

<https://doi.org/10.7577/formakademisk.3370>

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# Ecosystem Metabolisms and Functions

## An eco-literacy framework and model for designers

### **ABSTRACT**

*The framework and model describe ecosystem functions. Working within and towards systems of production that intend to be truly circular and regenerative necessitates that designers (and other stakeholders) have an increased understanding and intuition of how ecosystems function—an eco-literacy. To this end, the framework is based on foundational metabolisms (producers, consumers and decomposers), and their interactions with each other and ‘nutrient pools’ within their collective environment. The model proposes that ecosystems are fractals of plants and are one collective metabolism. Some ‘ecosystem concepts’ are also developed that can be worked with as they are or used as a base for analogies for those working directly with, or developing frameworks for, integrative systems of production.*

### **Keywords:**

Systemic design, ecological design, biomimetics, circular economy, systems ecology.

### **INTRODUCTION**

As a response to some accumulating issues of our time, including energy, the environment, climate change and food security (Capra & Luisi, 2014); du Plessis’ (2012) ‘regenerative sustainability paradigm’ proposes a transition from the mechanistic to an ecological or living systems worldview, which reconnects ‘human aspirations and activities with the evolution of natural systems—essentially co-evolution’ (Mang & Reed, 2012, p.26). This ultimately ‘means shifting human communities and economic activities back into alignment with life processes’ (Mang & Reed, 2012, p.26). This goal defined by Mang and Reed (2012) is also coherent with the definition of ecological design by Cowan and Van der Ryn (1996, p. 34), which ‘is simply the effective *adaptation* to and *integration with* nature’s process’.

Capra and Luisi (2014, p. 353) advise ‘that the first step in this endeavour must be to understand how nature sustains life’, by comprehending ‘the principles of organisation that ecosystems have evolved to sustain the web of life’. This understanding has become known as ‘ecological literacy’, or ‘eco-literacy’ (Capra, 1996; Capra & Luisi, 2014; Orr, 1992).

To support ecoliteracy in ecodesign (and related fields), a framework has been developed, viewing living systems through organisms different roles or *functions*, based on metabolism and behaviours. This is principally advanced visually with a model, which expresses different patterns of complementary and interdependent relationships, which together, form functioning ecosystems.

The paper begins with an introduction explaining the goals of the framework and models, some definitions of the main terminology, and clarification of the link between these and the goals. The second section outlines some biological and ecological foundations and complementary existing models. The third section describes the ecosystem function (EMF) model, while the fourth section discusses plants as a fractal of an ecosystem, the view of ecosystems as one collective metabolism and a list of proposed ecosystem concepts. Finally, the fifth section ends with what value the framework and model can bring to design and gives some conclusions.

### Key goals

The key goals of the ecosystem framework and models presented in this paper are as follows:

- To support *eco-literacy* for designers (and design educators) and other stakeholders engaged in the design and development of systems of production;
- To be a foundation for analogies and guiding patterns, for developing frameworks and models for integrative human systems of production that are regenerative by design; and
- To present a whole functioning ecosystem with its collective metabolism, including the interaction between its living and non-living elements.

### Frameworks and models

A framework is an entity between a model and a method and ‘is, or contains, a . . . structure or system for the realization of a defined result/goal. Many frameworks comprise one or more models’ (Verbrugge, n.d.). According to Carol Sanford (2016), frameworks also ‘invite the generation of a pattern, in this time and space, rather than follow[ing] a preset pattern’. In this paper, the framework is the view of ecosystems (and to a lesser extent, plants) through the conceptual lens of four foundational forms of metabolism, which are as follows: autotrophs (producers), heterotrophs (consumers), saprotrophs (decomposers) and mixotrophs (mixed); these are considered along with the foundational abiotic (non-living) elements—*nutrient pools* (NPs). This view supports the explicit examination of functionality within ecosystems in terms of how different organisms function in relation to others and their environment and how an ecosystem can function as a whole. The paper ends with some ecosystem concepts that were used for, and emerged from, the development of the models.

A model can be words, images or combinations of the two; however, it is usually in schematic form (Verbrugge, n.d.). Models, as the economist Raworth (2017) suggests, have the potential to ‘stick in the mind’s eye and wordlessly reshape [some part of] our view of the world’ (p. 14), as an image can help determine ‘what we can and cannot see, what we notice and what we ignore, and so shapes all that follows’ (p. 15). In the process, they potentially help ‘overturn [some] deeply held beliefs’ (Raworth, 2017, p. 14); they also ‘show how to replicate an existing pattern’ (Sanford, 2016). Within this framework, the EMF model has been developed (Figure 21), which attempts to potentially reshape how we view living systems by presenting a *functioning* ecosystem model, showing direct and indirect and trophic and non-trophic, functional relationships and *bi-directional* cycles of matter and the flows of energy, as well as living and non-living elements.

### The importance of eco-literacy in design

The intention is that, by supporting eco-literacy, there will be more talk about and understanding of regeneration, and individuals will actively practice ecological design, and will be ‘inclined to care for all living nature’ (Capra, 1996, p.12). If, for example, eco-design students are not taught about and engaged directly with living systems and are only taught topics, such as materials (e.g. material ‘black lists’, biodegradability and certification), the consequences may be that we maintain or simply slow (at best)—or even *worsen* (due to unforeseen consequences)—the predominant paradigm of ecosystem extraction and degradation and division between ourselves and our environment. In parallel, we can miss the abundant and *regenerative* services that living systems provide us, which can be integrated into or replace some of our synthetic and entropic systems.

Capra and Luisi (2014) put forward (from experience) that eco-literacy should not be imparted within a single isolated discipline, but instead, it should involve a central project spread across multiple curricula, including the sciences and the arts, and practice and application in concrete practical projects. Therefore, how this framework and these models are transmitted to different stakeholders is a complete work of potential creativity.

### **A foundation for integrative systems of production and regeneration**

Transforming our prevailing extractive and destructive systems of production into those that are congruent with the *regenerative* systems of Earth presents an existential challenge. Looking to nature for how this can be achieved makes sense, not only because natural systems provide abundant inspiration for designing systems of production but also because congruence necessitates that human production systems align and work with and within natural systems—within the so-called planetary boundaries (Rockström et al., 2009), while also regenerating—supporting ‘an expansion of natural capital’ (Cowan & Van der Ryn, 1996, p. 37; as opposed to purely sustaining it)—after a long legacy of ecosystem and community degradation. At the same time, it is important to ensure current and new activities are also constantly regenerative.

Human systems of production are arguably synthetic ecosystems; within these anthropogenic activities, we can find equivalent analogies (transferable patterns) of producers, consumers, decomposers and mixed groups; our systems of production interact with broadly the same abiotic nutrient pools and energy to build up and break down (and therefore, transform) matter to produce the goods and services we need. Therefore, in a paper that follows this one, the EMF framework and model are used as a foundation in the development of an *integrative systems of production* framework and model (Snow, 2020).

### **One collective metabolism supporting the five kingdoms and ecosystem functions**

Metabolism

is a process of chemical changes in living matter by which energy is provided for taking in new matter, building and repairing cells, collecting and excreting wastes. Metabolism is divided into two parts: *anabolism* and *catabolism*, the buildup and breakdown of body substance or *protoplasm*. (Sahtouris, 2000, p. 77)

By developing the model around Vernadsky’s proposal of the different forms of metabolism found in living systems (explained below), the model presents metabolism as the ‘activity of all Earth’s living matter taken together, as well as that of any particular organism’ (Sahtouris, 2000, p. 77).

This is also inspired by Vernadsky, and his holistic vision of *The Biosphere* (1926/1997), as well as a scheme in a paper by Bogush and Edmunds (2012; Figure 3 in their paper), written on Vernadsky’s legacy. Here, the EMF model makes the mineral explicit (see also the discussion on Linnaeus in the next section), along with the other key *non-living* elements (nutrient pools) that life collectively uses and transforms and recycles through metabolism. Models that do not include these non-living elements neglect how life actively transforms and interacts with its environment.

Pedagogically, the Five Kingdoms of Life (Margulis & Schwartz, 1982/1998; Whittaker, 1969; see next section) supports the understanding of the different ways that life has been expressed through its relational and historical context (*diachronic*)—along with different course-grained traits, illustrating how life has collectively evolved, within the framework of kingdoms. By comprehending this, via symbiogenesis, an understanding can be formed of how all life shares some of the same fundamental functional building blocks for metabolism at the cellular level (e.g. chloroplasts or mitochondria), as well as how life is also highly symbiotic.

The Five Kingdoms can be illustrated as a hand (e.g. Margulis & Schwartz, 1982/1998, Front cover), with the kingdoms forming the five fingers. However, what happens next? How do the different fingers now interact together—how do they all play the ‘piano of life’—with the non-living elements within ecosystems? In effect, this represents the transition from biology to ecology. Therefore, the EMF

model is intended to support the use of the Five Kingdoms framework *and* food webs (see more in the next section) by bringing environmental factors, non-trophic interactions, inter-kingdom interactions, and broader concepts of EMFs together, as Vernadsky proposed, by using metabolism as the core classification framework. The vocabulary and meaning(s) of ‘function’ is something that can be easily understood by designers, and therefore, it is potentially by understanding how organisms individually function and collectively interact to form functioning communities and ecosystems that designers may be able to design systems of production (integrating living or synthetic systems or both) that function within and with functioning living systems.

## **BIOLOGICAL AND ECOLOGICAL FOUNDATIONS**

Scientists have been attempting to systematically observe and describe biological diversity since Aristotle (Leroi, 2014; Ross, 1977). The way in which life is classified and visually modelled, including what is made explicit and implicit, and what is left out altogether, frames our view of what life is (and is not), and depending on the form of classification, how it (co)evolves, functions, interacts, differs and resembles, collaborates and competes and reproduces and sustains itself. This second main section provides a brief introduction to some evolving classifications of life, which have inspired the framework and models.

### **Classifying living and non-living elements together**

Linnaeus (1707–1778), a Swedish botanist, zoologist and physician, first classified all living organisms into Plantae, Animalia, and Mineral—however, the mineral ‘kingdom’ was later abandoned (LibreTexts, Biology, 2019). With this abandonment, an explicit link between life and physical and chemical geology was made within *biological* taxonomies of life, and this continues today within different classification systems (e.g. kingdoms and phylogenetics).

### **The biosphere**

Vernadsky (1863–1945) proposed that life is a geochemical process—it is principally rock rearranging itself (Sahtouris, 2000). In his seminal work—*The Biosphere* (1926/1997)—he developed the first holistic view of the *biosphere* (although the term was first mentioned by Lamarck). Here, he integrated living and non-living matter, which includes rocks (lithosphere), gaseous substances (atmosphere), water (hydrosphere) and dead organic matter. He proposed (and was able to show experimentally and theoretically) that there exists a continuous connection during respiration, nutrition and reproduction through a flow of atoms between the non-living and the living (Bogush & Edmunds, 2012).

### **Interactive evolution and Gaia**

Wegener (1880–1930) helped develop the theory of dynamic Earth, which described Earth’s geological evolution (Kutschera, 2011). The two evolutions—one for physical Earth and one for life—were proposed to be one *interactive evolution* (Lovelock, 2006), as Vernadsky imagined, and was later conceptualised within the Gaia theory, co-developed by Lovelock and Margulis. Through this work, the living and non-living are brought together (again) in some frameworks (see the Synade-model of macro-evolution, e.g. Kutschera, 2011), and within academic study, such as Earth system science and ecology.

### **Metabolic classification**

It was clear to Vernadsky that the activity of life was fundamentally metabolic, and so he sought to reclassify living organisms based on their metabolism (Sahtouris, 2000). He argued that the classification system using kingdoms (and their descending hierarchies) led to classifying organisms as related that are really not related in their natural context (Sahtouris, 2000). Therefore, he looked to classify organisms by the way in which they metabolised supplies from their environment (Sahtouris, 1999), and from this, develop a clearer view of their relationships in their natural and collective context. During this process, he found that the different forms of feeding had already been named by German biologist Wilhelm Pfeffer and proposed using these as a way to classify all life (Sahtouris, 2000).

The principal categories are autotrophs (or producers), meaning self-feeding, as these organisms can build their own complex molecules from simple molecules and elements; heterotrophs (or consumers), which feed off others, as these organisms need to eat ready-made molecules made by others; *saprotrophs* (or decomposers), which feed on the dead, and these organisms also turn large molecules into smaller basic ones that the autotrophs can (re)use; and mixotrophs, referring to organisms that can bridge or switch categories as required. There are then finer distinctions within each category. These different forms of metabolism can be thought about functionally, in that, collectively, they interact with each other and are essentially *interdependent*: the different functions collaboratively form *functioning* ecosystems.

### Functional groups

Functional ecology is a branch of ecology that historically and conceptually derives from Elton's work (1927, 1933) on *ecological niches* (Dussault, 2019), which he referred to as 'what [an animal] is *doing*' (1927, p. 63) in its community, emphasising '*relationships to food and enemies*' (1927, p. 64), in contrast to 'appearance, names, affinities, and past history' (Elton, 1927, p.64). Elton's 'niche' concept was inspired and 'used in ecology in the sense that we speak of trades or *professions* or *jobs* in a human community' (Elton, 1933, p. 28).

Contemporary functional ecology builds on Elton's work and looks at the context-based properties (or traits) of organisms, which determine how they potentially or actually interact with other organisms and their environment (Dussault, 2019). Some functional ecologists distinguish this *context-based* view from *history-based* properties (or traits) of organisms, which can consider their selective history—and therefore, evolutionary considerations (Dussault, 2019). The context-based understanding of ecological functions is explained by Jax (2010, p.79), clarifying that 'role' and 'function' are often used as alternative terms to describe the same thing:

Even if we can say that the bird actually has the role of being prey, we can also find other roles, e.g. its role to distribute seeds and nutrients, to be predator for insects, etc. That is, like a person within a human society, who may be teacher, spouse, child, politician etc., either at the same time or at different times, it can have several roles. Roles can change and the same person as well as the same species can even take opposing roles in time . . . . 'The' one and only role of a species does not exist. Roles are strongly context-dependent.

Modern functional ecology expands on Elton's work in two important ways. The first is with the study of traits of organisms and seeing how they determine their contributions to ecosystem processes—such as nutrient cycling, primary productivity and energy flows (Dussault, 2019). This can be described through, for instance, *feeding* (or 'trophic') interactions and food webs (Figure 2). The second is the study of traits of organisms and seeing how they determine their contributions to *non-feeding* (or 'non-trophic') interactions, such as one organism changing the environment in some way for another.

Although there have been attempts to provide clear definitions for the term 'function', significant misunderstandings remain; however, Jax (2005) identified four key variants as follows:

- The descriptions of processes and the causal relationships that create them;
- The *role* of an organism within an ecosystem;
- The processes maintaining an ecosystem, which determine its ability to function; and
- The services a system provides for humans or other organisms.

This framework and model focus primarily on the second of these (the role), which can be explained in (at least) four different ways (Figure 1), or types of 'functional groups' (FGs).

The first FG focusses on *what an organism eats*, which includes all resource–consumer trophic interactions, such as meat-eaters (carnivores), insect-eaters (insectivores) and plant-eaters (herbivores). These trophic food chains (Figure 2) within food webs help describe and understand many

aspects of ecosystems and organisms, particularly their morphology (form), physiology (their physical functioning) and behaviour.

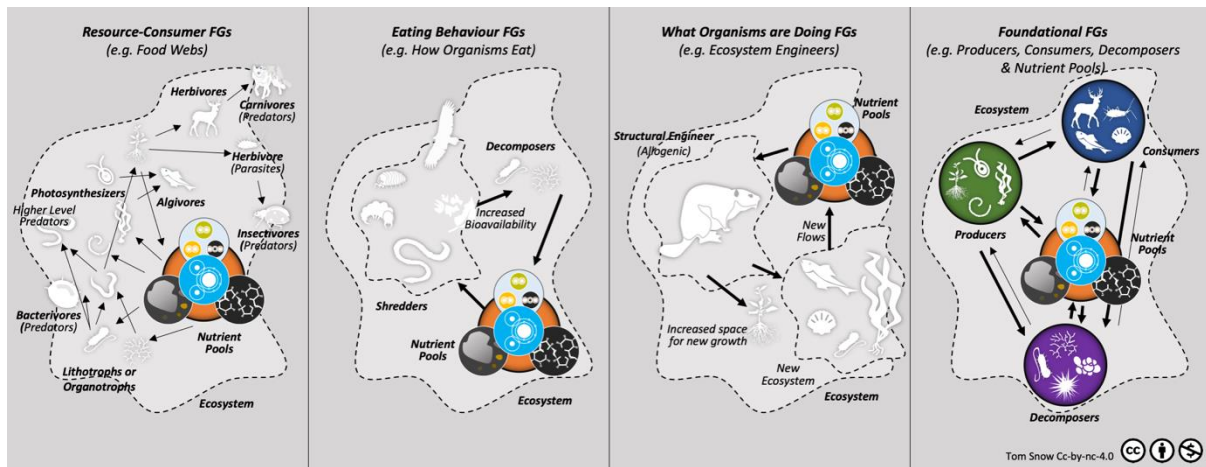


FIGURE 1. Four types of functional groups (Snow, 2020).

The second FG focusses on *how an organism eats*. Examples from a coral reef can include *brushers*, fish that brush particulate materials from algal turfs; *croppers*, fish that can nip off short algae from concealed microhabitats; *scrapers*, which scrape the outside of the reef; *excavators*, which bite into the reef; *choppers*, which remove the entire algal thallus; and *shearers*, which nibble on leaves (Bellwood et al., 2018). Some further terrestrial examples are shredders (e.g. earthworms) and scavengers (e.g. vultures). These types of FGs can have significant effects on other organisms and on the surrounding environment.

The third FG focusses on *what an organism does, regardless of how it does so—or which organism does it*. As described by Bellwood et al. (2018, p. 950):

The defining characteristic of [this] functional group (from an ecosystem perspective) is the extent to which it modifies or facilitates the transfer or storage of energy or material within the system. In this respect, a scraping parrotfish, a sand-winning goby and a sticky-tentacled sea cucumber would all be classified as particulate removers. They are, in this context, a discrete functional group defined by what they do regardless of how they do it.

Therefore, this group aligns with *ecosystem engineers* (described at the end of the next section), and it includes light, structure, water and chemical engineering functions. Although some species may be ecosystem engineers in one circumstance and not in others, it is possible to identify fundamental engineering roles in ecosystems independently of the specific species involved (Di Marco, 2019). Ecosystem engineers are explicitly illustrated in the model (Figure 21), clarifying some important non-trophic relationships between organisms and environmental elements.

