecology already contributes to astrobiology with concepts such as habitat and niche, which are used by astrobiologists to speculate about planetary habitability and the possible distribution of extraterrestrial biota. At scales between organisms (lowest ecological scale) and the biosphere (highest assumed scale), the intermediate levels of organization in ecology (populations, communities and ecosystems) have been very rarely explored in astrobiology, even though they form a large proportion of current ecological research. Finally, the ecology of the biosphere seeks to deepen our understanding of the limits to planetary homoeostasis (Lovelock, 2003), and perhaps this is where an intersection with astrobiology more clearly lies. This ecological vision of astrobiology could result in innovative ideas and may represent an important step forward to inspire researchers to address unsolved or new questions.

Here, we seek to explore how astrobiologists employ ecological ideas, review the extent of previous contributions by ecologists to astrobiology, and develop a framework for advancing towards the unification of ecological and astrobiological ideas and concepts by exploring the whole span of ecological levels from organisms to the biosphere, with the intent of identifying questions relevant to astrobiology.

The employment of ecology in astrobiology

How much is ecology employed in astrobiology? To diagnose and quantify the contribution of ecology to astrobiology in a more objective way, we looked for the presence – or absence – of ecological concepts and ideas in the *NASA Astrobiology Strategy* (Hays, 2015), which is widely cited and discussed as a framework for prioritizing research in astrobiology. It mentions six major research topics in astrobiology: 1. Identifying abiotic sources of organic compounds; 2. Synthesis and function of macromolecules in the origin of life; 3. Early life and increasing complexity; 4. Co-evolution of life and the physical environment; 5. Identifying, exploring, and characterizing environments for habitability and biosignatures; and 6. Constructing habitable worlds. In the approximately 165 pages of the text, the word 'ecology' appears only once (p. 87). The word 'ecological' is seen more often: 28 times.

The first topic to mention ecology is the third one: '*Early life and increasing complexity*'. Here, it is mentioned that the drivers of evolution are genetic and ecological mechanisms, which include the evolution of cooperation and symbiosis (both ecological interactions, p. 39, 40). Predation and competition are also mentioned as interactions that, being selective pressures, can lead to evolution (p. 55). Ecosystem engineering, which happens when communities produce environmental modifications, is cited in the text as a mechanism that affects the evolution of the 'engineer' species and the species that live nearby. Here, ecology is mentioned because of its evolutionary explanations. However, ecology is surely more than just evolutionary biology. Ecosystem engineering, for example, could be discussed in terms of organismal adaptation to extreme environments, which could possibly increase habitability parameters as one kind of organism could facilitate the occurrence of other kinds. More complex approaches could be developed to build on these ideas as we start to look at ecological phenomena not only for their evolutionary implications but also for their functional ones.

Another relevant topic is 'Constructing Habitable Worlds'. While the important concept of ecological niche (p. 136) is presented here, it seems to be misused relative to its ecological perspective. The Roadmap points to 'What Are the Processes on Other Types of Planets That Could Create Habitable Niches?' (p. 136) as being a key research question for astrobiology. It is worth noting that the term 'habitable niches' appears redundant. There is no such thing as an uninhabitable niche because niches are intrinsically related to the existence of life. Begon and Townsend (2021) noticed the common misunderstanding in the use of the term and explained that '(…) where an organism lives is its habitat. A niche is not a place but an idea: a summary of the organism's tolerances and requirements' (p. 33). However, in the glossary of the NASA Astrobiology Strategy (Hays, 2015), ecological niche (p. 168) and habitable niche (p. 171) share the same definition: '*the space in which an organism or community lives, uses resources, competes with other life forms, and has other behaviors related to the specific aspects of that environment*'. Ecological niche was a synonym of habitat when it was first used by Grinnell (1917), but in the following hundred years, the concept of niche has evolved as distinct from the concept of habitat (Sales *et al*., 2021). This is not a profound mistake, nor does it come to the detriment of a relevant discussion; however, the misuse of an ecological term could be easily fixed with stronger collaborations between astrobiologists and ecologists, probably also leading to new insights.