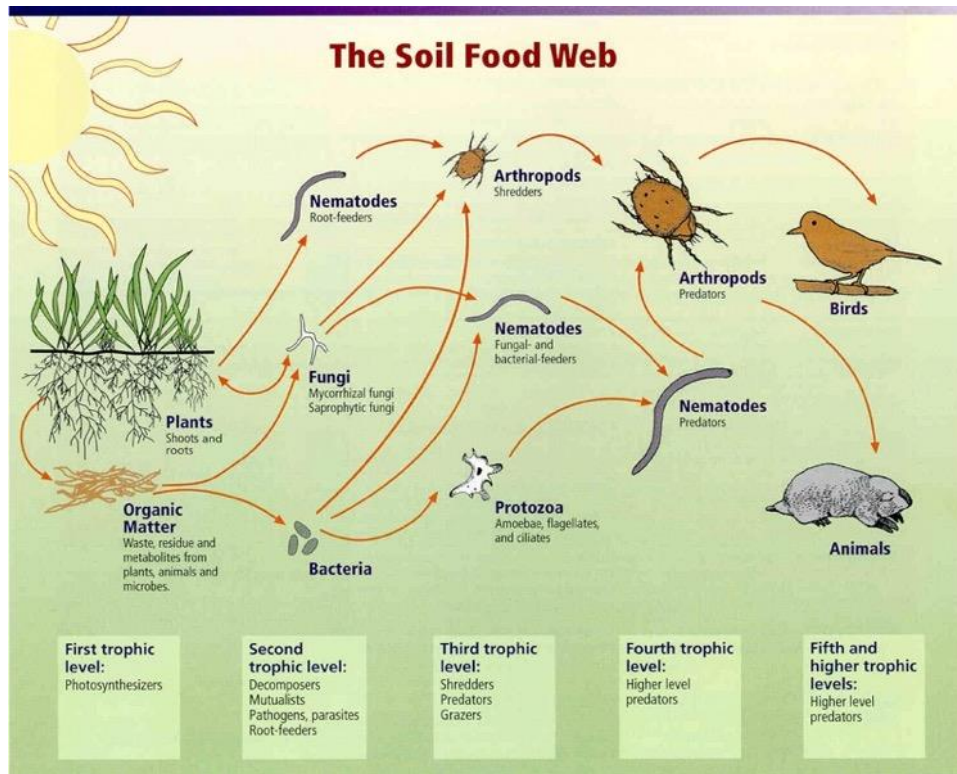
Arguably, the fourth and most foundational FG is far more distinctive and more specialised to certain kingdoms of life than the others are, and this is the function of *producers* (usually plants), *consumers* (usually animals) and *decomposers* (usually bacteria and fungi). The EMF model, illustrated in Figure 21 (described in the next main section)—places the emphasis from the right to the left within Figure 1 shown above.

### Food webs and biogeochemical cycles

Elton also pioneered the concept of ‘food webs’ in his 1927 book *Animal Ecology*, which describes the transfer of food energy between species in an ecosystem (basically, *who-eats-who/what*; Hui, 2012). A food chain examines and describes one linear energy pathway, and there are two types: The grazing

food chain starts with ‘autotrophs’, while the detrital food chain begins with dead organic matter (e.g. wastes, residues and metabolites from organisms; Hui, 2012). A food web (Figure 2) attempts to *mesh* several food chains together to illustrate all the potential energy pathways within an ecosystem (Hui, 2012). Food webs can also be used to describe and bring *biogeochemical cycles* to life.

## Five Kingdoms of Life



**FIGURE 2.** Trophic relationships between soil food web, plants, organic matter and birds and mammals. Image courtesy of the Soil and Water Conservation Society (SWCS, 2000).

The Five Kingdoms of Life include the Kingdoms Monera, Fungi, Protista, Plantae and Animalia. Proposed by Whittaker (1920–1980), this framework considers various ecological characteristics (Hagen, 2012). The criteria were based on his experience in ecological systems and biogeochemical cycles. A core concept was that kingdoms were defined by their functional role primarily and taxonomic grouping secondarily (Hagen, 2012), linked with their predominant mode of nutrition. His work later evolved to include symbiogenesis (see Margulis & Sagan, 1997; Margulis & Schwartz, 1982/1998) through collaboration with Margulis (and a work she continued independently). The following are some criteria Whittaker used in his framework (synthesised from Hagen, 2012), which are also relevant to this paper:

- The ecological functional role: producers, consumers and decomposers;
- The mode of nutrition: photosynthetic, ingestive and absorptive; and
- Pedagogic ends: useful, practical, theoretical and aesthetic.

## AN ECOSYSTEM FUNCTION MODEL

This third main section of the paper is a *progressive* deep dive into ecological interactions, which collectively describe how ecosystems function.

### Initial ecological grounding

The word *ecology* is derived from the Greek *oikos*, meaning ‘house’ or ‘place to live’. Therefore, in a literal sense, ecology is a study of organisms ‘at home’ (Odum, 1953, p. 3). Ecology is a distinct branch of biology that studies the interactions among organisms and their biophysical home. To create manageable system boundaries for study, ecologists use the concept of *nested hierarchies*, ranging in scale from genes to cells, tissues, organs, organisms, species, populations, communities, ecosystems, biomes, and ultimately, the biosphere (Nachtomy et al., 2002).

According to Eugene Odum (1953, p.9), ‘Living organisms [*biotic*] and their non-living (*abiotic*) environment are inseparably interrelated and interact upon each other’. Any entity or ‘natural unit’ made up of a biotic community (e.g. an assembly of plants, animals and microbes) and abiotic (e.g. air, water and wind) *factors, components* or substances that interact to produce a dynamically stable system, where materials are exchanged between the two factors, is known as an *ecosystem* (Odum, 1953). Ecosystems have no particular size and can be as large as a desert or as small as a tree; they include agroecosystems, aquatic and marine ecosystems, coral reefs (Figure 3), forests, savannas and tundra. To fit with the previous analogy, a *habitat* can be said to be an organism’s, or an entire community’s, ‘address’ (Odum, 1953, p. 15).

Ecosystems are controlled by external and internal factors. External factors include the *address, climate* and *parent material* of the underlying bedrock and topography. These factors highly influence the structure of an ecosystem and are primarily classed as ‘external’ because they are assumed to have no influence (or feedback) from the ecosystem; however, at least within the boundaries of Earth’s atmosphere (e.g. not Milankovitch cycles), organisms and/or communities of organisms can have influence on their environment in the long term or even the relatively short term (Bjornerud, 2018). Internal factors can include disturbances, succession and the types of organisms or species present.



FIGURE 3. Coral reef ecosystem (photo: Joakant, 2014).

Abiotic (chemical or physical) factors can include water and its availability, air and its composition (e.g. high or low oxygen or CO<sub>2</sub>) and important variables, such as pH, salinity, pressure, temperature, the amount of and quality of light, tides and wind speeds. Abiotic factors can affect living organisms in terms of growth, maintenance and reproduction.

Biotic factors include the *living* (and once living) components that affect other organisms or shape the ecosystem. At first glance, it may be less obvious that abiotic factors can also be influenced and controlled by biotic factors; however, linked to the point above, this is clearly the case. Examples include bacterial biofilms and fungal acids changing pH (in soils), corals building islands (Figure 3),



organisms (particularly bacteria) affecting the composition of the Earth’s atmosphere and all organisms building unique compounds and isotopes (Odum, 1953).

**Matter circulates, energy flows and dissipates**

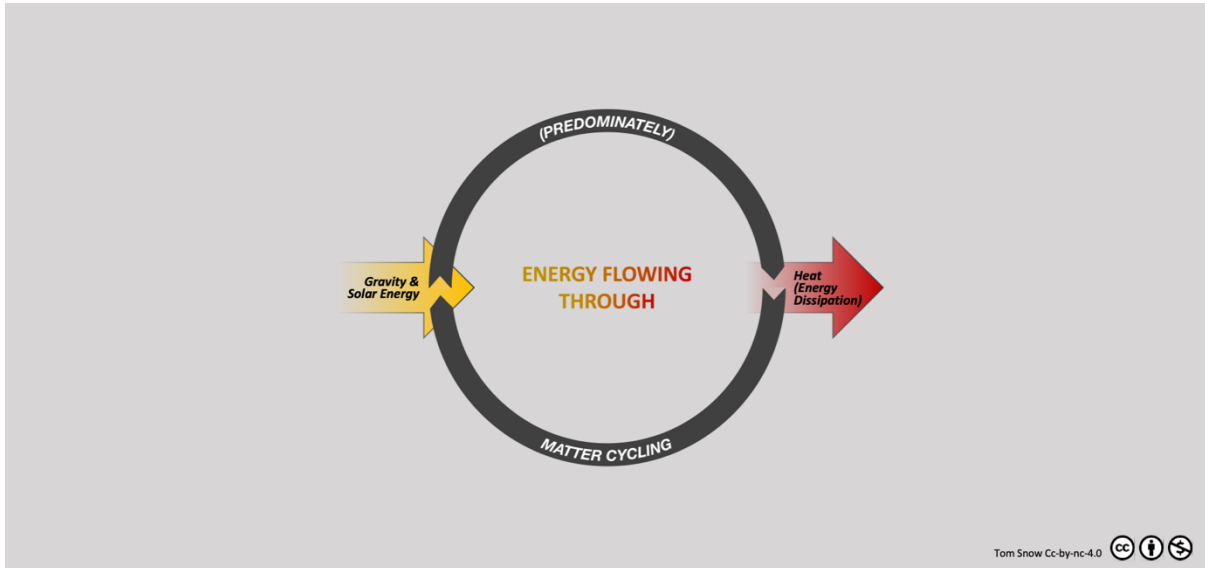


FIGURE 4. Energy flows and matter cycles (Snow, 2020).

Energy mostly enters terrestrial ecosystems via plants. Therefore, they are the ‘energy gatekeepers’. Through the process of photosynthesis, plants convert some solar energy that reaches Earth’s surface into chemical energy in the chloroplast.

To create energy for doing work, organisms with mitochondria in their cells (e.g. animals, plants, fungi and most protists) use glucose, for example, to produce adenosine triphosphate (ATP). ATP can be used to do work within the cell. Energy is released from ATP when one of its phosphates (it is made of three phosphate groups—hence, ‘tri’ phosphate) is broken off the molecule. The energy stored in the phosphate *bond* is the source of all the metabolic energy and keeps organisms like humans alive (West, 2017). Therefore, this process requires constant production of ATP, and thus, a constant input of energy, as mitochondria ‘stick’ the loose phosphates back onto the broken ATP (known as adenosine diphosphate, ADP)<sup>1</sup>; this creates a continuous loop process (West, 2017).

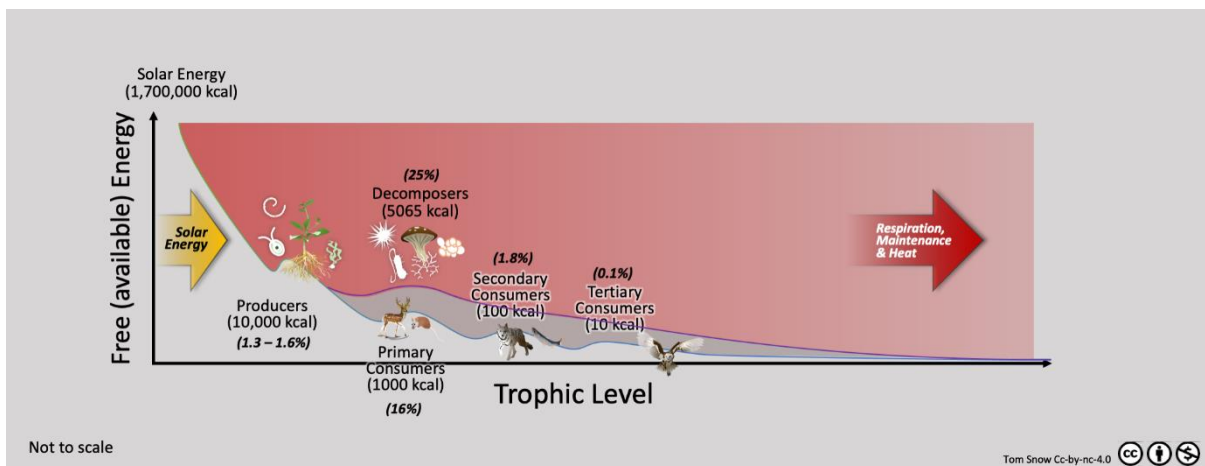


FIGURE 5. An illustration of energy flowing through an ecosystem (Snow, 2020).

Plants produce their fuel (glucose) and are known as autotrophs ('self-feeders'). Organisms like humans need to eat energy-dense foods (organic molecules, e.g. glucose) to power the process, so we are known as heterotrophs ('other-feeders').

Miller (1971), a chemist, calculated that a 'food chain' consisting of 1000 (US) tons of grass can support 27 million grasshoppers, which supports 90 000 frogs, which can support 300 trout, which can support 1 human for one year. He showed that only around 10–20% of the energy stored as biomass in the prey (food) is transferred and stored as *biomass* in the predator. A combination of reasons for this include the following: predators do not eat all the prey (e.g. some survive or die without being eaten), some elements are indigestible and are excreted (this can be around 20%) and a significant proportion is used to power respiration and is 'lost' as heat (this can be around 65%). Some of this heat keeps us warm while dissipating into the environment. See Figure 5 for a more detailed visual description.

The elements that cannot be digested are excreted from the body as faeces or urine and decomposed by certain bacteria and fungi and other detritivores ('debris eaters'). They extract the remaining energy from the system, while also respiring and dissipating heat. This is in fact a description of the *Second Law of Thermodynamics*, which states that 'whenever energy is transformed into a useful form, it also produces "useless" energy as a degraded by-product: "unintended consequences" in the form of inaccessible disorganised heat or unusable products are inevitable' (West, 2017, p. 14).

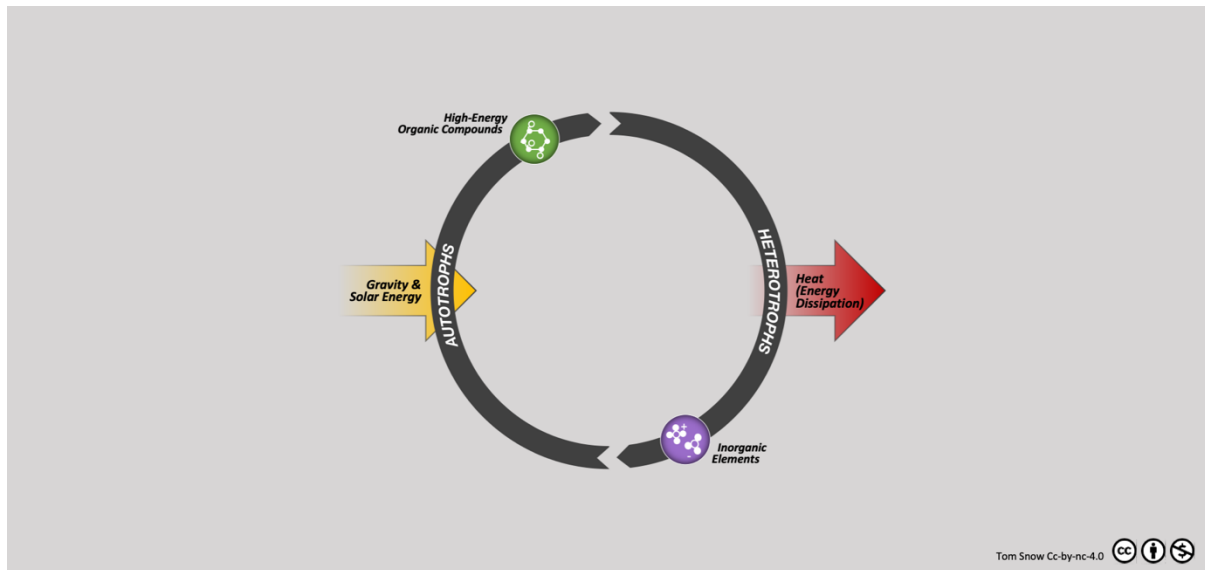
There are two points to underline here. First, that each transformation—as one organism eats another—'requires an expenditure of energy and results in the loss of energy' (Rifkin, 2011, p. 200). Second, unlike matter (particularly *inorganic* matter), which can cycle around an ecosystem—potentially hundreds of times—energy must be constantly replenished as it *flows through* an ecosystem via relatively short food chains (and is recycled, but relatively, very little), until what came in as solar energy is dissipated back out into the environment and then out into space as *heat* (Figure 4). This also describes the *First Law of Thermodynamics*, which states that 'energy is always conserved, and . . . no matter how far it is dispersed the total always remains the same' (Lovelock, 1995 p. 21). However, the quality of the energy has changed: It is now low energy heat, which is dissipated (disordered)—the manifestation of *entropy*; its ability to do work has been reduced.

Gravity is also an input to the system, although in a different way from the electromagnetic energy from the Sun. Gravity is a phenomenon that forms all the stars and planets in the universe and maintains them in their *interactive* orbits, grasping all the rocks, liquids, and gases—and in the case of Earth, all life—retaining them together as a whole. Along with solar energy, these two inputs put into motion the vast majority of Earth's cycles.

### **Autotrophs and heterotrophs, organic and inorganic matter**

The main metabolism categories can initially be separated into two principle groups: autotrophs and *heterotrophs* (Figure 6). All autotrophs can 'eat' air for food—extracting the essential carbon from carbon dioxide (CO<sub>2</sub>) in the atmosphere (Margulis, 1998), which they use to build *high-energy organic compounds*. These compounds can be used as the building blocks (the carbon backbone) for physical matter (biomass *de novo*) or the chemical energy previously mentioned.

The vast majority of autotrophs use sunlight as the external source of energy to predominantly break apart water molecules (H<sub>2</sub>O), providing the energy to 'fix' carbon and turn it into simple carbohydrates (photosynthesis). These are known as *photoautotrophs*, which include plants, algae, lichens and cyanobacteria. Some autotrophs do not use sunlight, and instead, use geological sources of hydrogen-rich inorganic compounds, such as hydrogen gas (H<sub>2</sub>), methane (CH<sub>3</sub>), hydrogen sulphide (H<sub>2</sub>S) or ammonia (HN<sub>3</sub>) as a source of energy to fix carbon (Margulis, 1998). These largely hidden microbes can be found in extreme environments, such as hot springs and hydrothermal vents at the bottom of oceans; others, such as nitrifying bacteria, can be found in soils, lakes and oceans (Strong, 2008). These are known as *chemoautotrophs*.



**FIGURE 6.** Autotrophic organic compounds, heterotrophic inorganic elements (Snow, 2020).

The vast majority of inorganic elements, such as essential minerals—or nutrients—in the form of ions and salts are made available to autotrophs by heterotrophs (Loreau, 2010). Heterotrophs are organisms that consume the pre-made high-energy organic compounds (alive or dead) originally made available by autotrophs. Through respiration (using the high-energy organic compounds for energy) heterotrophs (and autotrophs) ‘return’ carbon back into the air as  $\text{CO}_2$ , and through digestion, they make the inorganic elements available to the autotrophs. Combined with the fact that (many) photoautotrophs produce oxygen as a by-product from breaking water molecules apart, which is essential for respiration of all aerobic heterotrophs (and autotrophs), further underlines that this prevalent relationship between autotrophs and heterotrophs is the most fundamental and widespread interaction at the core of material cycling in modern ecosystems (Loreau, 2010; Figure 6).

Energy is *transferred* between organisms as one eats another (‘trophic interactions’). The external energy (mainly from the Sun) originally used by the autotrophs is *dissipated* (mainly) by the heterotrophs as they regenerate the inorganic elements *consuming* the organic compounds produced by the autotrophs. Therefore, *energy flows through* ecosystems from the point of fixation by photosynthesis to the point of heterotrophic (and autotrophic) respiration—again, there is essentially no energy recycled within the ecosystem (Loreau, 2010; Figure 6).

Unlike energy, *matter is greatly recycled* within ecosystems (Loreau, 2010). The internal cycling of a *healthy* ecosystem, for instance, accounts for most nitrogen and phosphorus used and released by organisms every year; typically, the recycled amount is an order of magnitude greater than the amount that leaves or enters the (terrestrial) ecosystem (Vitousek & Matson, 2009), which is enabled by life. The Earth system as a whole, which is made up of the biosphere, hydrosphere, atmosphere and lithosphere, is virtually a closed system for matter (except for a few rare inputs from meteorites) and an open system for energy, as energy enters from the Sun and dissipates as heat back out into outer space (West, 2017). Without the recycling of materials (in *limited* supply), the energy flow would quickly stop, leading to ecosystem collapse (Loreau, 2010). This is why ‘biogeochemical’ cycles (the interactions between life and non-life in the cycling of matter through the different ‘spheres’) are such a fundamental part of the functioning of the Earth—and why it is thought that the recycling of matter, such as the wastes of one organism becoming the resources for another, is so likely to emerge spontaneously through evolution (Loreau, 2010).

### Three different metabolisms and direct and indirect interactions

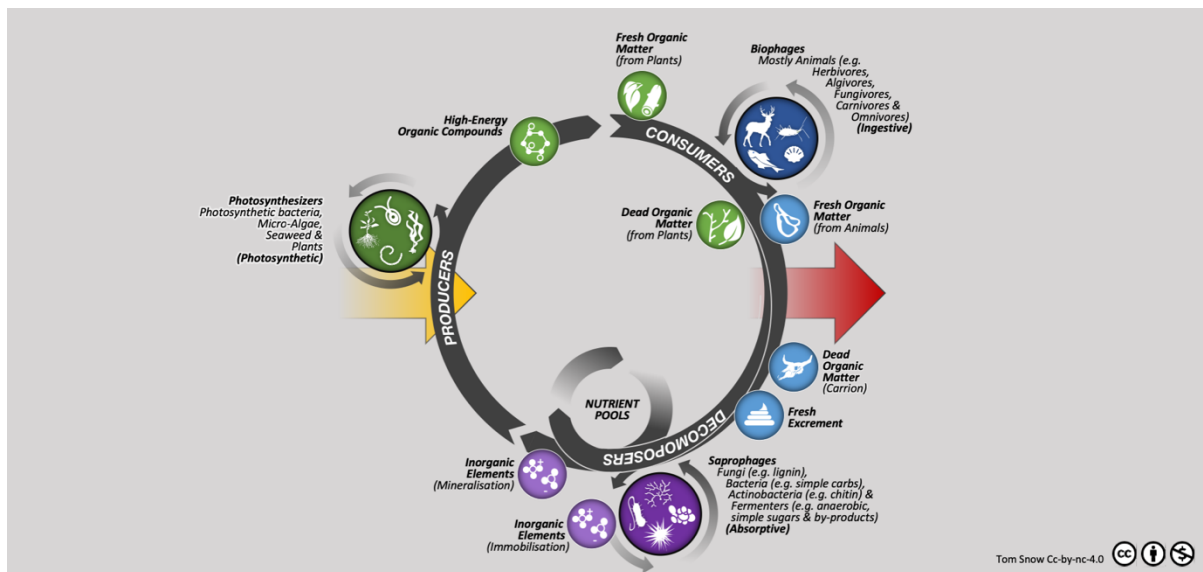


FIGURE 7. Three principal functional groups/metabolisms and nutrient pools (Snow, 2020).

In the previous subsection, the two main groups of autotrophs, photoautotrophs and chemoautotrophs, were discussed. There are also two main groups of heterotrophs, which are as follows: *biophages* (or biotrophs), including herbivores (which eat plants), algivores (which eat algae), bacterivores (which eat bacteria) and carnivores (which eat meat), which subsist on *living biomass* (Strong, 2008); and *saprophages* (or saprotrophs), which live off *dead biomass*, such as dead organisms and their organic by-products (detritus).

As can be seen in Figure 7, the term ‘autotrophs’ has been replaced with ‘producers’; and ‘heterotrophs’ is expressed using two terms, ‘consumers’ and ‘decomposers’. Figure 7 also distinguishes between living and non-living organic matter and introduces another important component—*nutrient pools*. Nutrient pools (or reservoir pools) are made up of *dead* organic matter and inorganic nutrients. There are principally two compartments or pools that are recognised, which are as follows: *i*) the large, slow-moving reservoir pool (sometimes called the unavailable pool), including lignin and humus (recalcitrant organic matter); and *ii*) the small, actively moving exchange pool (sometimes called the available pool), which is exchanged rapidly between organisms and their immediate environment. All ecosystems across the Earth, from the most barren deserts (e.g. Antarctica), to the most abundant (e.g. the Brazilian rainforest), include—at least—two of these three functional groups/metabolisms (producers, consumers, decomposers), and it is thought that all *modern* ecosystems include producers and decomposers (Loreau, 2010).

Producers predominantly *eat* via photosynthesis and need a source of light; therefore, they all exist near terrestrial or aquatic surfaces<sup>2</sup>. Decomposers predominantly eat via absorption by first decomposing some or all of their foods *outside of their bodies* prior to it entering the cell(s). They do this by expelling enzymes, and sometimes acids (by fungi), into their surrounding environment, to attach to and break down complex/large molecules into smaller/simpler ones. Once pre-digested, the simpler molecules can be transported across their membranes for use in biosynthesis<sup>3</sup>. The external form of digestion requires a large surface area to *absorb* the resulting nutrients; this is why all microbes (and all cells) are small, with the greatest possible surface to volume ratio.

There are also *fermenters*, which essentially include yeasts (single-cell fungi), anaerobic bacteria and Archaea. By *inefficiently* breaking down simple sugars, *yeasts* and *fermenting bacteria*, for instance,



**FIGURE 8.** Saprotrophic fungi decomposing woody lignineous matter (photo: Adege, 2018).

they extract some chemical energy and food while producing by-products, including ethanol or acids (such as lactic acid), carbon dioxide (CO<sub>2</sub>) and hydrogen gas (H<sub>2</sub>; Margulis & Sagan, 1995)<sup>4</sup>.

Consumers are primarily *animals* (Kingdom Animalia)<sup>5</sup> and predominantly all eat via *ingestion*, which is the physical process of taking food from the external environment and bringing it inside their bodies—generally through a ‘mouth’. This usually starts with the mouth at one end of the digestive tract and the anus at the other (known as a complete digestive system); however, there are some animals, such as jellyfish, that have one opening for both (known as an incomplete digestive system).

Decomposers (Figure 8) do not consume (eat) producers directly; instead, decomposers are said to indirectly consume dead organic matter from producers via the nutrient pools (Loreau, 2010). Through their action of decomposition (in relation to their predators, as discussed in a following subsection), decomposers mineralise the inorganic elements (notably nitrogen, phosphorus and sulphur) and release them in a soluble (dissolvable in water) inorganic form, which makes them accessible for plants; thus, this is a mutualistic relationship. Mineralisation is the opposite of immobilisation, which describes the process by which decomposers take up the inorganic elements and use them for their growth (biosynthesis) or store them for later use. When the inorganic elements are immobilised, they are not available (they are not ‘mobile’) for the producers.

Unlike decomposers, consumers consume (eat) producers directly—and for this reason, it can be less intuitive that this relationship can also be mutualistic (Loreau, 2010). The perception of a negative relationship is clearly accentuated in that humanity generally has long seen non-domesticated herbivore consumers of crops (e.g. certain insects, birds and deer) and secondary carnivore consumers of livestock (e.g. wolves and otters) as pests, which can be a danger to humans and can also be food or valuable materials for humans.

The mutualistic aspect was initially explained in the following observation by Alfred J. Lotka in 1925, p. 330:

The plant species alone . . . would have a very slow working cycle, because the decomposition of dead plant matter, and its reconstitution into CO<sub>2</sub>, completing the cycle of its transformations, is very slow in the absence of animals, or at any rate very much slower than when the plant is consumed by animals and oxidised in their bodies. Thus, the compound transformer (plant and animal) is very much more effective than the plant [and decomposers] alone.

This insight has since been defined within the *grazing optimisation hypothesis*, which states that the producer ‘productivity’, or even plant ‘fitness’, is maximised at an *intermediate* rate of herbivory (Hilbert et al., 1981; McNaughton, 1979; Owen & Wiegert, 1976, 1981); however, this has been fiercely



**FIGURE 9.** Migrating bison herd (photo: Tpsdave, 2016).

contested (see Belsky, 1986; Belsky et al., 1993; Lennartsson et al., 1997; McNaughton, 1986; Silvertown, 1982).

As herbivores, such as bison, feast on grassland plants (Figure 9), they excrete, urinate, and push mulch into the soil (Schwartz, 2013). This speeds up the cycling of inorganic nutrients—in the short term—and increases the *availability* of nutrients to the decomposers through ‘pre-digestion’ via the consumers’ stomach, as Lotka stated above. This describes an indirect mutualistic interaction between plants and consumers (Loreau, 2010). However, the consumption of *some* of the plant has obviously reduced the plant’s total biomass in the short term, and therefore, this is a direct negative effect (Loreau, 2010). Thus, for this hypothesis to hold, the positive interactions have to outweigh the negative ones for it to be an overall positive interaction.

Some additional indirect mutualistic effects include herbivores eating or pushing down dead or dry biomass, creating space and light for new growth (Butterfield & Savory, 2016), and through eating the plants, the plants are provoked to mobilise resources (e.g. sugars) stored in the roots, which are released to the decomposers, also boosting nutrient cycling (Schwartz, 2016). Perhaps the greatest, and the least (or non-) contestable, indirect mutualistic interaction by herbivores feeding on plants is that they reduce the amount of total *dry* plant biomass (e.g. by eating the drier grasses or keeping the grasses pruned, and therefore, not allowing grasses to elongate and age so much); thus, they convert a significant proportion of the total ecosystem plant biomass into their own meat biomass (their bodies). This reduction in *burnable biomass* reduces the total biomass lost during annual fires (Butterfield & Savory, 2016), and particularly, it reduces the loss of important inorganic nutrients, such as nitrogen, that are stored in grass biomass and released into the atmosphere (such that they are lost from the soils) during fires (Loreau, 2010; Schwartz, 2016).

Although consumers generally have a negative *direct* effect on plants through their consumption, they compensate for this with a potentially greater amount of positive indirect effects through improved productivity (including ‘fitness’; see Loreau, 2019, Chapter 8, for more about this point). This can also benefit the plants they do not eat.

The importance of this subsection is to principally underline direct and indirect interactions *and* the fundamental role of consumers in modern ecosystems, as well as why all three metabolisms are fundamental actors within healthy and functioning modern ecosystems—and therefore, are the foundations of this model. Thanks to generations of work by ecologists (e.g. works on keystone species and cascades), we have empirical evidence that this is really the case—and consumers are not just mentioned in this model simply because they exist. The understanding of this fact has brought about significant changes, for example, to ecosystem conservation (and regeneration) and regenerative agricultural practice (see Butterfield & Savory, 2016; Estes & Terborgh, 2010). To stress the point a little further: Some land plants (producers) can live with only decomposers (i.e. an ecosystem without

consumers) and a very few plants, even without soil; however, virtually all (if not all) modern, complex, healthy ecosystems include consumers and require them to be the vibrant ecosystems that they are.

### Nutrients pools as the central node and diazotrophs, lithovores and calcifiers

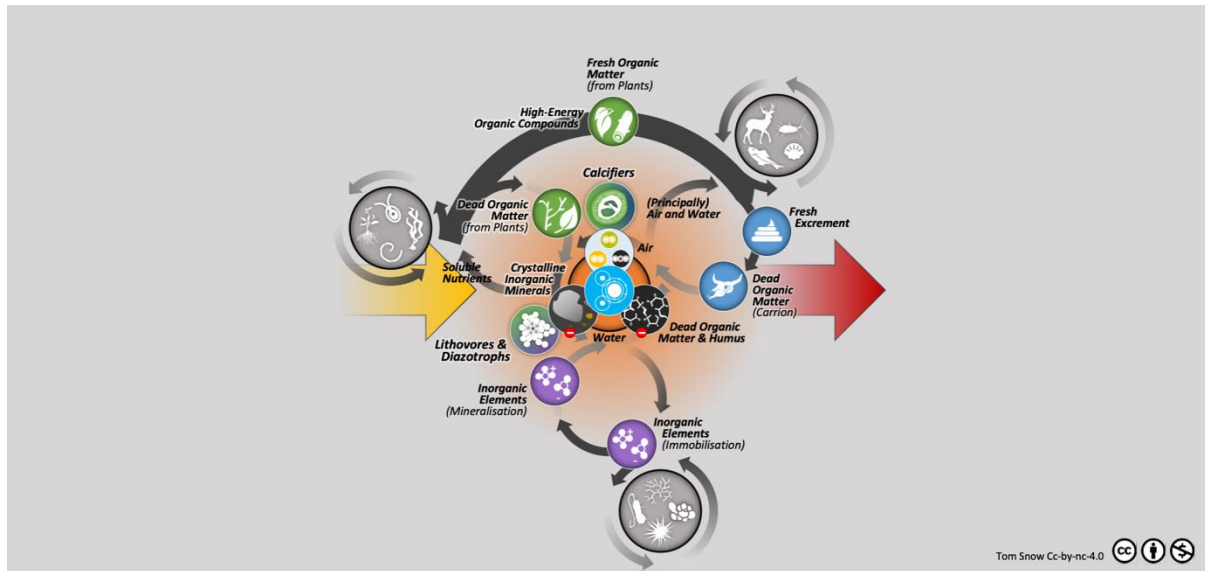


FIGURE 10. Diazotrophs, lithovores and calcifiers (Snow, 2020).

In Figure 10, the nutrient pool has shifted to the centre to illustrate how this unit interfaces with all the other biotic units. Water, air, crystalline inorganic minerals (e.g. rocks) and dead organic matter are now labelled explicitly, and the inorganic, fresh and labile (easy to decompose) elements are now freely moving around the system. It has also been coloured orange to depict that these elements have an important interaction with solar energy (and gravity) flowing through the ecosystem (e.g. the greenhouse effect and hydrological cycle). When matter cycles via the nutrient pools, this illustrates the *indirect* interactions between the three different biotic units described in the previous subsection, illustrated with the thinner circular arrows. This central node is inspired by Figure 3 in Bogush and Edmunds (2012).

At the centre is *water* (H<sub>2</sub>O), which plants use for photosynthesis, structure (turgor pressure), drawing in dissolved nutrients and taking up and releasing components, for instance, for evapotranspiration–cooling. Water is also produced as a by-product of respiration by all aerobic organisms (breaking down—usually—simple sugars for fuel), with carbon dioxide, and it is used, for instance, for its ability to break apart molecules (either on its own or with enzymes)—known as hydrolysis. Through these and other processes, it is possible to see how water is cycling around the indirect arrows and how it is fundamental for all life.

The *crystalline inorganic minerals* are the rocks, pebbles, sands, silts and clays that make up the bedrock (lithosphere) of the ecosystem<sup>6</sup>. Although the type of bedrock determines which minerals maybe released into the soil and the type of ‘texture’ (e.g. clay or sand), it is their *bio-availability that is* more important for life.

The *dead organic matter* (or detritus) typically includes the bodies (e.g. animals, plants, fungi, bacteria and Protista), or dead parts of organisms (e.g. leaves, bark, skin, bone, seeds, pollen) and faecal materials<sup>7</sup>. ‘Humus,’ which includes ulmic, fulvic and humic acids, is the by-product left over after repeated decomposition, where the material is converted into increasingly complex structures (Schwartz, 2016)<sup>8</sup>. According to (Christine) Jones, humus is a form of organo-mineral complex that contains carbon and nitrogen in specific ratios, plus a wide range of crystalline inorganic minerals (Jones,

n.d.) and masses of dead fungal hyphae, which collectively hold several times their weight in water (Schwartz, 2016). *Clays*, the smallest of the crystalline inorganic minerals and humus, have vast surface areas covered with negative electrical charges<sup>9</sup>.

In Figure 10, there are also three important types of organisms that have been added to the model, which are as follows: diazotrophs, lithovores (or lithotrophs) and calcifiers. Just over 75% of Earth's atmosphere (air) comprises nitrogen (Figure 11). In the atmosphere, nitrogen is mostly in the gas form of two nitrogen atoms, tightly triple-bounded together as dinitrogen ( $N_2$ ). In this form, it is virtually inert and completely unavailable to all forms of life. Unless dinitrogen is broken apart, and the single nitrogen atoms are somehow bound to hydrogen, no life on Earth can exist because there is nothing able to build some of life's key building blocks—*amino acids* (themselves the building blocks for



**FIGURE 11.** Lightning fixation of atmospheric nitrogen ( $N_2$ ) is estimated to contribute to around 10% of the total *non-biological* nitrogen, which enters the soil with rain (photo: BrinWeins, 2015).

proteins and enzymes) or *nucleotides* (Falkowski, 2015). There is only one kingdom of life that can break apart dinitrogen biologically; this is the Kingdom Monera—bacteria and Archaea (Falkowski, 2015)<sup>10</sup>. They transform the nitrogen into amino acids and proteins in their bodies, and either exchange it if in a *symbiotic* relationship or enter into the *decomposer predators* if they are eaten. The predators subsequently excrete high-nitrogen manure into the soil, and thus, the decomposer predators are the important mineralisers (Lewis & Lowenfels, 2010); this will be expanded on below. If soils are anaerobic (or low in oxygen), *denitrifying bacteria* can use nitrates or nitrites as a form of respiration, and in the process, transform them 'back' into  $N_2$ , closing the 'short' nitrogen cycle. Therefore, denitrifying bacteria do not help the fertility of soils; however, they are essential for maintaining the longer nitrogen cycle (Lewis & Lowenfels, 2010). *Lithovores* (from the Greek, meaning 'eaters of rock') are a diverse group of bacteria and Archaea that can use *inorganic minerals* (usually of geological origin—i.e. *crystalline* inorganic minerals from rocks, not those produced by decomposers) for different metabolic functions<sup>11</sup>.

Within soils of slightly alkaline pH, an important group of aerobic bacteria can be active, known as *nitrifying bacteria*. The first group is nitrite-oxidising bacteria, such as *Nitrosomonas* or *Nitrosococcus*. These bacteria can use the energy released from breaking apart the ammonium ( $NH_4^+$ ) through oxidation ( $2O_2$ ) to 'fix' carbon from carbon dioxide—not like plants or cyanobacteria in photosynthesis—also releasing hydrogen oxide ( $2H_2O$ ) and nitrogen, now in an oxygenated form, and a negative mineral—an 'ion' ( $NO_2^-$ ) known as *nitrite*. The second group, *nitrate-oxidising bacteria* (e.g. *Nitrobacter* spp.), also use oxygen ( $O_2$ ) to release energy from the nitrite, transforming it into *nitrate* ( $NO_3^-$ ). The significance of this to plants is expounded on below.

Phosphorus is the least abundant macronutrient and the second-most important limit to crop growth after nitrogen (Biklé & Montgomery, 2016). Most of the world's phosphorus is held in certain rocks, and it readily forms insoluble compounds with iron, calcium, magnesium and aluminium, which makes it unavailable to plants (Biklé & Montgomery, 2016). Phosphorus-solubilising bacteria (e.g.



*Azospirillum* and *Burkholderia*) can produce acids (e.g. fungi) that convert phosphorus into a soluble form (that plants can also take up). In organic matter–rich soils, the dead organic matter can also provide half of the total phosphorus in soils (through recycling) and sometimes up to 95% (Biklé & Montgomery, 2016)<sup>12</sup>.