Use of the term 'astroecology' and its correlates in the scientific literature has been scant, which sometimes attempts to define a crossroads discipline between astrobiology and ecology, as in here, but otherwise has been used in more specific designations (Table 1). For this review, we see astroecology as a good term for this proposed combination of astrobiology and ecology, which aligns with the definition proposed by Mendonça (2014). Whether this word will be widely used or not is up to the community of scientists who could feel encouraged to work on these themes, although we hope that the ideas presented here resonate with current research trends.

Table 1. *Appearances of the term 'astroecology' and derivatives in the literature and definitions proposed by the authors*

Term	Definition	Reference
Exoecology	The study of the interaction of extraterrestrial organisms with their extraterrestrial environment.	Jones (2001)
Astroecology	Concerns the relations between life and space resources.	Mautner (2002a, 2014)
Astroecology	A new scientific branch mingling ecology and astrobiology.	Mendonça (2014)
Astroecology	An approach to showcase a recent example of an interdisciplinary collaboration.	Buettel *et al*. (2018)
Astroecology	A merger of ecology and astrobiology as a self-aware scientific endeavour.	This paper

The definitions of exoecology by Jones (2001) and astroecology by Mautner (2002b, 2014) do not need to be discarded but can be encompassed within the scope of the definition proposed here. The first one restricts the study to outer space and does not take terrestrial life into account, while the second one includes terrestrial life but primarily focuses on space resources. Both ideas can be valuable and provide useful insights for astroecology research since they do not disagree with the broader concept presented in this paper. Meanwhile, the concept of astro-ecology by Buettel *et al.* (2018) is part of an essay on the capacity to use methodological interdisciplinarity to study well-defined questions about complex systems such as forests and galaxies. In that case, ecologists adapted an astronomical model to analyse fallen trees in forest plots. The merger of ecology and astronomy can result in relevant theoretical modelling (see also Keddy, 1994) but does not present the panoramic view that is being advocated here, since ecology deals primarily with biological systems. Given that astrobiology is already an interdisciplinary science that addresses numerous questions related to life itself, ecology can take a more prominent role in this field as described in the following sections.

Can ecology go beyond Earth? – presenting astroecological levels

As explained above, ecology can be divided into five main hierarchical levels of study: organisms, populations, communities, ecosystems and the biosphere. It is important to note that division does not mean lack of connection, since the functioning of each level depends crucially on the functioning of the level below it; however, each level has its own emergent properties and is investigated using different methodologies (Begon, Howarth and Townsend, 2014). The following subsections suggest how the five (or even more) levels of ecology can be studied under the lens of astrobiology.

Organisms

In organismal ecology, the focus is on how individuals are affected by their environment and how they respond to it, from a basis of physiology and behaviour (Begon, Howarth, and Townsend, 2014). It can be a powerful tool in conservation studies for understanding organismal responses to environmental changes (Bozinovic and Pörtner, 2015; Lyons *et al.*, 2019), especially while trying to predict responses to global climate change.

The adaptations of many extremophile organisms for surviving in hot, cold, salty, acid and metal-rich extreme environments have been extensively studied in terms of their physiological ecology (Shu and Huang, 2022). Studying the physiology of such organisms helps astrobiologists hypothesize about the origin and maintenance/presence of life on other planetary bodies. The relationships between Earth-based organisms and their ability to survive in extraterrestrial environments has also been the subject of research. For instance, Beblo-Vranesevic *et al.* (2022) studied the survival of facultative anaerobic microorganisms on Martian soil, while Mautner (2002b) investigated mesophile and cold-tolerant algae on meteorite minerals, both falling within the scope of geomicrobiology (Cockell, 2010). Recent experiments have demonstrated that plants can grow in lunar regolith, which expands the range of life forms that can be considered in such environments (Paul, Elardo and Ferl, 2022).

Another way that organismal ecological understanding can contribute to answering astrobiological questions draws upon recent suggestions on the use of ecological scaling laws, sometimes called metabolic ecology (Brown *et al.*, 2004). Kempes *et al.* (2021) explored size distributions of cells of known organisms to derive stoichiometric relationships expected of life, which relates to biosignatures as well, for example: (1) stoichiometry of living things should differ in specific ways from non-living systems (given particle sizes); (2) specific particle size distribution in itself is expected of living systems as well (a power law). One implication is that studying cell size as a functional trait in extreme and/or extraterrestrial environments could perhaps suggest ecological limits to cell size. This possibility was shown in the purported fossils retrieved from Martian meteorite ALH84001 that were supposedly too small to have been living (McKay *et al.*, 1996), and such limits are worth considering in the context of proposed sample studies from Mars and icy moons.