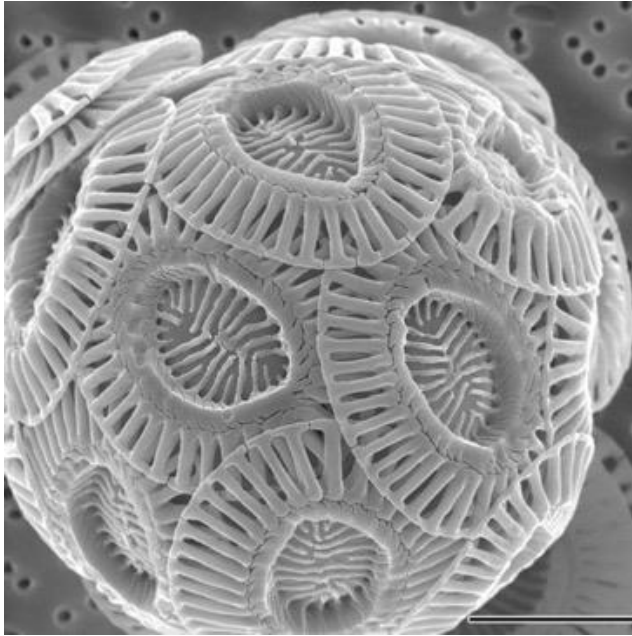


FIGURE 12. *Emiliana huxleyi* (coccolithophore; photo: Taylor, 2011).

Sulphur is also an important micronutrient, and some Archaea can oxidise sulphur from rocks—often in extreme environments, such as volcanic pools or thermal vents. Through food-web interactions, this sulphur eventually works its way around the abiotic and biotic units (Lewis & Lowenfels, 2010).

The last group of organisms discussed in this subsection comprises those that can perform a particular type of bio-mineralisation. Bio-mineralisation is the process by which organisms produce minerals—especially in the form of hard or stiff tissues (not to be confused with mineralisation). It is suggested that, in what started as a form of by-product or waste removal, the innovative recycling led to a system of protective and structural support (Margulis, 1998). Many forms of life are capable of this process—from all kingdoms<sup>13</sup>.

The group of ‘bio-mineralisers’ discussed further here are the *calcifiers*, due to their importance in the long carbon cycle. Calcifiers can be photosynthetic and include many types of animal, hence their location in the model. The major carbonate within the long carbon cycle is  $\text{CaCO}_3$ , and it is mainly in the form of either *calcite* (e.g. within coccolithophores and coralline algae) or *aragonite* (e.g. within corals); some bivalve molluscs, for instance, can be a mixture of the two.

When  $\text{CO}_2$  mixes with water vapour in the atmosphere, it forms a weak acid known as carbonic acid ( $\text{H}_2\text{CO}_3$ ). This can dissolve rocks, such as basalt and granite (known as calcium silicate rocks; Harding, 2009). By reacting with the calcium and silicates, they are realised into solution and can eventually be washed into the ocean. The weak acid can also dissociate into a bicarbonate ( $\text{HCO}_3^-$ ) and a hydrogen ion ( $\text{H}^+$ ; Harding, 2009). The dissolved silicates can be bio-mineralised by the diatoms, and the released calcium can be used by the various calcifiers with bicarbonate to build their calcium carbonate structures.

*Coccolithophores* (meaning the ‘carriers of little stone berries’) are a group of marine micro-algae (single-cell) that live at the surface of cold oceans (Harding, 2009). They form wheel-like calcium carbonate shapes outside their bodies (Figure 12), and as they die, they accumulate on the seafloor, building up light porous chalk or denser limestone (depending on the conditions; Harding, 2009).

*Coralline algae* are a form of red algae that are the main builders of algal reefs in the temperate Mediterranean Sea (the *Corallignène*), typically accumulating on rocks. In these areas, the beach sands are primarily composed of particles left from their decomposed bodies—literally building beaches (Todd, 2019). Along with other hard corals and molluscs, for example, these aquatic organisms are an important part of the long-term carbon cycle, concentrating carbon into the deep ocean sediments, which are locked up for tens of millions of years before finally being returned to the atmosphere through coastal plate tectonics and volcanic eruptions (Bjornerud, 2018).

All organisms produce by-products during metabolism and respiration throughout their lives, and when they die, they become part of a constantly *regenerated* stream of potential resources for other forms of organisms. As life has evolved, different organisms have evolved in different niches, functioning within (at least) one of the three basic ‘biotic units’ or metabolisms (producer, consumer and decomposer), collectively taking from and giving back to the dynamic ‘abiotic unit’. Therefore, these four foundational basic units (three biotic and one abiotic) make up the vast majority of *modern* (and untouched) ecosystems (Odum, 1953).

### Mutual direct interactions

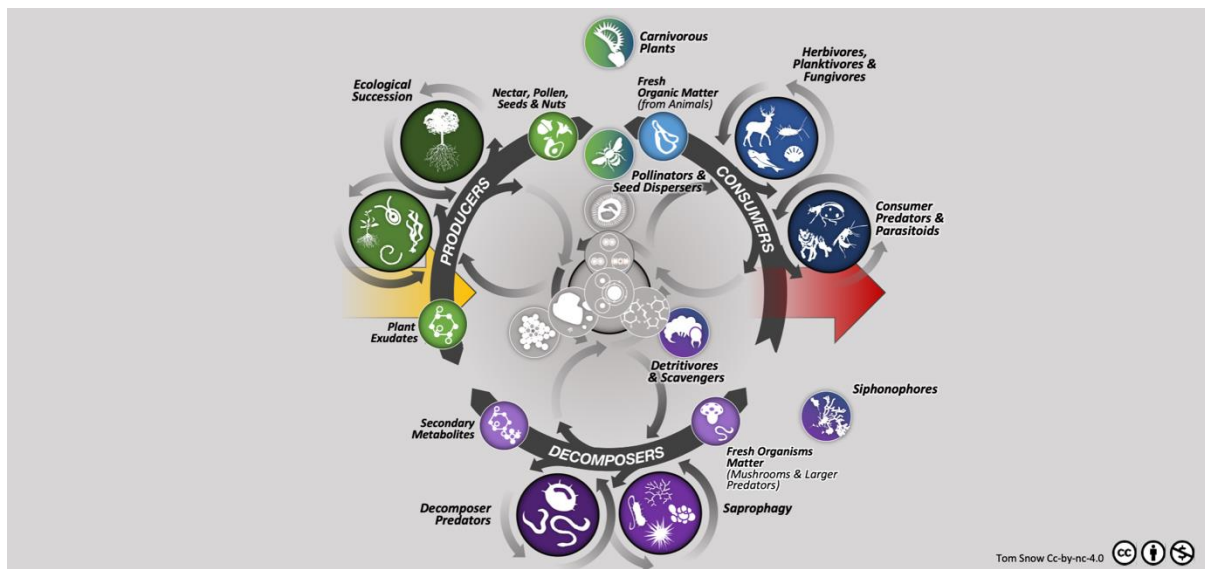


FIGURE 13. Important mutual and direct interactions (Snow, 2020).

This subsection builds on the previous one by introducing some more important *trophic interactions*—direct and indirect (Figure 13). Direct interactions are direct, whilst indirect interactions (or effects) can be defined as the impact one organism or species has on another that is mediated or transmitted by a third (Moon et al., 2010), whether abiotic or biotic.

The first important *direct* relationship, which has yet to be revealed, is between producers—particularly plants on land—and decomposers. Plants produce *exudates*, which are mostly (but not exclusively) excreted from the roots. These are in the form of carbohydrates, some amino acids, proteins, vitamins and phytochemicals (Biklé & Montgomery, 2016; Lewis & Lowenfels, 2010). They attract specific beneficial bacteria and fungi into the rootzone. The beneficial fungi and bacteria cover the roots, stems and leaves, feeding off the exudates and dead cells. Plants transfer sugars into the rootzone, where the proportion depends on the plant type<sup>14</sup>. This forms a ‘micro-biome’ around the rootzone, which attracts the microbe *predators* to feast on the bounty. As bacteria are extremely nutrient, and importantly, nitrogen dense (Lewis & Lowenfels, 2010), the predators, which proportionally need far less nitrogen, excrete large amounts of nitrogen in the form of ammonium

( $\text{NH}_4^+$ ) and other important minerals into the soil. The plant can then absorb nitrogen in the form of nitrate ( $\text{NH}_3^-$ ) or ammonium ( $\text{NH}_4^+$ ), depending on the soil pH<sup>15</sup>, which is created by the type of microbiome community that the plant has provoked (Lewis & Lowenfels, 2010)<sup>16</sup>. Occasionally, beneficial bacteria in the rhizosphere will produce secondary metabolites that help the producer (plant) in different ways (Biklé & Montgomery, 2016)<sup>17</sup>. These interactions are also direct.

Consumer predators comprise ‘secondary consumers,’ which are those that prey on primary consumers, including carnivores and omnivores. ‘Tertiary consumers’ include apex predators, which may feed on both primary and secondary consumers, and they can be fully carnivorous or omnivorous (e.g. eagles, wolves, bears, humans); tertiary consumers can also include *keystone species*—those species that have a disproportionately large relative effect on their ecosystem compared with their biomass or number<sup>18</sup>.

Some *consumer* predators also feed on some of the *decomposer* predators<sup>19</sup>. These two food chains—producer–predator food chains and decomposer–predator food chains—can combine into complex food webs. These interactions are also direct.

Decomposers (saprotrophs) can also be separated into two subgroups—saprophages and detritivores. *Saprophages*, which include bacteria, fungi and many protists discussed so far, are unable to ingest discrete lumps of matter, and instead use a range of ‘unbinding’ enzymes to *decompose* organic matter outside of their bodies. *Detritivores* are usually invertebrates (animals lacking a backbone) and digest via *ingestion*—‘shredding’ organic matter into smaller pieces (e.g. termites)<sup>20</sup>. Larger consumer predators, such as vultures, which eat dead meat (carrion), are also crucial ‘shredders’ in ecosystems, breaking up large carcasses and bones, making them available for decomposers (Cortés-Avizanda & Pereira, 2016). These large shredders are known as *scavengers*.

*Carnivorous plants* (e.g. Venus flytraps) are both producers and consumers, making it possible for them to grow in nutrient-poor (especially low in nitrogen), water-logged and acidic environments (like bogs). They still fix carbon through photosynthesis, but they also have the ability to trap small animals, such as insects and other arthropods (or protozoans)<sup>21</sup>.

Some plants (producers) can provide a ‘resource’—a food for a specific consumer that does not (generally) result in the plant being eaten (like with the exudates), and in return, the consumer provides a ‘service’—which does not include a resource input. This is known as a form of *service–resource relationship*. The most common example is the relationship between flowering plants and animal pollinators. Here, insects pollinate (entomophilous) flowers, while birds pollinate (ornithophilous) flowers. The plants provide nectar (a sugar-rich liquid) or pollen to feed and attract the pollinators, and ‘the service in return’ provided by the pollinators is pollen dispersal. In this relationship, plants are not *eaten* (their green biomass is not reduced directly); however, they do use energy and resources to produce the nectar (which could have been used for growth or maintenance)<sup>22</sup>.

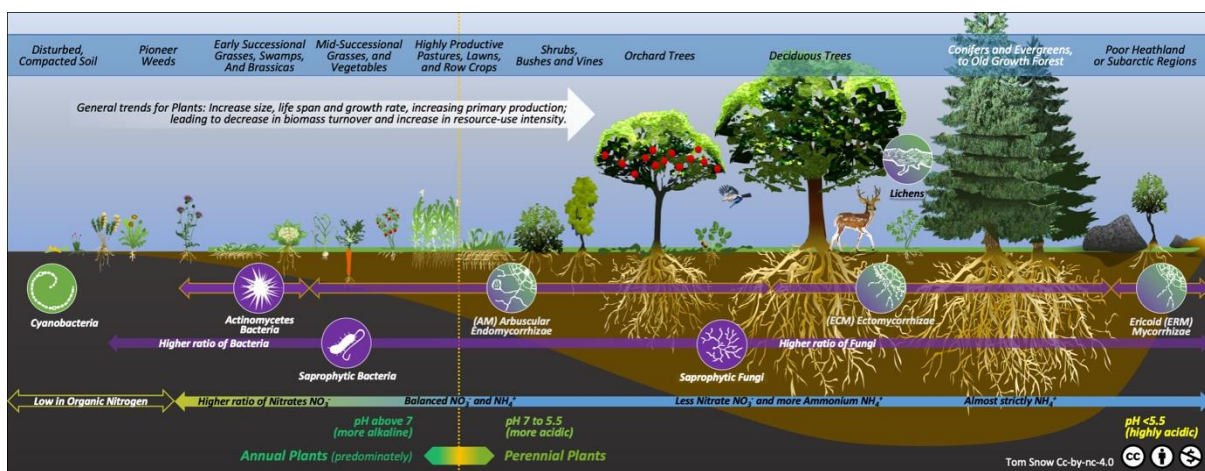
Another important service–resource relationship between animals and plants is known as ‘zoochory’. This is the dispersal of seeds of plants by animals. This is similar to pollination, in that the plant produces a food resource (e.g. fleshy fruit or overabundance of seeds) and consumer animals disperse the seeds (as the service)<sup>23</sup>. All large tree seeds, such as beech and hazelnuts, are also taken by birds; therefore, if birds are killed, then this has an effect on tree populations<sup>24</sup>. A further service–resource relationship is between the gorse bush and certain ants: Gorse bushes can eject seeds away from the bush; however, ants take them much further (Whitfield, 2014). The seed has a small package of nutritious food that the ants like, and so they take the seed to their nests to share with the rest of the colony; in the process, they help disperse the seed further and sow it.

*Consumer/decomposer predators* can also have indirect interactions (and benefits) for producers. For example, Hairston et al. (1960) first stated a hypothesis that carnivore consumer predators help control herbivore populations, thereby releasing plants from *over* control by herbivores in most ecosystems (Loreau, 2010). This later became known as the ‘trophic cascade’ concept (Carpenter et al., 1985) after empirical evidence from ecosystems (showing the indirect interaction). *Predators* can also have a positive *downward* effect on their prey<sup>25</sup>. As long as their numbers are kept in check—for instance, through higher predators eating some of them or their prey avoiding them—

then the predator’s food source can remain plentiful. Decomposer predators can also eat plant *parasites*, such as plant root-eating nematodes, which also benefits the plant.

The relationship between predators and their prey also influences the ‘fitness’ of both, in that individuals must feed and avoid being fed upon to survive and reproduce (Stevens, 2010). Fitness essentially comprises the genetically determined *traits* that improve an organism’s ability to survive (through improved predation or predation avoidance) and to reproduce, which tends to be positively selected, passing on to offspring (Stevens, 2010).

Producer and consumer communities show an orderly change in species composition and community structure as they colonise newly available ecosystems (e.g. land raised above sea-level after tectonic activities) or after a major disturbance (e.g. fire) in an existing ecosystem (Loreau, 2010)<sup>26</sup>. This remarkably predictable process—over the long run—is known as *ecological succession* (Figure 14), and it is used to describe the process of change in biological communities, for instance, from bare rock to mature grassland and forest (Butterfield & Savory, 2016). In this process, and as there are no plants



**FIGURE 14.** Some prominent variations through ecological succession, inspired by ‘Plant Succession’ illustration in Ingham and Rollins (2011, p. 30; Snow, 2020).

that eat plants as such (parasites will be discussed in a moment), ‘ecological succession’ is positioned within producers in the EF model (Figure 13), as producers are the base of the food web, and so they fundamentally drive everything else. ‘Higher’ plants can gradually replace other plants within ecological succession until the previous plants are no longer present (or are present in very reduced numbers); this means that it also includes *dynamic competitive interactions* (as well as mutualist and parasitic ones).

One of the most prominent features of ecological succession (Figure 14), is the displacement of species with those of greater size, lifespan, colonisation abilities and growth rates (increasing biomass, particularly in plants, and increasing production, particularly in primary production). All these attributes contribute to decreasing biomass turnover rates and increasing resource-use intensity (Loreau, 2010). The ecosystem’s cycling efficiency also increases as producers and decomposers use their organic and inorganic resources more efficiently, which reduces direct losses of these resources (Loreau, 2010)<sup>27</sup>.

A relationship in this subsection, which has only been touched on thus far and is *not* illustrated in this framework explicitly, relates to *parasites*. In parasitism, an individual organism (the parasite) consumes nutrients from another living organism (its host). In most cases, parasites do not kill the host, but those parasites that cause a disease within the host are referred to as *pathogens* (Stevens, 2010). Parasites are discussed more in the next section<sup>28</sup>.

Finally, a *siphonophore* is a colony made up of individuals with specialised forms and/or functions (Sloan Wilson & Wilson, 2008). One well-known example is the Portuguese man-of-war, which is not a jellyfish—it is not even an ‘it’: It is a ‘they’, an *animal* made up of a colony of different individual

members. The colony comprises four different ‘polyps’, which are as follows: *i*) a gas-filled bladder (which makes a sail); *ii*) the tentacles that sting (protect and kill prey); *iii*) the digestive organs; and *iv*) the reproductive organisms. Similar to a siphonophore are *slime moulds*, an informal name given to various kinds of eukaryotic organisms that can live as single cells, but also have the ability to aggregate together to form multicellular structures<sup>29</sup>.

This subsection has described some more of the direct mutualistic relationships, predator–prey relationships (primarily within each form of metabolism), parasitism and ecological succession. Through these different interactions and processes, it can further be seen how layers of complex relationships knit the different metabolisms together in complex food webs, and with the ‘service–resource relationships’, there is an introduction to how some organisms can provide benefits for other organisms in *non-trophic* ways.

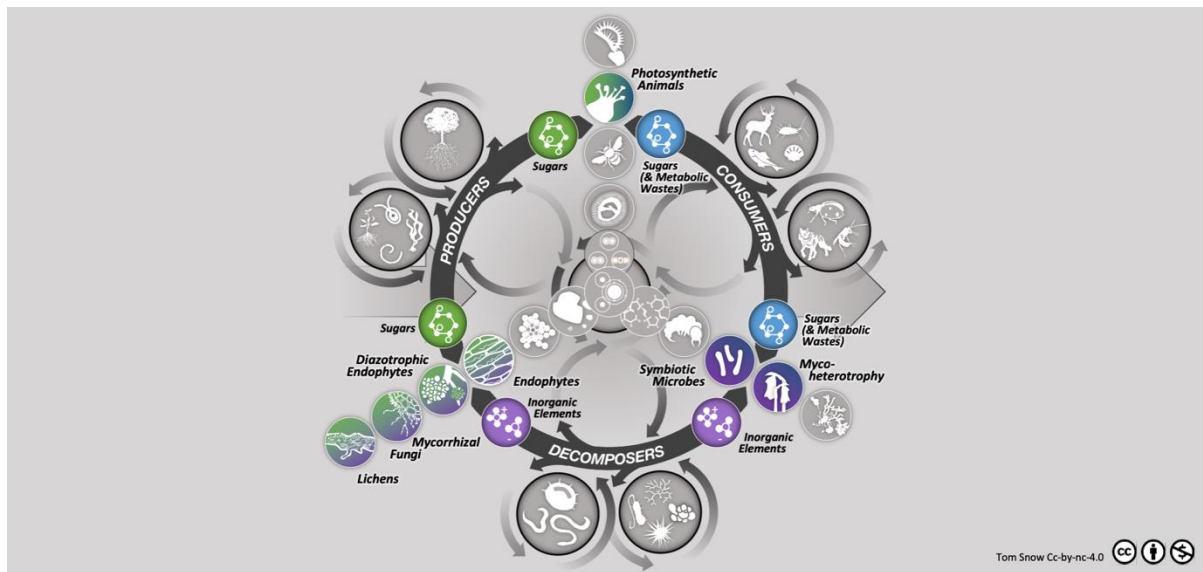


FIGURE 15. Conjunctive symbiosis (Snow, 2020).

### Conjunctive symbiosis

Symbiosis (from the Greek meaning ‘living together’) is any type of close and long-term biological interaction between two different organisms, whether it is *mutualistic* (win–win), *commensalistic* (win–no loss or gain) or *parasitic* (win–loss). Some of the co-evolutionary relationships described in the previous section, such as those between plants and pollinators, can be classed as symbiotic; however, this subsection looks at those symbiotic relationships that require some form of physical attachment (which usually includes some form of physical transformation by those involved)—in which two or more organisms create a bodily union; this is known as *conjunctive symbiosis*. When one organism lives on the surface of another, it is known as *ectosymbiosis*, and *endosymbiosis* is when they live inside.

As can be seen in Figure 15, by coming together as symbionts, the organisms ‘straddle the line’ between the different forms of metabolism—therefore, many are collectively mixotrophs, helping each organism to meet some of the fundamental needs of the other as a collective whole. Conceivably, it is through this perhaps most compromised form of collaboration that they are often the foundational organisms in an ecosystem (discussed more below). Relatedly, these collaborative organisms can create a niche in early ecological succession ecosystems, where nutrient cycles can be poor, the environment can be highly demanding—and neither may be able to survive alone.

For continuity from the previous section, although they are relatively rare in nature, this subsection begins with *myco-heterotrophs* (or monotrophs). So far, all plants have been described as producers, animals as consumers and microbes as decomposers. However, there is an interesting

example where this is not the case, with the subfamily of plants that are actually consumers; these help drive an anti-clockwise flow of carbon. This is a subfamily of Ericaceae flowering plants called Monotropaceae (or monotropes). These often red or white plants are unable to photosynthesise, and therefore, they need to consume fixed carbon from somewhere else (McCoy, 2016). The provider of this carbon comes via a relationship with certain mycorrhizal fungi (discussed further below). As fungi are heterotrophs (and recyclers of carbon), they also need to source carbon from somewhere else—so they also associate with a photosynthesising plant (i.e. a producer), which in this case, is typically a nearby coniferous tree (McCoy, 2016). This *unidirectional* anti-clockwise flow can logically be described as *parasitic*; however, there is evidence that the monotropes also share some precious phosphorus with the surrounding trees via the fungal network (McCoy, 2016), potentially making this beneficial to both the fungi and the tree.

The next conjunctive symbiosis example is between fungi (decomposers) and plants (producers), known as *mycorrhizal fungi*. These physical associations are known to occur in around 80% of all flowering plants and gymnosperms (non-flowering plants, e.g. conifers; Biklé & Montgomery, 2016). Within this relationship, the producer provides the sugary carbon source from photosynthesis, and in this case, the fungi heavily depend on the carbon from the plant, and in return, provide it with minerals, such as phosphorus (Lewis & Lowenfels, 2010). Mycorrhizal fungi are actually weak decomposers; instead, they support the plant by extending their single-cell tubular strands (hyphae) into the soil, increasing the area accessible to the plant. These fungi can bring water and double or triple the uptake of phosphorus (and other nutrients) per unit root length (Biklé & Montgomery, 2016). This relationship is often between one plant and one fungus; however, it can sometimes be between many plants of the same species or different species, sharing nutrients around a community.

There are seven types of mycorrhizal fungi, which can be categorised in two main groups, according to the way the fungi associate with the plant root cells; these are as follows: endomycorrhizal and ectomycorrhizal (EM). There is also a third, rarer type of ecto-endomycorrhizas, which can develop different forms of endo- or ecto-relationships over time.

Arbuscular mycorrhizae (AM) are part of the phylum Glomeromycota, and they are the most abundant *endomycorrhizal fungi* on Earth, forming mutualistic symbiotic relationships with an estimated 70–90% of all plant species (over 400 000 different plants), on which they completely depend for carbon sugars. AM also produce a sticky protein-rich glomalin that helps stick soil macro-aggregates together and extract metals from rocks<sup>30</sup>.



**FIGURE 16.** Classic ectomycorrhizae (EM) fungi with red pine root as the host (photo: Backpackerin, 2015).

EM fungi (Figure 16) form a dense sheath (known as the mantle) around the roots, which can create stubby roots with a reduced amount of root hairs. The hyphae do not penetrate into the root cells; instead, they develop around the surfaces, creating what is called a Hartig net between the cells<sup>31</sup>.

An *endophyte* is any microbe (usually a bacterium or fungus) that develops a conjunctive symbiotic relationship within plants without causing disease (White et al., 2019). Endophytes include the endomycorrhizal fungi already mentioned above. All (or most) plants have endophytes, and in most cases, they are transmitted to the plants via the seed from the parent plant, supporting growth and plant health from the moment of germination (White et al., 2019). In addition, some plants can ‘recruit’ endophytes from the soil (White et al., 2019), potentially more than once, cycling them in and out of



**FIGURE 17.** Different species of lichen living on a tree branch (photo: Makamuki0, 2014/2016).

the root cells into the rhizosphere as required (White et al., 2019)<sup>32</sup>. Many symbionts bio-defend their host plants<sup>33</sup>.

The most well-known endophytic bacteria are the *diazotrophic bacteria*, and the main types of symbiotic diazotrophic bacteria are *symbiotic cyanobacteria*, *rhizobia* and *Frankia*. In all cases, the outer symbiont provides a controlled environment for the diazotroph, as the iron in the nitrogen-fixing enzyme (nitrogenase) is highly susceptible to oxygen rust<sup>34</sup>.

*Lichens* (Figure 17) are a form of conjunctive symbiosis between certain types of fungi and a photosynthetic partner (or *photobiont*), which can be a green alga or cyanobacteria (White & Torres, 2009). The fungi create a protective body (the thallus) and situate themselves in a place suitable for catching sunlight; they are capable of dissolving rocks (lithotrophic) or woody substances (decomposer) and sourcing water, which they provide to the photobiont partner in return for sugars (photosynthates) (White & Torres, 2009). With the ability to colonise bare rocks and trees and survive extreme climates, lichens are one of the great pioneers (McCoy, 2016)<sup>35</sup>.

There are also various marine animals (consumers) that have developed conjunctive symbiotic relationships with certain algae and cyanobacteria (producers). Many *corals* (as well as others in the same cnidarian group, such as sea anemones) have formed conjunctive symbiotic relationships with *dinoflagellate algae* (‘*zooxanthellae*’). Corals are sessile animals that consume zooplankton and small fish (using stinging cells). However, most corals attain most of their carbon energy and nutrients from the dinoflagellates<sup>36</sup>.

Finally, this subsection discusses the conjunctive *symbiotic microbes* (e.g. bacteria, archaea, fungi and protozoa) that live within (and on) *consumers*, which make up their microbiome. Humans have a vast microbiome, which is estimated in number to be greater than the number of human cells in the human body—and more than the number of stars in our galaxy (Biklé & Montgomery, 2016). Like plants, the foundations of our microbiome are passed to us from our mother (in this case, via vaginal birth; Biklé & Montgomery, 2016) and are initially fed by particular nutrients in the mother’s breastmilk as babies grow. The microbiome changes over our lifetime. Gut microbes (particularly in our colons) can support us through the training and priming of immune response, producing vitamins, such as B12, K and K2 (Biklé & Montgomery, 2016); in return, the colon microbes feed (through fermentation) on

complex carbohydrates (polysaccharides)—also known as ‘dietary fibre’, which is not digestible by us alone (Biklé & Montgomery, 2016). Many (if not all) animals have symbiotic microbes, which also provide critical functions that the host could not perform alone. A famous example is the fermenting microbes in the stomach of cows, which produce the appropriate enzymes to break down cellulose in grass (Lewis & Lowenfels, 2010)<sup>37</sup>.

Through the *division of labour* and *fusion*, a single holobiont is formed (Margulis & Fester, 1991)—an assemblage host with other species living within it (or around it)—and this becomes a discrete ecological unit. Because of their diverse abilities and activities across metabolism types, they are often foundational and early ecological successional species, helping to colonise new environments and put into action the primary stages of pedogenesis—the building of new soils and soil crusts.



FIGURE 18. Ecosystem engineers (Snow, 2020).

### Non-trophic interactions and ecosystem engineers

To this point, the model has principally described various trophic interactions, which have been richly studied from the early days of ecology; however, there are also important non-trophic interactions (Figure 18), and these have often been neglected (Bruno et al., 2003), particularly as they do not easily fit within traditional food-web models. The service–resource relationships, described previously, are the bridge to this section; however, they still include a one-sided resource transfer (often a sugary food). Conversely, this subsection focusses only on non-trophic interactions and on one particular form: ecosystem engineers (Jones et al., 1994). Ecosystem engineers are defined by Jones et al. (1994, p. 373) as

organisms that directly or indirectly modulate the availability of resources to other species, by causing physical state changes in biotic or abiotic materials. In so doing, they modify, maintain and create habitats. Autogenic engineers (e.g. corals, or trees) change the environment via their own physical structures (i.e. their living and dead tissues). Allogenic engineers (e.g. woodpeckers, beavers) change the environment by transforming living or non-living materials from one physical state to another, via mechanical or other means. The direct provision of resources to other species, in the form of living or dead tissues is not engineering. Organisms act as engineers when they modulate the supply of a resource or resources other than themselves.



Building on this, Berke (2010) developed four main categories of ecosystem engineers. The first category comprises ‘structural engineers’—organisms able to alter or create relatively durable structural features within and of their surroundings; the second includes ‘bioturbators’—organisms that burrow, excavate, disturb and mix materials in their surroundings. The third category comprises ‘chemical engineers’—organisms able to modify the chemistry of water, air or soil through processes like respiration, photosynthesis or metabolism, or for instance, moving or depositing materials. The final category includes ‘light engineers’—organisms that, through shade or light scattering, can alter local patterns of light transmission and intensity. All four of these categories can be either autogenic or allogenic.

Moore (2006) developed a range of groups and subgroups (for animals in stream ecosystems), adding some richness to those by Berke. One is ‘habitat creation’ (essentially the same as structural engineers). A second is also called ‘bioturbation’. However, Moore (2006) adds the subgroups ‘nest digging’, ‘foraging’ and ‘movements’ to this. The third group is ‘bio-consolidation’—comprising organisms that modify their habitats by consolidating benthic sediments (reducing erosion and leaching of nutrients). Finally, the fourth is ‘particle matter processing’, incorporating organisms that physically modify the size and location of particulate matter in their ecosystem.

There are some overlaps in these definitions given here (and others exist); however, these categories provide a sufficient base to frame some examples. The discussion starts with the decomposers, as they are generally the least commonly known and are particularly important ecosystem engineers in terrestrial (soil) environments.

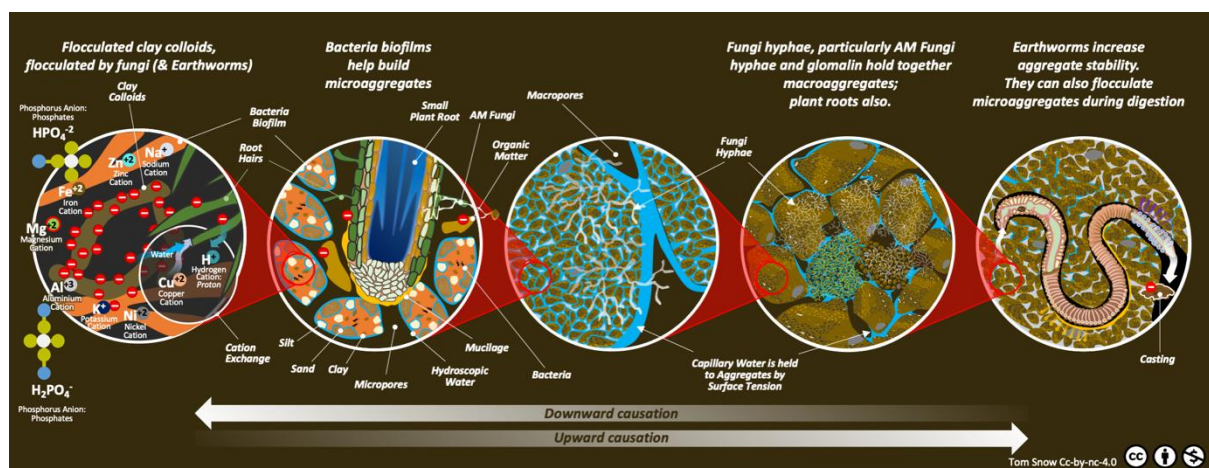


FIGURE 19. The foundational process of soil structure development (Snow, 2020).

*Saprotrophic bacteria* in soils and on surfaces within aquatic environments, just like producers and consumers, build vast structures; however, unlike many producers and consumers, which primarily build their physical bodies, single-cell organisms produce vast structures outside their bodies, known as *biofilms*. Biofilms are a sticky matrix made up of simple sugars, proteins and DNA (Lewis & Lowenfels, 2010). Some bacteria use these biofilms as a means of transport, saving them from drying out (desiccation), and they can be a defence against antibiotics produced by other organisms (up to 1000 times more resistance; Lewis & Lowenfels, 2010)<sup>38</sup>. In soils, biofilms also bind *micro-aggregates* of soil together (Lewis & Lowenfels, 2010), representing the smallest building blocks of soil structure. In aquatic environments, bacteria biofilms are usually the first layers, and they are able to attach to surfaces and take hold<sup>39</sup>.

Biofilms are also slightly alkaline (with a pH above 7), which is enough to change the pH in their soil habitat and help *buffer* the pH in the area (Lewis & Lowenfels, 2010)<sup>40</sup>. Therefore, bacterial biofilms (and nitrifying bacteria—see xxxii) are examples of how soil bacteria and their biofilms are also important *chemical engineers*.

Unlike bacteria, *saprotrophic fungi* predominantly build autogenic structures using their bodies (hyphae) to hold micro-aggregates together, building macro-aggregates—the larger structures in soils (Lewis & Lowenfels, 2010; SWCS, 2000). AM mycorrhizal fungi also produce significant amounts of glues, known as *glomalin*<sup>41</sup>. As a gluey substance, glomalin helps build soil macro-aggregates, and with its wax-like properties, it is not very soluble; therefore, it helps maintain the stability of soil aggregates during rain events (Schwartz, 2016)<sup>42</sup>. Humus can also hold significant amounts of water, which is a by-product of decomposition, particularly by fungi; some mycorrhizal fungi create water storage structures around plant roots, helping to keep plants hydrated during periods of water scarcity (Lowenfels, 2017). Collectively, this makes saprophytic and mycorrhizal fungi critical *autogenic structural engineers* and *water engineers*—helping bacteria and their biofilms build the ‘carbon soil sponge’ (see Schwartz, 2016).

All fungi, like bacteria, decompose organic matter using enzymes; however, many fungi also use a range of *acids*<sup>43</sup>. For this reason, fungus-dominated soils tend to be slightly more acidic (the pH is below 7)<sup>44</sup>. As fungi move through soils, they spread calcium and help *flocculate* (line up horizontally and break apart) collapsed clay colloids<sup>45</sup>. Therefore, due to effecting changes in soil pH and flocculation, saprophytic fungi are also important ‘chemical engineers’. *Actinomycetes*, as a group of single-cell bacteria that grow in long hyphae-like strands, also bind micro-aggregates, making them *autogenic structural engineers*.

As a transition to *consumers*, earthworms, which are decomposer predators, are great ecosystem engineers. As engineers, they are *burrowers* (like ‘micro-ploughs’), as they pull organic matter down from the soil surface underground—making it bioavailable for many other organisms, fungi and bacteria, and speeding up cycling of dead leaves, for example, from 1–2 years to around 3 months (Lewis & Lowenfels, 2010)<sup>46</sup>. Earthworms increase soils’ porosity through tunnelling, and therefore, support water and air flow through the soil. Collectively, this means that earthworms are (at least) important *bioturbators* (and *burrowers*), *particle matter processors* and *water engineers* (see Figure 19 as a summary so far).

*Bioturbation* is performed by many other animals, and therefore, consumers. Fiddler crabs (*Uca pugnax*) in new England salt marshes (Bertness, 1985), blind mole rats (Heth, 1991), prairie dogs (Whicker & Detling, 1988) and pocket gophers all dig and tunnel, moving large amounts of soil, increasing the replenishment of the water table and minimising erosion and runoff (Schwartz, 2016). Burrowing animals in marine benthic environments also play a dominant role in determining the physical structures of sediments, altering the suitability of habitat for other species (Jones et al., 1994). Bottom feeding fish also keep sediments in motion (bioturbation) while searching for food<sup>47</sup>. This relates to beavers, which build dams (*allogenic structures*), which ecologists think defends them from predation (Howard, 2017). Beavers help hold back nutrient-rich sediments and spread and slow river water over larger areas (Schwartz, 2016), creating new aquatic ecosystems (e.g. ponds), which has a profound effect on a range of resource-flows used by other organisms (Jones et al., 1994).

*Filter-feeding* consumers, such as (marine animals) clams, krill, sponges and whales, are able to trap/strain materials floating or suspended in a water solution or in the air, playing an important role in *purifying* their environment and benefiting other organisms. Therefore, filter feeders are important ‘light engineers’ that help keep aquatic systems clear enough for photosynthetic organisms (e.g. photosynthetic corals) to survive and thrive.

As mentioned above, corals are fundamental for reef ecosystems, serving as autogenic ‘structural engineers’. This is also true of ribbed mussels, which secrete byssal threads (silk-like fibres) that help form dense beds of mussels on marsh edges, protecting sediments and helping to reduce erosion and disturbances from storms (Jones et al., 1994).

Elephants are important *allogenic structural engineers*. Through their feeding, digging (often for minerals in sediments), dung and migrating behaviours, they alter fire regimes, affect the food supply and population dynamics of other animals, and ultimately, can change elements of the environment, including soil formation, riparian zones and biogeochemical cycling (Jones et al., 1994)<sup>48</sup>.

Cow pats can be viewed as effecting allogenic structural engineering. They create lush environments for invertebrate communities, providing both shelter and concentrated foods, such as non-digested lipids, for fly maggots.



**FIGURE 20.** Seagrass (*Thalassia testudinum* König) concentrating sediments (photo: St. John, 2011).

Plants—particularly trees—create important *autogenic structures* that are used by microbes, insects, birds, small mammals and many other plants, from mosses to vines and lichens. Plants also act as ‘litter trappers’ (Zona & Christenhusz, 2015), which are able to catch falling leaf litter and other organic debris; on a larger scale, riparian woodlands can hold riverbanks together, and seagrasses (Figure 20) help form and maintain a store of coastal nutrient-rich sediments. In this process, they concentrate sediments and organic matter and create new *autogenic structures* and ecosystems<sup>49</sup>.

Plants, through the loss of dead leaves and branches, generate *litter* under and around them. This keeps soils cool from the hot Sun; reduces water loss through evaporation; protects soil from direct rainfall (which compacts bare soils); reduces germination of young plants, which need plenty of light; creates habitat for soil macro fauna; and becomes an unfrozen water zone in winter, where soil fungi can eat and thrive (while others lie dormant). In these different ways, plant litter also makes plants *light, water* and *autogenic structural engineers*.

Trees (and other plants) can create wind and sunshade for animals and other plants. (Some plants profit, while others can suffer). In particular, micro-algae in coral reefs can have a large effect on the amount of light getting to the photosynthetic corals below. These corals need clear water, and without it, they will suffer from lack of light for their photosynthetic symbionts. This is another example of producers being important *light* (and wind) *engineers*.

Bog moss, such as sphagnum moss, builds large blankets or raised bogs on accumulated peat. The sphagnum peat develops low oxygen and high pH environments, cycling nutrients so slowly that many other plants cannot survive (but making peat bogs highly important stores of carbon). Thus, sphagnum moss belongs to the category of *chemical engineers*.