In organismal ecology, the concept of ecological niche is fundamental since it is closely related to the particularities of a given organism (Kearney, 2006). Ecological niche modelling (ENM), which is sometimes (and more correctly) referred to as species distribution modelling or habitat modelling (Soberón and Nakamura, 2009), involves estimating the geographic distribution of organisms and then identifying suitable habitats for them by matching their environmental requirements with environmental condition maps. The insights provided by ENM not only enhance our understanding of Earth-based ecology, such as the implications of climate change for species distribution dynamics, but also help us evaluate the probability of Earth-like life to survive in extraterrestrial environments. For example, *Bioclim*, an envelope-based model, was used to investigate the possibility of mapping methanogen niches into Enceladus plumes, and the results suggest that this is indeed possible (Tenelanda-Osorio *et al.*, 2021). Further, if we can model the ecological niches occupied by extinct organisms, such as ancient bacterial and archaeal biota, from paleoclimatic-derived data, this would expand the scope of habitats that we know could be occupied by organisms in general, and consequently, expand the roster of potential extraterrestrial habitats as well.

Populations

A population is a group of individuals belonging to the same species that are found in the same defined space and time (Krebs, 2014). Population ecology is concerned with understanding the underlying reasons for the distribution and abundance of organisms and making predictions about them (Krebs, 2015). This discipline has made significant advances in mathematical modelling and statistical methods. Given the expectation that theoretical principles of population ecology remain constant across different environments (Wilkinson, 2003), we certainly have grounds to extend its models to astrobiology.

One of the most studied concepts in population ecology is the spatial dynamics of organisms as they disperse across heterogeneous environments to form metapopulations and metacommunities. A metapopulation is a population of populations (Levins, 1969), and metapopulation ecology studies 'the dynamic consequences of migration among local populations and the conditions of regional persistence of species with unstable local populations' (Hanski, 1998). This concept has parallels in astrobiology, particularly with the lithopanspermia hypothesis, which suggests that life can be transferred between inhabitable solar system bodies via solid material ejected from planetary surfaces (Cockell et al., 2007). Experiments have shown that organisms can survive the harsh conditions of space and re-enter Earth's atmosphere (Slobodkin *et al.*, 2015). Given that interplanetary organismal dispersal is possible, albeit improbable, typical population ecological processes involving dispersal may have this foothold in space as well as on Earth. In the basic model of a metapopulation (Levins, 1970), a population is divided into subpopulations distributed among habitable patches. With this parallel, the dispersal of organisms between patches here on Earth could be a system similar to the dispersal of organisms between planets; as a set of populations linked by dispersion is called a metapopulation, a set of biospheres linked by dispersion would be called a metabiosphere (Mendonça, 2014). In this sense, the concept of a metabiosphere is an extension of a well-established Earth-bound ecological concept applied to the context of the cosmos. Example of indirect evidence for the concept of a metabiosphere include the discovery of Earth-like life (e.g. in biochemical composition or genetic code) on Mars, Europa or Enceladus (which could mean common ancestry rather than independent origins of life) or the detection of biosignatures on sets of neighbouring exoplanets of other planetary systems (e.g. TRAPPIST-1 system). Table 2 presents some implications of extrapolating the distribution and dispersal of organisms to space.

Population ecology has already been applied to astrobiology, but there is still a vast landscape to explore. For instance, Simpson's (1940) 'sweepstake' dispersal route proposed an indeterministic migration process that happens randomly and cannot be correlated with other events in space and time. Although this model was deemed inadequate to explain the colonization of Madagascar by mammals (Stankiewicz *et al.*, 2006), the probability values derived from Simpson's equations could still be significant when applied to the context of random meteor bombardments over billions of years.