*Producers* are fundamental participants in the water cycle. Plant shade cools the land below, and as the plants transpire, they create a cooling effect (Runyan & D’Odorico, 2016). Some plants (particularly certain *trees* with microbe symbionts) also support the formation of low, thick clouds (which also provide a shade-cooling effect); by releasing aerosol/nuclei, they create the core that water needs to form a water droplet. The droplets can then form a haze and rise and form into clouds, later falling as rain (Schwartz, 2016)<sup>50</sup>. The ‘biotic pump theory’ suggests that these large transpiring areas of natural forest support the drawing-in of fresh ocean moisture inland (through an air-pressure differential). Therefore, deforestation of interior areas can result in continents becoming dry a few hundred kilometres inland (Schwartz, 2016)<sup>51</sup>.

*Coccolithophores* (calcifying micro-algae) release sulphur-based nuclei, supporting the formation of ocean clouds along coastlines (Harding, 2009) and priming the biotic pump into motion. (Terrestrial water flows from the ocean to replace water lost to the oceans by the rivers). In this way, producers are also fundamental water engineers—and light engineers—as low, dense clouds, which can cover an estimated 50% of the planet at any one time, are critical for planetary cooling (via shade and heat transfer into space; Schwartz, 2016).

The last example in this subsection describes three biotic units functioning together. Seagrass meadows accumulate vast amounts of organic matter, representing an important nutrient reserve for the plants—although, over time, this will eventually cause toxicity, which is detrimental to the plants. However, bivalve clams filter the water by feeding on the organic matter collected by the plants, and with the support of sulphide-oxidising bacteria that live on their gills, *detoxify* the water for the seagrass and the clams (Todd, 2019).

### The complete ecosystem Metabolisms and functions model

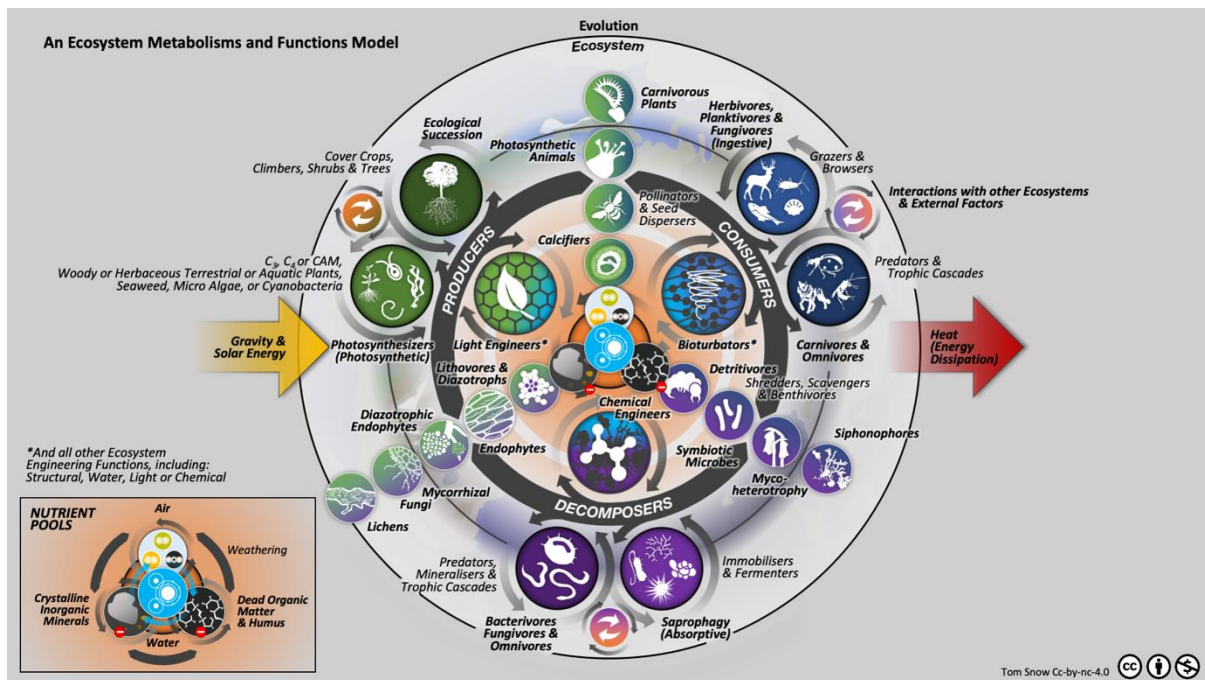


FIGURE 21. Ecosystem metabolisms and functions model (Snow, 2020).

Figure 21 shows the model in its complete—*holistic*—form. Sahtouris, 2000 (p. 49) provides a Vernadsky style perspective of life, which is an appropriate ‘book-end’ synthesis of the EMF model:

Vernadsky called life "a disperse of rock," because he saw life as a chemical process transforming rock into highly active living matter and back, breaking it up, and moving it about in an endless cyclical process. Vernadsky’s view is... [that] life is rock rearranging itself—like music come alive—packaging itself as cells, speeding its chemical changes with enzymes, turning cosmic radiation into its own forms of energy, transforming itself into ever-evolving creatures and back into rock.

### FRACTALS, ONE INTEGRATIVE METABOLISM DISCUSSION AND SOME CONCEPTS

This fourth main section is a relatively short discussion of the model at a different scale and through the focus of one integrative metabolism, ending with some ecosystem concepts.



## Integrative metabolisms of an ecosystem discussion

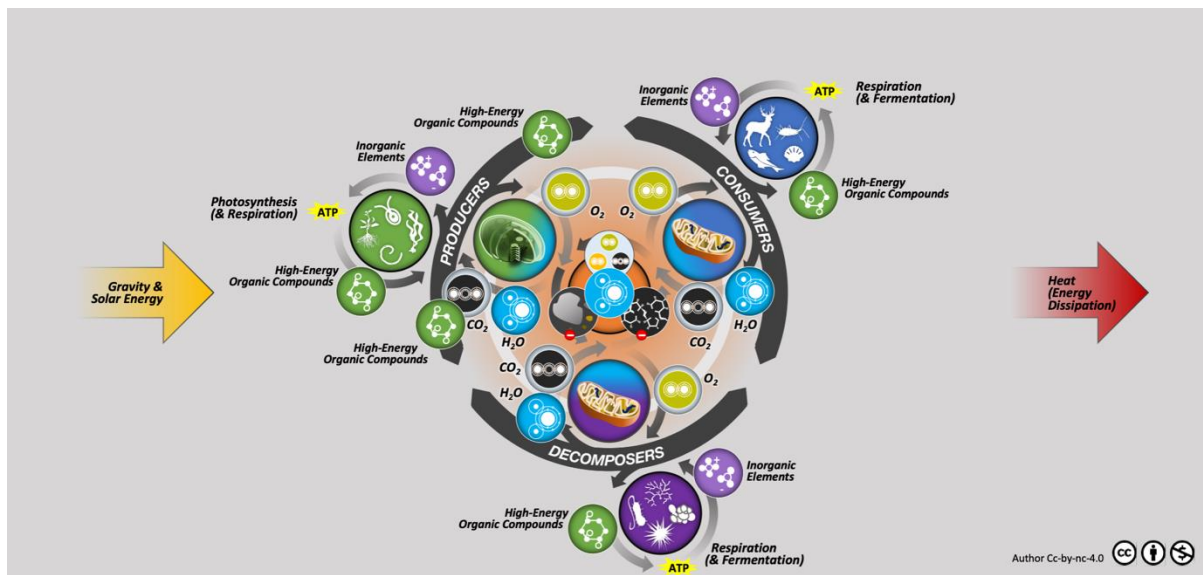


FIGURE 23. Integrative metabolisms of an ecosystem (Snow, 2020).

Figure 23 is a view of the EMF model showing the central foundational physical metabolism organelles—the small organs of the cell (or equivalent). As shown in Figure 22, plant producers have chloroplasts *and* mitochondria. However, to distinguish them in this model, only the chloroplasts are shown. Animal consumers have only mitochondria. Multicellular fungal decomposers also only have mitochondria, while all the single-cell fungi and bacteria (which are single cell) generally have the equivalent function within their single cell. The fermenters (e.g. yeasts) are the exception and have a less sophisticated metabolic system.

The smaller icons show the principal forms of organic and inorganic matter that each different group takes in and produces, along with the principal gas and water wastes during respiration. The point to underline here is that the plant producers create the oxygen (O<sub>2</sub>) ‘waste’ and the high-energy organic compounds, which the heterotrophs (consumers and decomposers) rely on; the heterotrophs produce the CO<sub>2</sub> *and* the water waste and inorganic elements the producer plants rely on. At the scale of an ecosystem, biome and the planet, this describes the foundational view of one integrative metabolism—without even adding all the functional inter-relations already reviewed in the previous main section.

Kleiber’s Law postulates that an animal twice the size of another requires only 75% more food per day (West, 2017). This can be described with a simple  $\frac{3}{4}$  power scaling (‘scaling rule’) for the *basal metabolic rate*, and it is proposed to apply to other taxonomic groups, including bacteria and plants (West, 2017).

Some generic network properties behind this apparent phenomenon include space filling (the need to feed all cells in the body), fractals and the approximate optimal (evolution tends to evolve to the optimal; West, 2017). Geoffrey West postulates that the fractal nature of these networks, *within* an organism, has allowed them to operate beyond the three dimensions of space, instead working at a fourth dimension (West, 2017); basically, the larger the organism, the greater the number of fractals and the more efficient they are.

From these astounding (and here, simplified) insights into scale, it could be suggested that this is purely an efficiencies-of-scale and economies-because-of-scale phenomenon. Indeed, these scaling laws of *individual organisms* have been applied as analogies to city design with this in mind (West, 2017).

Conversely, looking through the EMF framework and model ‘lens’, it can be argued that metabolism is a collective *ecosystem activity between* the different biotic units (as studied in ecological energetics) and between the different plant-cell organelles and between certain microbe communities.

Thus, individual metabolism essentially does not exist (see Figure 21, Figure 22 and Figure 23). How much metabolic energy (e.g. expended by a producer) was used, for example, to re(produce) the food for the so-called more efficient consumer? See Figure 5 for more on this topic. An exception (perhaps) involves certain forms of chemoautotrophs; however, they are (basically) individual single cells, which also suggests that an organism cannot evolve larger than a single cell without being part of a complex ecosystem.

It can be proposed that increases in scale, and with them, increased complexity and function, are made possible through internal *and external* fractal and non-fractal networks. Therefore, this is not a disagreement with the insight that a scaling law(s) may exist; rather, it tends to question how it exists and what we can learn by this for our design of systems of production—and cities. Perhaps city designers should not look at economies because of scale of a *single* organism as a guide to designing modern cities; instead, it may be better (a more appropriate analogy) to learn from ecosystem integration and ecosystem scaling rules (yet to be defined?) to be more efficient, zero-waste and healthy. Perhaps collectively, the 3 FGs (producers, consumers and decomposers) co-create the 1 emergent nutrient (therefore, 3 + 1), forming a 4<sup>th</sup> dimension (the nutrient pool being the 4<sup>th</sup> dimension in this case) that West proposes in his work. (See also see Pauli, 2010, for his concepts on energy held in relationships).

This brief discussion highlights the potential care we need to take when extracting analogies and patterns from living systems and the potential issues of viewing organisms without considering their relationship(s) with their abiotic and biotic environment. Finally, how ecosystems potentially evolve—as single organisms and/or as integrative communities and metabolisms—is outlined briefly in the endnotes.<sup>52</sup>

### **Ecosystem function concepts**

This final subsection introduces some concepts that can act as synthesis of some of the main points raised during this ‘deep dive’ into ecosystems.

Concepts related to energy are as follows (the last three in this list are not discussed in detail), but they are mentioned here because they are considered important within the overall theme):

- *Gravitational energy is primary before solar energy*: Earth is an open system to energy and is powered by direct sunshine around half a day on roughly half of the Earth’s surface and gravitationally powered 24 hours a day everywhere (Pauli, 2010).
- *Energy quality changes as it flows through ecosystems*: Energy flows into Earth as mostly high-quality and powerful light; eventually, all energy is transformed and flows back into space as low quality, dispersed heat (infrared), with virtually no recycling. This relates to the First Law of Thermodynamics and the concept of energy and transformity.
- *Plants drive energy into the biosphere*: Energy flows into the biosphere via producers (mainly plants on land and algae in our oceans), and it is transferred to other lifeforms in the form of high-energy organic compounds (see Soil and Water Conservation Society [SWCS], 2000).
- *Recycling energy requires energy*: Through each transformation, as one organism eats another, there is an expenditure of energy, which results in a loss of total available (free) energy (Rifkin, 2011). This relates to the Second Law of Thermodynamics.
- *Water cools*: Plants transpire, and particular plants (some with or some without symbiotic bacteria) can support the formation of clouds. Transpiration and cloud formation have a local and planetary cooling effect and can potentially draw water inland from the oceans. Plants cannot transpire if there is no carbon soil sponge—water held in the soil thanks to a healthy soil food web and organic matter (Schwartz, 2016).
- *Cellular energy is driven by hydrogen batteries and adenosine triphosphate ‘currency’*: Many producers extract hydrogen from water using the energy of sunlight to create a hydrogen *differential*. This generates flow, driving a ‘turbine’ (adenosine triphosphate [ATP] synthase) that produces ATP. ATP is a stable form of energy transport in the cells that can work in various

ways. Respiration uses a similar hydrogen differential in the process of producing ATP from high-energy organic compounds (e.g. glucose), while producing water as a by-product.

- *The ecosystem economy is based on sugar:* Producers use ATP (and electron carriers) to power the fixation of CO<sub>2</sub> and produce glucose. Glucose is the base of fuel in cellular, inter-cellular and inter-organism transport (exchange and use), as well as for making many structural molecules (e.g. cellulose). Glucose can be transformed for transport (e.g. sucrose), sharing with others (e.g. fructose) or storage (e.g. starch).
- *Lipids store large amounts of energy:* Lipids, such as fats and oils, store vast amounts of energy. Lipids also form biological membranes and can be used for communication.

Matter is related to the following concepts:

- *Matter cycles:* Earth is practically a closed system to matter. Ecosystems are open systems to matter and energy (Jørgensen & Mitsch, 2004). Matter (re)cycles many times around the biosphere and through the other spheres (biotic and abiotic) at different rates and in different forms. This affects and is affected by life.
- *Matter cycles and is bi-directional:* Matter flows indirectly via nutrient pools and directly through trophic relationships. Matter flowing through trophic relationships predominantly moves from producers to consumers to decomposers; however, matter also flows in both directions, between producers and decomposers and symbiotic decomposers and consumers. Therefore, direct trophic relationships are truly circular (not linear) and bi-directional (see SWCS, 2000).
- *Life creates structures:* All forms of life can build (biosynthesise) different forms of carbohydrates, lipids, proteins and nucleic acids (macromolecules) as building blocks for more complex structures (e.g. polymers, or enzymes) and secondary metabolites. Ecosystems store information in the structures (Jørgensen & Mitsch, 2004).
- *Matter is never truly consumed:* What is consumed comprises the qualities—the concentration, the purity and the structure—of matter and the ability of energy to perform work (Robèrt et al., 2010).

Concepts related to life are as follows:

- *Life is autopoietic—self-making:* The main characteristics of life are that life self-maintains (with a persistent input of energy) through an internal network of chemical systems that reproduces itself continuously, within some form of boundary of its making (Capra & Luisi, 2014/2015).
- *Life is self-organising and self-replicating:* Living systems are self-organising networks; unlike chemical reactions, they can replicate themselves (Pross, 2012).
- *Functions emerged through life:* There are no true functions in the abiotic physical and chemical systems of Earth or any planet. Functions emerged from life at all scales—from rubisco enzyme that fixes CO<sub>2</sub> to a heart that pumps blood, an ear that can hear (see Pross, 2012) or a *living* watershed that cleans water.
- *Functions are nested:* As we continue to remove (kill or make extinct) different species from ecosystems, we are not only removing a direct or indirect food source for other organisms, but we are also removing a functioning individual whole within an assemblage whole and greater ecosystem whole.
- *Organisms develop multi-functionality:* Fats keep us warm or plants cool (by reflecting light), and they are highly efficient in storing energy. Roots hold a plant to the ground and soil macroaggregates together, and they collect, store and share nutrients with living soil.
- *Forms of metabolism can define all forms of life:* Healthy, modern ecosystems usually consist of three foundational functional *biotic* groups or metabolisms, which are as follows: producers,



consumers and decomposers. These are all inseparably integrative and interact with their environment, the nutrient pools and each other (Sahtouris, 2000; Vernadsky, 1997).

- *Life interacts directly and indirectly through trophic relationships*: Organisms can be eaten by another directly or indirectly via nutrient pools; they produce secondary metabolites for their use or for direct exchange with other organisms; and they produce by-products or 'wastes', which can be (unintentionally) foods for other organisms.
- *Waste for one is food for another*: Metabolic wastes of one form of metabolism can be food for others in the *same* metabolism group (but not directly between producers, although plants do share nutrients via fungal networks) or other metabolism groups (see simplified version by Margulis & Sagan, 1995). On land, virtually all wastes of producers and consumers are food for decomposers; in the oceans, microscopic aquatic *producers*, such as micro-algae (which are from the Kingdom Protista) and cyanobacteria (Kingdom Monera) can also absorb organic wastes.
- *Functions can be trophic and non-trophic*: Organisms interact directly and indirectly in all directions through different *trophic functions*, including who-eats-whom, eating behaviours and modes of nutrition (photosynthetic, ingestive and absorptive); and *non-trophic functions*, such as ecological engineering (e.g. structural, light, chemical and water engineers and bioturbators).
- *Life collectively creates living soil*: Life both uses what it needs from living soil (as opposed to non-living regolith) and creates and regenerates it. Soil is alive with microbes, plant roots, and many animals and insects, which create its structure and other abiotic properties (Ingham & Rollins, 2011). Soil is the interface between all the abiotic spheres on Earth (e.g. hydrosphere, lithosphere, atmosphere) and life (the biosphere).
- *Consumers are value adding*: Consumers may not be obligatory organisms in all modern ecosystems; however, their presence can support greater cycling rates of nutrients (principally by increasing the bio-availability of nutrients for decomposers), defence, pollination and seed dispersal of plants, provoking change to or maintaining ecosystem communities, changing hydrological flows and reducing loss of biomass into the atmosphere, for example, during annual fires (Butterfield & Savory, 2016; Schwartz, 2016). Therefore, they can be considered obligatory for highly functioning, bio-diverse and healthy ecosystems.
- *Collaboration and division of labour exist in living systems*: Conjunctive symbionts (those that bond together in a physical way) show that many organisms give up individual freedom for the benefits of living with and within a host, either permanently or temporarily. The host creates an appropriate environment (e.g. appropriate pH, water and oxygen levels, food and shelter from the environment or predators), and in return, the symbiont can fully focus on what it does best—producing an important nutrient, such as glucose or nitrogen, or helping break down wastes.
- *Pioneer and foundational species are often conjunctive symbionts*: Conjunctive symbiotic organisms are often structural and/or pioneer species in early ecological succession ecosystems. Some are eventually displaced, while others remain as important foundational organisms.
- *Life is foundationally symbiotic*: At a cellular level, all eukaryotic forms of life are symbiotic (symbiogenesis), and all plants and animals are symbionts of some sort (often with bacteria, fungi and/or protists). What started out as cooperation between separate bacteria in the early evolution of life ended in the creation of one indivisible cell, illustrating a general principle: 'Sometimes, social groups become so functionally integrated that they become higher-level organisms in their own right' (Sloan Wilson, cited in Brown, 2003). Life involves competition, but at the same time, it is highly symbiotic, integrative and interdependent (Margulis & Sagan, 1995).
- *Plants are a fractal of a functional modern ecosystem*: At the cellular level, plants can be seen as one of the most advanced organisms on Earth; they are a fractal of a functioning modern

ecosystem. That is to say, they have organelles that function in similar ways to producers, consumers and decomposers at the ecosystem level.