Table 2. *Important concepts for the study of organismal dispersal, their usual definition and how they fit into astrobiology. The last column specifies the sources for the origin of the ideas as applied to astrobiology*

Concept	Usual definition	Why is this astroecology?	Source of idea
Patch	A surface area differing from its surroundings in nature or appearance that allows a species to occur (Wiens, 1976).	Planets hosting life can be seen as occupied patches. Unoccupied patches refer to planets that are habitable, meaning they have conditions suitable for life, but currently lack any inhabitants. (Cockell *et al.*, 2012).	Mendonça (2014)
Matrix	The 'non-habitat', which is inhospitable to some existing species in a region. Patches are surrounded by matrices.	Outer space itself can be seen as a matrix.	Mendonça (2014)
Dispersal filters	Processes that hamper the dispersal of organisms.	Dispersal filters in space are atmospheric exit, interplanetary transfer (…), atmospheric entry and finally inoculation on the new planetary surface.	Cockell et al. (2007)

Another idea is the suggestion by Ginsburg, Lingam and Loeb (2018) that panspermia could happen on galactic scales, and extremophiles that survive the journey could seed the entire galaxy with life, similar to the island-continent metapopulation models. There are still many other ecological models that could be revisited with new astrobiology perspectives in mind (Table 3).

Biological communities

Theoretically, biological communities include all populations of species that occur in a defined location and time. However, given the difficulties in studying all organisms in an area, ecologists frequently research partial communities based on taxonomic or functional groupings (Begon and Townsend, 2021). Also crucial for community ecology are the myriad interactions among individuals and species, such as competition, mutualism, etc. Community ecology is often used in applied ecology, for example, dealing with ecological restoration, which may be relevant for the debate on terraforming other planets (Smith, 2022). Ecological succession theories have been widely used in restoration research (Wainwright *et al.*, 2017), but they can also be examined in the context of astrobiology (Graham, 2004). Another important subject that relies on community ecology in most instances is microbial ecology, and technical improvements may reveal new understandings for astrobiology (Walker and Pace, 2007).

Ecological succession, which describes the sequence of communities from colonization to the climax community of a given ecosystem (Clements, 1916), is a central concept in ecology and an important characteristic of communities (Krebs, 2014). The facilitation model of primary succession, in which pioneer organisms help the establishment of those arriving later in sterile areas, may have relevance for astrobiology. Fiedler and Mendonça (2023) explored this concept in terms of propagule arrival on planets through lithopanspermia events, which led us to ask new questions: what if ejecta arrive with live organisms repeatedly throughout the history of a planet? Can invasion ecology help us understand this process? Why do we not find this pattern on Earth? And here we can propose an extension to Fermi's

Table 3. *Population ecology models, suggested applications to astrobiology and an example of current usage of the model (for Earth-based ecology)*

Ecological model	Application to astrobiology	Origin
Basic metapopulation model	Biospheres linked by dispersal create metabiospheres (Mendonça, 2014)	Levins (1970)
Source-sink	Organisms from terrestrial planets with favourable conditions (sources) dispersing to terrestrial planets with less favourable conditions (sinks) (Mendonça, 2014)	Gotelli (1991)
Seed bank	Persisting ejecta in space distributing propagules across time (Mendonça, 2014)	Gotelli (2008)
Predator-prey competition	Proposed as a solution to the Fermi paradox (Forgan, 2019)	Lotka-Volterra equations (Lotka, 1925 and Volterra, 1926)
Rescue effect	Recolonization can protect a biosphere from reaching extinction (Mendonça, 2014)	Brown and Kodric-Brown (1977)
Infection dynamics spatial patterns	Modelling hypothetical bio-dispersal (Kovačević, 2022)	Kermack and McKendrick (1927)
Island-continent	A single inhabited planet (continent) seeding other habitable planets (islands) (Mendonça, 2014) or the Galactic Center as a life seeder (Ginsburg, Lingam and Loeb 2018)	Gotelli (1991)
Sweepstake dispersal route	Calculating probabilities for intergalactic dispersal 'by chance' (this review)	Simpson (1940)

paradox: if life is common in the universe, then why did it not arrive here multiple times throughout history from space rocks?

When discussing panspermia, it is important to remember that life might not get established on all habitable-yet-uninhabited planets, resulting in what is known as vacant habitats: places where organisms could thrive but in which they are simply not there now (Cockell, 2011). Vacant habitats can also exist on Earth (Cockell, 2011). True vacant 'habitats', without any kind of living being present, are not even habitats by definition, but 'will-dwells', where life meets a limit that not even 4.5 billion years of opportunity for the evolution of terrestrial biota were apparently able to overcome. Further research is necessary to provide convincing explanations for the existence and persistence of 'will-dwells' on Earth.

Considering the possibility of extraterrestrial life (or Earth-based life that would be able to live elsewhere), we usually assume that life will be microscopic; this is why astrobiologists should also utilize concepts from microbial ecology (as many already are). Microbial ecology focuses on the same topics as community ecology in general: abundance, diversity and distribution of microorganisms, their specific interactions, and the effect they have on ecosystems (Gray and Head, 2008; Ladau and Eloe-Fadrosh, 2019). Microbial communities appear to have emergent properties (Prosser and Martiny, 2020), and despite ongoing challenges, the rules governing their assembly are gradually being unveiled due to advances in research areas such as molecular biology and bioinformatics (Mony *et al.*, 2020). The study of microbial communities in extreme environments and extraterrestrial analogues within a microbial ecology framework can also deepen the habitability discussion and potentially enhance astrobiology research protocols (Cockell *et al.*, 2019; Meslier and DiRuggiero, 2019). These concepts are relevant for exploring expected microbial communities like those on Mars subsurface brines, on ocean worlds like Europa or Enceladus or even on the clouds of Venus.

Ecosystems

Ecosystems reveal the relationship between ecological communities and their environment, and ecosystem ecology is concerned with understanding the functioning of the relevant portions of Earth in terms of energy and matter flow (Begon and Townsend, 2021). Some ecosystem principles can be seen as universal, as Jones (2001) has stated: '*Ecology exists wherever there is an energy source and living things can employ some method to capture, store, and use the available energy*'. Dynamic systems with environmental interactions and material cycling are not restricted to Earth, and so ecosystem ecology might help astrobiologists identify and characterize extraterrestrial sites where life could occur as proper ecosystems.

Some locations on Earth are often considered analogues for extraterrestrial environments and thus are used as field sites for exploring new organisms, studying habitability, validating biosignatures and understanding possible past life on our planet to decipher the signatures of extinct life (Preston and Dartnell, 2014). Examples of analogue environments where extremophiles can be found would be terrestrial caves and desert soils (Coleine and Delgado-Baquerizo, 2022). Extreme environments may also be used to test ecological theories that address limits and absolute restrictions, such as specific resource availability, temperature and water availability, that are not typically found in conventional ecological studies (for a modelling of an extreme ecosystem, see Fisher and Schulze-Makuch, 2013). These studies can reveal the role of functional traits, such as adaptations to extreme conditions, and ecological interactions, such as mutualisms and facilitation, in enabling organismal survival and can also aid in understanding the reasons underlying 'ecological extinctions' (Warren-Rhodes *et al.*, 2022).

Many questions discussed in ecosystem ecology, like habitability and biogeochemical cycles, are derived from global/biosphere ecology as well as ecosystem ecology, an unsurprising fact since Earth itself can be considered an ecosystem (Krebs, 2014). Taking habitability as an example, we can try and classify planetary objects as either habitable or not (global ecology), but this approach comes from the study of their specific environments (or possible exoecosystems). Nevertheless, the question remains: can a single inhabited ecosystem on a planet suffice to deem the entire planet as

habitable? As habitable ecosystems emerge, does the habitability of the planet 'increase', being thus quantifiable, and justifying using terms such as 'superhabitable' (Heller and Armstrong, 2014)? Studies of habitability began by examining current Earth ecosystems, but as habitability research widens its scope and scale, perhaps ecology can be instrumental in developing more sophisticated approaches.

Ecosystem ecology is also important in the uncovering of ecological patterns. One of the most significant global patterns is the latitudinal gradient in biodiversity (LGB): there is more biodiversity (e.g. taxonomic, functional and phylogenetic) at low latitudes and less at high latitudes (Chown and Gaston, 2000). Although the LGB is global and has been present throughout geological eras, its causative factors are still explained by local environmental and population hypotheses, not by global feedback (Willig *et al.*, 2003). Recent ideas suggest the availability of energy (such as sunlight on Earth), resources (such as water) and environmental conditions (such as temperature) are the key factors driving higher productivity in tropical regions, which leads to faster ecological and evolutionary processes such as speciation and extinction (Mittelbach *et al.*, 2007). Spatial arrangements also play a role, with south and north tropical areas being contiguous while temperate zones are separated by the tropical regions (Rosenzweig, 1995).