- *Life is one integrative and interdependent metabolism:* There is no such thing as a fully independent metabolism of a single multi-cellular organism (Sahtouris, 2000; Vernadsky, 1997). Perhaps collectively, the three fundamental forms of metabolism (producers, consumers and decomposers) co-create the one emergent NP (therefore, three + one), forming a *fourth dimension* in the ecosystem of collective efficiency. It is proposed that increases in scale, and with them, increased complexity and function, are made possible through internal and external fractal and non-fractal networks between the different forms of metabolism and NPs.
- *Life integrates and separates:* As well as integrating (e.g. biosynthesis or anabolism), organisms also separate substances (see Pauli, n.d.), such as through catabolism—breaking down complex molecules into smaller molecules (usually releasing energy in the process), which can then be used for the anabolism of other complex molecules (requiring energy; Sahtouris, 2000). Decomposers decompose minerals and organic matter into mineral elements using enzymes. Mineralisation is an advanced form of decomposition by organisms into inorganic elements.
- *Evolution can also occur at the ecosystem level:* Life on terrestrial Earth evolved through collaborations between fungi, plants and bacteria, and later, animals (Margulis, 1998). There are potential mechanisms that lead to the evolution of foundational biotic/metabolism groups (producers, consumers, decomposers) with their environment, through ecosystem-level selection of ecosystem properties. In this way, the fitness of the species that make up an assemblage is potentially determined by their collective behaviour, selecting for optimum assemblage performance (see Todd, 2019).

## VALUE ADDING AND CONCLUSIONS

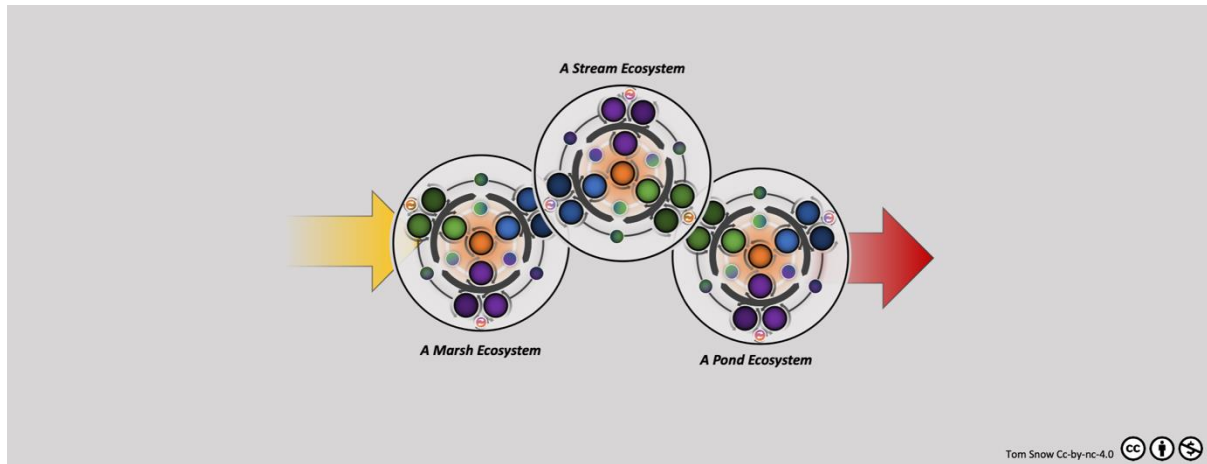
This fifth and final main section discusses some of the value that the framework and model intend to bring to existing frameworks and models, some potential practical applications (beyond pure pedagogical learning) and some conclusions.

### The ecosystem metabolisms and functions model and its use

To this point, the EMF model has been used in academic environments at the university level and in consultancy work (with farmers, industrial actors and economists), and in all cases, it has been communicated in a progressive way, similar to the different stages in this paper (to the level required). With the aid of animations of the model and the support of videos and photos, the model has proven to provide a good foundation for non-‘eco-literates’ and eco-literates alike. The depth to which the model is described can be tailored to the audience, time and objective of the classes (and knowledge of the person presenting). From experience so far in an academic setting, if context allows, a primer in Earth Systems Science topics, such as gravity, thermal dynamics, principle biogeochemical cycles and climate—which also provides some grounding in geophysics and geochemistry; followed by the Five Kingdoms of Life (including symbiogenesis), form a solid base prior to presenting the models delineated in this paper.

As well as an education tool, the EMF model can be used directly within the practical design process, principally for those working directly with living systems, such as designers of various forms of regenerative agriculture. For example, the EMF model can bring value to thinking about (and explaining to others) integrative and regenerative farming practices. The following is an example of an existing form of practice: Once cows have left a pasture, flies can lay eggs in the cows’ faeces. After several days, these eggs develop into maggots, which feed on the remaining lipids (fats) in the cows’ excrement (as the microbiome of the cows cannot break this down very easily in the anaerobic conditions of a cow’s rumen). Once the maggots are large enough, chickens are allowed into the pasture to feed on the maggots. (Chickens are omnivores). This provides a protein source for the chickens, and as they scratch and dig in the cow dung, they also spread it around the field (Pollan, 2006)—which is a bioturbator *function*. All the different organisms are from the Kingdom Animalia (cows, flies, maggots and chickens),

and thus, these interactions cannot be described between *different* kingdoms; in addition, they include a non-living element—the faeces, which is also an important part of the system. The EMF model can help explain these interactions as it includes living and non-living elements and functions.



**FIGURE 24.** ‘Eco-machine’ assembly made of different ecosystems, inspired by Todd 2019 (Snow, 2020).

The framework can also be modified to illustrate *specific* ecosystems (e.g. bogs, grasslands, ponds or pine forests). Thus, the framework can be used directly for supporting the design of ‘mesocosms’ (also known as ‘eco-machines’)—those (usually aquatic-based) systems that are often designed to carry out ‘work’ for society, such as cleaning water, growing food or fuels, or remediating polluted landscapes, based on *ecological design* (Todd, 2019; Figure 24).

An important point to underline is that this model does not detail any specific assemblages of organisms in any particular ecosystem. As Todd (2019) highlights in some of his work, often, even with a good understanding of what different functions may be required, it is through the process of mixing many microbe species together in a system, for example, that we can see what new assembly *emerges*; over relatively short periods, these systems can potentially self-assemble into an optimum assemblage. Finally, it was already mentioned in the introduction that the EMF framework and model can be used to develop *analogous* framework(s) for many types of human systems of production (e.g. agriculture, product-life-extension activities and the bioeconomy), including how these different types of production systems interact and function with each other and the environment (as in the EMF model)<sup>53</sup>.

## Conclusions

The EMF framework has emerged from the teachings from many experts and experienced practitioners (directly and indirectly), from different fields of biology, ecology, regenerative agriculture and geology; however, this paper is the first written presentation of the framework in the public domain. Therefore, there may be some (hopefully not significant) errors; however, it is my intention that the main model and framework is solid and flexible enough (like bamboo) to adapt and change if need be, while still being a valuable structure as it is today.

As already mentioned, this model and framework has primarily been created for designers working within systems of production; however, the design of these systems is clearly not only made by ‘designers’. The act of design can be carried out by a broad range of different disciplines, often in collaboration; therefore, the intent is that this framework will also communicate and bring value to this diversity. Perhaps one of the key roles of designers in this new paradigm is to support collaboration and shared awareness and clarification across diverse stakeholders (much like mycorrhizal fungi) and help illuminate how complex systems function and where we came from, where we are and where we collectively want to go.

The core of the paper, which lays out the main EMF model, tries to push towards a high level of detail in an attempt to present the terrain in one place (with additional endnotes to go even further). The paper could have remained at an introductory level; however, this can keep the understanding at a level that may not be high enough for us to make real transformations to the way we see the world and proactively work within it. Learning about life and our local ecosystems is a lifetime journey—including observation, experience and interaction—with these complex systems. The EMF model attempts to visualise some complexity, not necessarily simplify it.

In explaining these topics, some instructors experience that the first hurdle for those learning can be that these topics are viewed as ‘science’ (or scientific)—and that science is too complicated, something that was left behind at school. The second hurdle is that students may not be able to deal with the high complexity of these topics (for varying reasons, from work overload to reduced capacities for concentration or these topics being perceived as beyond their abilities). The result can be a dumbing-down (fragmentation or ‘simple-stupid’)—and potentially ‘dumb design’ (Cowan & Van der Ryn, 1996, p. 26). Conversely, in developing this model and paper, the following question was asked: How can we express the most—at the highest possible potential? Complexity is real; we need to reconnect with it.

As Cowan and Van der Ryn (1996, p. 43) point out, the idea of ecological design is not new: It has already, *by necessity*, ‘been brought to a high level of excellence by many cultures faced with widely varying conditions’. For example, ‘Australian aborigines use stories and rituals to preserve an exquisitely detailed ecological map of their lands’ (Cowan & Van der Ryn, 1996, p. 44). With the myriad of issues humanity faces today (as briefly discussed in the introduction), I think that eco-literacy and eco-design are necessities (again) for *all of us*.

As a non-scientist, I understand from personal experience that it is possible to comprehend, experience and apply these concepts. If we have the right teachers/community of practice and tools, and we are motivated, we can all arrive at high levels of eco-literacy (while retaining a sense of humility about the limits of our ever-evolving co-understanding). Through different approaches and activities in the ‘real world’, science practiced by a supposedly objective observer can evolve into direct observation, learning, data collection *and* adaption and interaction involving a proactive participant and partner. As we continue to learn, through study, experience and collaboration, how life regenerates the conditions for more life, through a myriad of relationships, it may help us evolve our relationships as an active part of these living systems (collectively forming Earth) to ones that have greater congruence and respect and are regenerative by intention.

#### ACKNOWLEDGEMENTS

The seeds for *knowing* that I needed to understand living systems far more deeply, were first hydrated during a Blue Economy (ZERI in action) course in Hungary. I would like to thank my teachers, Gunter Pauli, Silvia Barbero, Tibor Kiss, Ivanka Milenkovic, and Curt Hallberg; and the support of Katalin Hartung, Péter Fodor and my classmates. I would like to thank my teacher in soil biology and compost, Dr. Elaine Ingham; from this deep and instructive dive into the rich microcosm within living soils, I was gifted a foundational scientific structure to build from. Furthermore, I would like to thank Chiara Battistoni for first proposing that I enter a paper into an RSD conference, and Tom Hoppen and Désirée Driesenaar for insisting that I should get my ideas and models ‘out there.’ I would further like to thank Ben Sweeting for his initial help with this paper; and later Marie Davidova for her challenges and probing into the details and the voids that needed addressing. Finally, I would like to thank Paul Fleckney for his encouragement and feedback, and Birger Sevaldson for his succinct, but impactful encouragement after the fledgling paper was first presented at the RSD conference.

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## END NOTES

<sup>1</sup> Every day, for example, humans produce around 80 kg of ATP (West, 2017)! This means that the mitochondria are very busy—and the reason why there are around 500–1000 in each of our cells (and more in muscle cells).

<sup>2</sup> There are principally three types of *producer*: photosynthetic bacteria, photosynthetic Protista and plants. *Photosynthetic bacteria* (Kingdom Monera) include cyanobacteria (e.g. *Prochlorococcus*, *Anabaena*, *Nostoc* and *Spirulina*), which are understood to be the major contributors to the oxygen in our atmosphere (Margulis, 1998); however, some can be toxic in some cases (e.g. *Microcystis aeruginosa*, which can create toxic blooms in water systems). *Photosynthetic Protista* (Kingdom Protista—unicellular, colonial or multicellular—mostly microbial – organisms that have a true cellular nucleus), such as some species of Dinoflagellata (e.g. endosymbionts within some corals) and Euglenophyta (e.g. Eutreptiales and Euglenales) and Chlorophyta (e.g. *Chlorella*), as well as Phaeophyta (brown algae/kelp) and Rhodophyta (red algae). *Plants* (Kingdom Plantae) are characterised by three attributes: They contain chlorophyll ‘a’ and ‘b’, they have specialised structural elements (e.g. organs, roots, stems and leaves) and their cell walls contain cellulose (Todd, 2019).

It is important to mention that several strains of microalgae (Figure 6), have the capacity to use different carbon sources and grow heterotrophically, using organic compounds (e.g. glucose, acetate and glycerol) as their only source of carbon (Barros et al., 2019). Those that ferment these organic compounds can also do this without a source of light (Liu et al., 2016). Microalgae species can also absorb inorganic nutrients like plants (e.g. nitrates, nitrites and ammonium) and phosphorus for their growth, and they have capacities to remove heavy metals and toxic compounds from their environment (Abdel-Raouf et al., 2012).

<sup>3</sup> There are essentially two types of decomposers, which are as follows: saprotrophic (which describes this *extracellular* digestion of decayed—dead or waste—organic matter) fungi and bacteria. *Saprotrophic fungi* help to release nutrients through the continuous recycling of dead or decaying organic materials, using enzymes (e.g. cellulase) or acids (e.g. oxalic acid [C<sub>2</sub>H<sub>2</sub>O<sub>4</sub>]) and potentially hydrogen ions (H<sup>+</sup>) to break down cellulose in dead green plant matter, tougher substances like hemicellulose and lignin in woody materials. Some saprotrophic fungi are also able to break down inorganic crystalline materials (i.e. clays, sands, silts, clays, pebbles, stones and rocks) – known as ‘bio-weathering’; some are also able to break-down keratin and collagen from animal biomass.

Collectively, with this vast range of enzymes and acids, saprotrophic fungi are the ‘great decomposers’ across all terrestrial and oceanic ecosystems, helping to break down (recycle) 90% of all nutrients on Earth (Lewis & Lowenfels, 2010), with bacteria following behind in distant second place. However saprophytic fungi are specialised in breaking down tougher woody materials, meaning that they are generally more abundant in woodlands (than bacteria) and less abundant in areas where the plants are more predominantly cellulose, such as grass-pastures (which are more bacterial dominated). Fungi can be large in mass, but their mass is made up of large, interconnected lengths of microscopic strands or chains, known as *hyphae*.

*Saprotrophic bacteria* freely ‘swim’ around the plant root zone (Rhizobacteria) and use their array of enzymes to principally feed on *simple carbons*. However, particularly important saprophytic bacteria, *Actinobacteria*, are some of the few bacteria that can break down *chitin* (the tough material that makes up, e.g. the fungal outer wall and the shells of insects), as well as other complex carbons (SWCS, 2000).

<sup>4</sup> Since the wastes of the fermenters still contain some energy (thanks to the inefficiency of fermentation), other microbes (e.g. other fermenting bacteria and Archaea) can form a *consortium*, continuing to metabolise further, producing other by-products (which may also be further metabolised), such as butyric acid, acetones, acetate, carboxylic acids and formate. Methanogens (a type of Archaea) are considered the ‘final step’ in the decomposition of biomass, with their ability to convert acetate into (bio)methane.

<sup>5</sup> Kingdom Animalia can be divided into nine ‘phylum’ groups: Annelida (segmented worms), Nematoda (roundworms), Platyhelminthes (flatworms), Porifera (sponges), Cnidaria (coral, jellyfish), Mollusca (snails, clams, octopi), Echinodermata (starfish, sea urchins), Arthropoda (different invertebrates—no backbone: insects, spiders, barnacles, etc.) and Chordata (different vertebrates—with backbone: amphibians, reptiles, birds, mammals, fish, etc.).

<sup>6</sup> Although around 90 different chemical elements can be found in soil, most rocks mainly comprise *silicon* (Si), *aluminium* (Al) and *oxygen* (O) – with the first two often bound to oxygen; and to a lesser extent *iron*, *magnesium*, *calcium*, *sodium* and *potassium* (Biklé & Montgomery, 2016). All have a charge at the molecular level and combine to make up different minerals (Biklé & Montgomery, 2016).

Crystalline inorganic minerals can *move* into an ecosystem, often on slow timescales, via deposits from erosion. *Weathering* is the process of rocks being broken apart within the *same* area, and this can occur through abiotic processes, such as rain, wind, frost and ice conditions, or biotic processes (*bio-weathering*), such as by plant roots breaking rocks apart through turgor pressure or bacteria and fungi chemically breaking down rocks with their enzymes or acids. *Erosion* describes the process of how materials move into or out of an ecosystem. Factors that affect the rate of erosion include the slope, altitude and aspect, temperature and type of soil texture, and geological erosion includes winds, rain and water and ice flow. *Bio-erosion* is a term that is usually used to describe erosion by organisms in *aquatic* environments, such as molluscs and parrotfish, that ‘drill’ or ‘scrape’ coral reefs in search for food. *Isostasy* is the process by which erosion initiates the *uplift* of rocks from deep within the Earth, which means that erosion not only removes material from an ecosystem but also induces ‘fresh’ rocks to move up towards the surface to replace what has been lost (Montgomery, 2012). Once soils form, bio-weathering is the predominant process, breaking down bedrock faster than abiotic processes do (Montgomery, 2012). For soils to form and persist, weathering rates need to be equal to or greater than erosion rates (Montgomery, 2012).

<sup>7</sup> Detritus is the food-web ready for recycling—where many organisms, particularly microbes, such as fungi and bacteria, separate once living materials, and through their actions, make them available again for other existing or new lifeforms to use to put together. Dead organic matter is in various stages of decomposition—from fresh to decomposing, and finally, complex humus. Carbon is the main constituent of soil organic matter, comprising around 60% of its dry weight (Schwartz, 2016), and it is chiefly found in autumn leaves, bark, woodchips, seeds and branches (Lewis & Lowenfels, 2010). Another important constituent is nitrogen, which is found in higher amounts, for example, in fresh grasses, urine and faeces.

<sup>8</sup> It is estimated that the decomposers only respire around half of the carbon in organic matter back into the atmosphere (Biklé & Montgomery, 2016); the remaining is left as decay-resistant carbon compounds, with only fungi able to break down the most complex components (SWCS, 2000).

<sup>9</sup> Nutrients flowing in the soil water have either a positive charge (cations) or negative charge (anions); the nutrient *cations* are attracted to the free available sites on the clays (only around 1% of cations remain in water; Lewis & Lowenfels, 2010). Plant roots also bear a negative charge by actively pumping out *hydrogen ions* (H<sup>+</sup>) as a (weak) form of nutrient uptake (Lowenfels, 2013). Decomposers also have a negative charge due to their small size, and so bacteria and fungi can hold some nutrients on the outside of their bodies. Anions (if not taken-up by an organism) can be more easily lost to leaching.

<sup>10</sup> The nitrogen-fixing species within these sub-kingdoms, are collectively known as *diazotrophs* (see icon in FIGURE 10). Through the use of a specific enzyme (*nitrogenase*), these diazotrophs evolved the ability to break apart the strong bonds holding the two nitrogen atoms together. The ability to make the specific enzyme to fix nitrogen is distributed (and maintained) across different branches of the Monera 'tree'—which is thought to have been shared/acquired by horizontal gene transfer (Falkowski, 2015). Diazotrophs in the soil fix around 225 kg/hectare/year of nitrogen (Biklé & Montgomery, 2016).

<sup>11</sup> Such as a hydrogen source for carbon dioxide fixation (and therefore, biosynthesis) or as a source of energy to produce ATP (via aerobic or anaerobic respiration; Biklé & Montgomery, 2016). The chemoautotrophs described in the first subsection are a form of lithotroph (e.g. cyanobacteria); however, there are also other important non-photosynthetic forms, such as nitrifying bacteria, phosphate-solubilising bacteria and sulphur-oxidising Archaea.