Would this be relevant for other kinds of biospheres (Brodie and Mannion, 2023), such as icy worlds with underground oceans, in which solar energy may not be the main source for life? Would energy show any relevant spatial pattern there, or even on Mars, if life there is buried deep and based on chemolithotrophy? Superhabitable planets could sustain a tropical zone larger than Earth today (Schulze-Makuch *et al.*, 2020), but would that mean we should still expect an LGB on those planets? Or would there be stronger unknown factors affecting the distribution of life? Once more, this is a relevant question for ecology, which ultimately suffers from the statistical limit of having a single data point to study. And finally, would we expect a sharp biodiversity gradient along the 'terminator' region of tidally-locked planets? This is the circular band dividing a hemisphere in permanent daylight from another in permanent night in the case where the planet is in synchronous rotation around its star, expected of M-dwarfs – a possible habitable region where available solar energy would change drastically across a sharp gradient (e.g. Wandel, 2018; Lobo *et al.*, 2023).

Another significant pattern in nature is the tight association between high biodiversity and mountains. The geology and climate systems of mountain regions provide an environment where many biogeographic processes, such as speciation, diversification, adaptive radiation and dispersal, can occur (Rahbek *et al.*, 2019a). Although mountains make up only 25% of Earth's landmass, their regions host approximately 87% of the world's species of birds, amphibians and mammals; understanding the underlying mechanisms remains challenging (Rahbek *et al.*, 2019b). Considering mountains as a 'generator and reservoir of biodiversity' (Perrigo, Hoorn and Antonelli, 2019) could raise new astrobiologically relevant questions. Observing mountains may reveal internal (buildup of lava on Mars) or external (mounds or ridges created by asteroid impacts) planetary processes (McTier and Kipping, 2018). Such observations may also depend on the presence of plate tectonics, a geological feature on Earth that may be crucially linked to the maintenance of habitability (Korenaga, 2012). As discussions about exoplanet topography are beginning (Landais, Schmidt and Lovejoy, 2019) and selenography techniques are advanced, we can broaden such considerations by questioning the ecological implications of having mountains on an exoplanet or moon. Should we expect more forms of life to be found on planetary objects with mountains? Should a higher percentage of mountains be a relevant factor when we classify planets as superhabitable (Schulze-Makuch *et al.*, 2020), or is this an Earth-specific pattern due to the relatively small percentage of mountain regions on Earth today? Are there other geologic features that could be more common on planets other than Earth, which could lead to such patterns, but because of other factors? Will the discipline of mountain microorganismal biodiversity, which emerged only a decade ago but is evolving rapidly (Wang *et al.*, 2022), reveal relevant astrobiological insights?

Biosphere

The biosphere is Earth's entire ecosystem (Krebs, 2014), where living organisms can survive and reproduce. Global ecology as a field began with Lovelock's Gaia Hypothesis as a central concept (2000) but

has widened its scope as measurements at both local and global scales became easier, more common and more detailed (Schimel and Schneider, 2019). The Gaia Hypothesis remains controversial; however, it helped us conceptualize Earth as a nearly-closed planetary system that maintained its habitability despite all disturbances across deep time (Stolz, 2017). Since the number of planetary objects that can be studied *in situ* is very small compared to the number of known planetary objects, most of what we know about planets beyond Earth is based on limited observations at a distance. Given such restrictions, developing a systems-based approach towards understanding exoplanets and other solar system bodies falls under the scope of a biosphere-level ecology as well. Studying the integration among subsystems (geological, atmospheric, hydrological and cryological) can help determine whether an ecological subsystem could also be present, which could serve as a definition of a biosignature from a different point of view.

We suggest the most relevant astrobiology theme for contributions from biosphere ecology is habitability. This term has been defined astronomically in some detail in the recent past (Seager, 2013), but the concept continues to face conceptual changes as new ideas and research respond to (1) our growing understanding of the limits for life on Earth (Yung *et al.*, 2018); (2) the variety of environments found in our solar system (e.g. icy moon oceans; Paganini *et al.*, 2019); and (3) the results of our searches for habitable exoplanets and the diversity they reveal (Tsiaras *et al.*, 2018). The habitable zone (HZ), within which liquid water could exist on the surface of a planet, is determined by astronomical variables such as star size and temperature. But the primary reason for this definition as it stands is operational: the HZ is a place in which we can search for evidence of life using space telescopes. There are certainly ideas for how planets outside the HZ might be habitable, but the difficulty is also identifying ways that evidence of such life could be detected. For example, a subsurface biota may have little or no interaction with the atmosphere (Horne *et al.*, 2022), so detecting these life forms, especially on an exoplanet, may not be possible. Further extensions of the concept of the HZ may have limited applications when attempting to characterize exoplanets (Nicholson *et al.*, 2018), but such an approach does not necessarily consider the concept of habitability from an ecological perspective.

In a thought-provoking review, Méndez *et al.* (2021) highlighted the lack of integration between different concepts of habitability in astrobiology and advocated for the incorporation of ecological methodologies, such as Habitability Suitability Models. While astrobiologists have been using various criteria for habitability, ecologists have well-developed and established frameworks for modelling habitable environments. As the authors postulated, 'ecology methods are more capable than our limited planetary and astronomical data allow, but they also provide the basic language and framework to connect Earth and astrobiology science for decades to come'. We fully support this viewpoint and aim to underscore its significance in this article.

Biosphere ecology has yet to determine any limits to planetary homoeostasis produced by life, but for astrobiology, understanding such habitability limits is a crucial problem. If planetary homoeostasis is difficult to achieve and thus rare, then habitability is lower than could be expected (Chopra and Lineweaver, 2016). Life in the universe may be common, but how common is planetary homoeostasis achieved by biological processes (in other words, Gaian biospheres)? This raises two major problems for astrobiology: the ease with which life arises and the likelihood of persistent biospheres evolving, the latter of which is not often discussed. Ecology is thus an important factor: the extent to which biospheres on other planets and moons would be able to alter and maintain abiotic conditions adequate for life is a crucial question that astrobiology returns to biosphere ecology. Many abiotic factors related to habitability, like the age of rocky exoplanets (Unterborn *et al.*, 2022), ice surface coverage (Wilhelm *et al.*, 2022) or the presence of a satellite (Nakajima *et al.*, 2022), have been examined. However, taking a Gaian approach (e.g. the enhancing/optimizing Gaia model; Kleidon, 2002) can lead to somewhat different, biological-centred answers compared to the ones that rely uniquely on chemistry and physics (Nicholson *et al.*, 2018). We can begin right now to try and deepen theoretical explorations using biosphere ecology since some ecological ideas can bear fruit in the light of astrobiological phenomena.

As above, we finish by highlighting a set of examples of ecological biosphere-level questions related to current astrobiological problems. If life is present on Mars, then why is its atmosphere not clearly

chemically unbalanced and indicative of a biosphere present (were Lovelock & Margulis right in 1974)? Is the Martian methane question (e.g. Lefèvre, 2019) an answer to this? Is it possible for life to arise and not strongly affect its environment globally – so could there be 'weak biospheres' (potentially like Mars) and 'strong biospheres' (like Earth)? Alternatively, is life on Mars now the very last remnant of life on a dying planet, in which cosmic and areological (Martian geology) factors impeded biosphere maintenance, with perhaps no more remaining living biomass left to significantly affect planetary processes (a form of swansong biosphere, O'Malley-James *et al.*, 2013)?

Conceptualizing further levels of integration

The biosphere is accepted as the uppermost level to which ecology is relevant (Begon, Howarth, and Townsend, 2014) and involves all other ecological levels. However, the search for life elsewhere in our solar system suggests a direct question from astrobiology to ecology, which no ecologist seems to have addressed, as far as we know: are biospheres completely isolated? If panspermia is in any form a plausible process (lithopanspermia, at least, is seriously discussed but only likely depending on a series of factors; Nicholson, 2009), then biotas from life-bearing planets might interact by a form of, ecologically speaking, interbiospheric dispersal. So far, we have already mentioned a series of ideas related to this one, and we could further include efforts at space settlement/colonization, such as plans to send humans (and their microbiomes) to Mars, mining asteroids, etc – which could be considered a form of directed panspermia (c.f., Crick and Orgel, 1973). One approach towards understanding this ecological process is to study and describe patterns resulting from similar systems at different scales, and the metabiosphere model (Mendonça, 2014) is one such proposition, although not the only one.

An alternative take on this broad and important question is: if biospheres are numerous and they can interact, does this represent a further, sixth level of understanding for ecology? Although this has been mentioned briefly in the context of metabiospheres (Mendonça, 2014), the concept has never been seriously discussed. And even then, the metabiosphere model appears to be more adequate for describing biospheres that share a common origin: metapopulations arise when the same population is distributed among different patches, and metabiospheres arise when the 'same biosphere' (i. e. common ancestry) is distributed among different planetary bodies. Most level definitions in ecology involve describable, independent and repeatable units that act on each other – that is, interact – such as organisms interacting, which leads to population processes if these units belong to a reproductive lineage or community processes if populations of different species are interacting (Krebs, 2014). If biospheres that are phylogenetically distinct do interact, what would we call this astrobiological level of ecology, and at what scales is it relevant? Is the concept of metabiospheres appropriate to also describe this process? How would astronomical distances factor into this kind of system? Interacting biospheres within a given planetary system could lead to different dynamics than if interstellar dispersal is possible (e.g. in star-forming clusters; Adams and Spergel, 2005) – could this be different enough to suggest a seventh level for ecology? This discussion is even more relevant given the Fermi paradox, which is an ecological hypothesis when taken from this point of view. Colonization (in the ecological sense, along with the cultural sense) by an intelligent extraterrestrial biota could be expected to be rather common but has not been detected so far in our own biosphere, at least.

Five (or more) levels of astroecology: a summary

We hope to have shown that ecology can contribute relevant ideas to the interdisciplinary field of astrobiology. The possibilities of research presented here are still incipient; there is much to be done, and certainly more ideas are yet to come. However, we have provided the first steps by recognizing previous work, gaps and opportunities for the future. The theoretical foundations of ecology and its levels (organisms, populations, communities, ecosystems, biospheres and perhaps further) have a lot to offer to astrobiology. Figure 1 summarizes the topics we suggest that could lead to future insight.
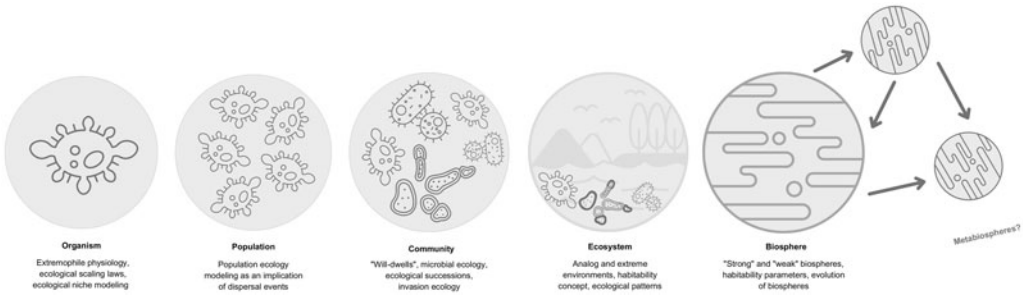
Figure 1. *Hierarchical levels of ecology and study opportunities they might present for a self-aware astroecology.*
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We hope this paper will encourage astrobiologists to take ecology consciously into account when studying the origin, evolution and distribution of life in the universe. New partnerships with ecologists, both in individual (astrobiologists and ecologists conducting studies together) and collective (astrobiology organizations working with ecology organizations) ways, should be established as the astrobiology community integrates one more discipline into this huge interdisciplinary field. Theoretical research in astroecology is just beginning, but it is also time for us to put these ideas into practice by conducting experimental astroecology in the laboratory and field campaigns – here on Earth and 'out there'.

If astrobiologists work together with ecologists, then our speculation does not need to appear unbridled, as mutual checks would be put in place. New patterns and processes can be hypothesized, and different paths could open up new ideas if we think about ecological questions in astrobiology. Ecology may seem a little 'too close' for those who study planets that are trillions of kilometres away or farther, but perhaps we should seek new ways to look at Earth while we observe far beyond it.

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