<sup>12</sup> An important short diversion is that phosphorus-solubilising bacteria develop a mutualistic relationship with certain fungi, which can take up the freed phosphorus and deliver it to plants (Biklé & Montgomery, 2016); it may be the case that the fungi stimulate the plants to produce sugars in exchange (Lewis & Lowenfels, 2010).

<sup>13</sup> Examples include calcium phosphate, which is the primary constituent of bone, teeth and fish scales; calcium carbonates, which are prevalent in marine environments, such as the shells of clams, snails, molluscs, corals and certain types of algae; silicates, which are prevalent in Diatoms (a form of algae), Radiolaria (a form of protozoa) and some sponges; and chitinous (a modified polysaccharide that contains nitrogen) exoskeletons of arthropods and in the membranes of fungi.

<sup>14</sup> However, around 50% of the sugars in the root zone are subsequently pumped out into the soil (mostly in the spring), when the plant is in full growing mode (Biklé & Montgomery, 2016; Lewis & Lowenfels, 2010). This means that most of the soil's active bacteria and fungi are around the rootzone of the plants (Biklé & Montgomery, 2016; Lewis & Lowenfels, 2010).

<sup>15</sup> The soil *Eh* (redox potential) factor is also related to and potentially as important as pH within soils, which the plants and their microbiome are adjusting. See works by Olivier Husson for more about this.

<sup>16</sup> The decomposer predators in soils, consist of primary predators (e.g. root nematodes and algae-eating diatoms), which predominantly eat the producers (and therefore, can be pests from a producer—and often human—perspective); secondary predators, which include bacterivores, fungivores and omnivores (e.g. bacteria-eating nematodes and protozoa, fungus eating nematodes, protozoa and mites and omnivore springtails); and *tertiary consumers*, including 'apex' predators (e.g. predatory nematodes and earthworms) and other predators, such as predatory mites, spiders, ants and potworms (worms found more commonly in woodland environments; SWCS, 2000).

<sup>17</sup> The three major groups of these bacteria are Actinomycetes, Firmicutes and Bacteroidetes. Principally, Actinomycetes produce a wide diversity of compounds that interfere with bacterial, fungal and viral pathogens for example (Biklé & Montgomery, 2016). Other potential compounds include *gibberellins*—plant growth regulators widely used in the nursery and agricultural industries—and *cytokinins*—plant growth regulators that promote cell division and greatly support plant health and development (Lewis & Lowenfels, 2010).

<sup>18</sup> Predators are rare relative to their prey and are forced to range over much larger areas than their prey do (Estes et al., 2010).

<sup>19</sup> Such as moles that feed on earthworms and can be eaten, for instance, by wolves or animals that eat mushrooms (the fruiting body of certain types of fungi), which can also help spread the fungal spores, supporting their reproduction (McCoy, 2016).

<sup>20</sup> These organisms usually have teeth or crushing internal 'crops'—like earthworms, which are able to shred larger materials (and are often called '*shredders*') and pull them underground, making them more *bioavailable* for other soil decomposers (Biklé & Montgomery, 2016). This group includes certain species that are specialised in eating fresh animal faeces, known as *coprophages* (e.g. dung-beetles); these species are fundamental in helping recycle nutrients in many different ecosystems. *Termites* are also important detritivores. Thanks mainly to symbiotic protozoa in their hindgut, they can break down cellulose. Termites are also able to break down the tougher parts of woody plants (*lignin*) with the help of fungi, which they farm inside their mounds. The fungi break down the termite's faecal pellets, which contain high quantities of undigested lignin, and after a few weeks, the substance is broken down enough for the termites to re-ingest and digest it (Cox & Cohen, 2013). It has been estimated that around 90% of all the lignin in a park in northern South Africa is returned to the ecosystem thanks to the termites and their farmed fungi (Cox & Cohen, 2013).

<sup>21</sup> It is thought to have evolved nine times, in five different orders of flowering plants (Givnish, 2015). They are mentioned here less for their overall importance to ecosystems and more to highlight that, in nature, there are no hard lines between virtually any attribute—and its corresponding form of taxonomy. Carnivorous plants have fascinated scientists since at least pioneering studies by Charles Darwin in 1875, particularly as they have seemed to 'turn the evolutionary table on (some) animals'—consuming them as prey, with the aid of astounding lures, traps, stomachs and even speed of movement (Givnish, 2015). This is an example of a *direct* trophic interaction between consumers and producers.

<sup>22</sup> An interesting exception to this is seen in some orchids that do not produce nectar (and therefore, do not use resources producing it), instead producing flowers that look or smell like female insects (usually bees or wasps). Males are drawn to the flower to mate with it, and in doing so, provide the ‘service’ of pollen dispersal—without a resource in return (University of Chicago Press Journals, 2009).

<sup>23</sup> For example, the oak tree relies significantly on the spreading of its seeds away from the shade of the forest to more open grasslands (which its seedling needs to grow and thrive), through burial by jays (among the smallest members of the crow family; Whitfield, 2014).

<sup>24</sup> In addition, if eaten, some seeds can survive the digestion acids in the consumer stomach to remain fertile on the way out—and some actually *need* the weakening of the seed coat (the outer layer) through digestion to help germination (Whitfield, 2014).

<sup>25</sup> For example, increasing bacterial predator populations, such as protozoa, can counterintuitively *increase* bacterial populations (Lewis & Lowenfels, 2010). This can arise because fewer bacteria (after predation by the protozoa) mean less competition for resources between the remaining surviving bacteria. The remaining bacteria can then grow and divide quickly on the available resources; this provides more food for the protozoa (Lewis & Lowenfels, 2010), which can also grow and reproduce (at a slower rate than the prey).

<sup>26</sup> Relatedly, decomposer communities also show a predictable composition change, particularly in the ratio of fungi to bacteria, which also determines the types of decomposer predators (Lewis & Lowenfels, 2010). Outside of ecology, in legal medicine, *successions* of necrophagous insects (those that feed on dead or decaying flesh) are placed on corpses to estimate the time of death (Lewis & Lowenfels, 2010).

<sup>27</sup> In a seminal paper by E. P. Odum (1969), the study of ecological succession is extended to a broader concept of ecosystem development. This integrative concept includes changes in material and energy flows, combined with species history traits, species diversity, food-web structure and many other properties of ecological communities.

<sup>28</sup> The line is blurred between parasites and predators, in the case of *parasitoids* (which is mentioned in the framework). The best-known parasitoid includes several species of wasps, which immobilise (they do not kill) their host by stinging it. The female then carries the host to the burrow, where she lays her eggs (within the host’s body). As the larvae hatch, they consume the host from inside out, which kills it (Stevens, 2010). These parasitoid wasps often eat parasitic insects, such as caterpillars, moths, greenfly and scale insects to the benefit of plants (and us), while the adult feeds on the nectar supplied by the plants (i.e. another *service–resource relationship*). Parasitic plants are those that derive some or all of their nutritional requirements from other plants. They are estimated to make up around 1% of flowering plants (angiosperms) found in most ecosystems. They have modified roots (called haustoria) that can penetrate the host plant, connecting them to the xylem or phloem (or both) conductive systems; where they can extract water and nutrients. Mistletoe is one example of a well-known *obligate* parasitic plant; another, *Monotropa uniflora*, is discussed in the next subsection.

<sup>29</sup> This incredible ability has amazed scientists for decades; as John Tyler Bonner (MacPherson, 2010) contends, slime moulds are ‘no more than a bag of amoebae encased in a thin slime sheath, yet they manage to have various behaviours that are equal to those animals who possess muscles and nerves with ganglia – that is, simple brains’.

<sup>30</sup> Mycorrhizal fungi can then directly share some of these nutrients with the host plant. These can include (if they are available in the soil) many of the important metals, such as copper, nickel, magnesium, manganese, zinc, iron and sodium; metalloids like boron; non-metals, such as nitrogen, sulphur and phosphorus (it is estimated that some host plants can source up to 80% of their phosphorus from AM fungi); and water (AM fungi can be critical for plant hydration, e.g. cacti in deserts).

<sup>31</sup> EM fungi develop a conjunctive symbiotic relationship with approximately 5% of all land plants. Most of these plants are forest trees, such as pine (*Pinus*), beech (*Fagus*), birch (*Betula*) and myrtle (*Myrtus*). Twenty-five per cent of EM fungi can also form ‘fruiting bodies’ – commonly known as *mushrooms*—both as underground mushrooms, such as truffles, and above-ground ones, such as boletes and morels, which are from the Ascomycetes and Basidiomycetes phyla.

<sup>xxxii</sup> Endophytic fungi live inside virtually all above-ground plant tissues, such as leaves, bark and stems (there are also some roots dwellers too, though much rarer), and in virtually all environments. These fungi work themselves in between the cell walls of the plant, but do not enter the cells. Currently it is thought that all plants have at least one type of endophytic fungi relationship, with the most extreme example found so far, being the Douglas-Fir tree, which hosts an estimated 100,000,000,000 *Rhizoglyphus* individuals, within a single tree! Many endophytic fungi are from the Ascomycetes (sac fungi) phylum, and most seem to live mutualistically with their host, although they can also be pathogens.

<sup>33</sup> For example, some will react to pest eggs being laid on their host plant by subsequently infecting the particular food source (e.g. galls) that the hatching larvae need to grow—resulting in their starvation. Others are able to produce toxins (mycotoxins) to kill aphids or even produce alkaloids that put off larger ruminants from eating their host (as they can cause sleepiness in the animals), such as in the case of camel weed grasses (*Lolium temulentum*). Other types, like *Trichoderma*, attack and feed on other types of fungi—specifically one type, or many, depending on the type. One particular form of *Trichoderma*, T-22, helps reduce the nitrogen needs of its host corn plants by an estimated 30–40%.

<sup>34</sup> Examples of conjunctive symbiotic cyanobacteria associated with plants include some liverworts (Bryophytes) and Azolla fern. In the case of the Azolla fern, the bacteria associates with the plant throughout its lifecycle and is automatically transmitted from generation to generation. These tiny aquatic ferns grow in rice paddy fields, where it becomes a green manure when it dies, providing a huge source of nitrogen for the decomposers to supply the rice plants (estimated to provide 50–75% of the rice’s nitrogen requirements).

Rhizobium bacteria associate mainly with leguminous plants (Family Fabaceae), such as wisteria, clovers, peas, beans, soybeans and lupins. Some legumes species can associate with many types of Rhizobium bacteria (though one at a time); others only associate with

specific Rhizobium bacteria. In the association, these plants release specific exudates into the soil to attract the specific type of Rhizobium bacteria. If they are present in the soil, through an absorption process, they enter into the root hair; once inside, the plant continues to supply the sugars, and the bacteria start to colonise and grow enlarged forms called bacterioids; through their rapid reproduction, the bacterioids make the area bulge out into a nodule known as a symbiosome.

*Frankia* bacteria are a form of symbiotic filamentous actinobacteria, and the eight families of plants they associate with are collectively called *actinorhizal plants*; they include alders (*Alnus spp.*), sweet ferns (*Comptonia spp.*) and myrtles (*Myrtus spp.*). These plants are predominantly trees and shrubs (except for the genus *Datisca*), which are also often early pioneer species—those that come, for instance, after fires, volcano eruptions or glacier retreats—and the relationship with the *Frankia* bring important amounts of nitrogen to the actinorhizal plants in these the poor soils environments, which is also supported by their ability to form symbiotic relationships with mycorrhizal fungi.

<sup>35</sup> In forests, lichens can produce anti-herbivore chemicals, primarily to protect themselves, and this consequently allows them to protect a host tree. In the desert; moreover, the forest *cyanolichens* are important nitrogen fixers, bringing an estimated 50% of all nitrogen, for example, into temperate rainforests (or up to 75% into a Douglas fir environment). Horsehair lichens are the main winter forage for keystone species of caribou (they are the base of this Arctic food web), as well as a few other fungivore mammals (McCoy, 2016).

<sup>36</sup> Including additional oxygen, glucose, and glycerol—and a waste-removal service, as the algae consume (and benefit from) many of the coral waste products (acting as decomposers), such as CO<sub>2</sub> and phosphorous and nitrogenous wastes (as well the protected environment; Barnes, 1987). Young corals are not born with the algae: They acquire them from their water solution.

<sup>37</sup> Earthworms also have microbe symbionts (bacteria, fungi and protozoa) in their digestive tracts, helping them digest certain materials (Lund et al, 2014); and as previously mentioned, termites rely on endosymbiotic gut *diazotrophic* bacteria, which help supplement their nitrogen-poor diet.

<sup>38</sup> Biofilms can contain multiple types of different bacteria (and Archaea) species, with the metabolic wastes being food for others (see microbial cross-feeding or '*syntrophy*')—some biologists compare them to *primitive circulatory systems*.

<sup>39</sup> Once this occurs, other organisms, such as different types of micro-algae and other protozoa, can attach to the biofilms, which attracts crustacea, such as limpets. This process is known as *epibiosis* (and when happening on the bottom of a boat, 'biofouling'). Therefore, soil and aquatic bacteria are important *micro-autogenic structural engineers*.

<sup>40</sup> In slightly alkaline soils, an important group of bacteria, known as *nitrifying bacteria*, can be active. As already mentioned in a previous subsection, these bacteria transform ammonium (NH<sub>4</sub><sup>+</sup>; the main form of nitrogen waste, e.g. from the decomposer predators) into nitrate (NO<sub>3</sub><sup>-</sup>) in a two-stage process, via two different types of bacteria (Lewis & Lowenfels, 2010). Different plants 'favour' these two forms of nitrogen in different ratios (Lewis & Lowenfels, 2010), depending on their type—generally, annual plants prefer more nitrates, and woody plants prefer more ammonium—and lifecycle; higher nitrates can, for instance, facilitate growth spurts in annual plants, while too much or not enough of the right form of nitrogen can lead to unhealthy plants (Lewis & Lowenfels, 2010).

<sup>41</sup> This carbon-rich protein, a sticky substance, is hard to break down (unlike bacterial biofilms); it acts as a form of waxy coating, helping to seal leaks in the fungi hyphae and transport materials over longer distances and through pressure changes in pockets of water and air (Montgomery, 2017).

<sup>42</sup> It also

makes some soil pores impermeable to water, but not to air. So the air in pore spaces can escape when the spaces fill with water in a soil with aggregates stabilised by glomalin. But when water fills pores in a soil with aggregates that are not stabilised by glomalin, the air can't escape, which can increase the air pressure in the remaining voids enough to break up the aggregates. Thus... stabilis[ing] passages through which water moves and can be stored. (Montgomery, 2017)

These inter-aggregate voids (spaces) are essential for fungi, plant roots, and many other organisms to move through (as well as for flow of air and water).

<sup>43</sup> They use these acids, such as oxalic acid (C<sub>2</sub>H<sub>2</sub>O<sub>4</sub>), to chemically break down crystalline matter in rocks (bio-weathering), or other acids to break down keratin and collagen in animals and dead plant organic matter (e.g. cellulose in dead plants, and tougher substances, such as *lignin*, and *hemicellulose*, in woody materials).

<sup>44</sup> Therefore, fewer nitrifying bacteria are active, and so the ammonium (NH<sub>4</sub><sup>+</sup>) remains predominantly as ammonium (Lewis & Lowenfels, 2010).

<sup>45</sup> Fresh clays have an extremely large surface area, which can be arranged like the thin pieces of paper that make-up a playing card. The thin sheets are silicates, with many different cations (e.g. potassium, calcium and magnesium) sandwiched in-between (Montgomery, 2012). Clays can collapse if calcium concentrates drop too low relative to magnesium. Fungi store more calcium on their hyphae than any other organism, in the form of calcium oxalate crystals (Jacke et al., 2005).

<sup>46</sup> As they consume 10–30% of their body weight each day (soil filled with microbes—particularly bacteria), they break down, mix and blend organic matter into smaller and smaller particles (Biklé & Montgomery, 2016) and disperse it as vermicastings. Vermicastings are 50% higher in organic matter than the soil (that has not passed through the worm) is, increasing the cation exchange capacity (CEC), and they have, for instance, around seven times more available phosphate, ten times more available potash and five times more available nitrogen (Lewis & Lowenfels, 2010) thanks, in part, to the symbiotic microbes in the worm's gut.

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<sup>47</sup> For example, sea snails; some *demersal fish*, such as species of catfish, sharks and carp; and many flatfish, such as halibut, flounder, plaice, sole and eels.

<sup>48</sup> Due to their size and longevity, these large animals have a significant impact on *ecological succession* (e.g. *constraining* a savannah from turning into a woodland, or changing a woodland area into savannah), which affects all forms of life in the ecosystem (Haynes, 2011). Opening up woodland areas can increase, for example, the numbers of mixed feeders and grazers in the area (Haynes, 2011); the splintering and cracking of trees by Kenyan elephants creates more habitat and supports larger populations of lizards than found in areas without elephants.

<sup>49</sup> Plant roots are also obvious autogenic structures, helping to hold soil macro-aggregates (also held by the decomposers) together. Plants like mangroves act like the ribbed mussels, for example, buffering coastlines from waves and high winds, as well as trapping sediments running off from the land to the ocean.

<sup>50</sup> It is estimated that 95% of the Amazonian rainforest rain is generated through this process, and water cycles across the region (known as a short water cycle; Schwartz, 2016)—making it the largest remaining block of humid tropical forest left on Earth.

<sup>51</sup> To add to the last example, plants cannot help to produce clouds (and help cool the Earth) if there is no water in the soil to transpire in the first place. This means that the water engineering functions of the decomposers and certain consumers (e.g. beavers and perhaps even elephants and migrating herbivores), which support the development of the ‘carbon-soil sponge’, are critical for trees to achieve their function. Therefore, biotic units functioning as an integrative system (a team of multidisciplinary engineers!) is required for an abundant (and stable) water cycle across continents.

<sup>52</sup> The traditional theory of evolution is outlined by Loreau (2010) as the following:

Evolution [is] the result of a two-step process: trait variation is first generated at random by mutations or recombination of the genetic material, and natural selection then acts on this variation to sift out those traits that confer better adaptation to the environment. Since genes are carried, expressed, and transmitted by individual organisms, the individual organism is widely regarded as the main unit of selection, while the ecosystem in which the individual organism lives is viewed as part of the broad environmental context that determines the direction and strength of natural selection.

Ecologists see ecosystems as integrative wholes; therefore, they tend to search for laws and principles that govern the *evolution* and development of these larger wholes (Loreau, 2010). Thus, at least since Lotka in the early 1920s, ecologists (and others) have been proposing ways that evolution may *also* act at levels ‘higher’ than individuals—such as the ecosystem.

Loreau (2010) identified three different scenarios in which groups (or ecosystem) properties could evolve. First, evolution of individual species, through individual-level selection, can drive changes in ecosystem properties indirectly. This means that ecosystem effects are by-products and do not need feedbacks of the ecosystem acting on the evolution of the individual. Second, organisms indirectly change ecosystems, and there are feedbacks from these changes that affect the evolution of the species (affecting their ‘fitness’). ‘Ecosystem engineers’ and ‘niche construction’ (see Odling-Smee et al., 2003) enter into this theory. Both theories (and the next) acknowledge *co-evolution*. Third (and most contentious), there could be mechanisms that lead to the evolution of ecosystem properties through ecosystem-level selection of ecosystem properties. In this situation, the collective behaviour can (but does not always) determine the fitness of the organisms that make up the ecosystem; natural selection *can* operate between organisms from different ecosystems such that the fittest species assemblages are selected (Loreau, 2010). Loreau (2010) proposes that this

scenario requires stringent ecological conditions. Not only does it require that the species involved play a significant role in the ecosystem and that species interactions be sufficiently long-lasting, it also requires that species interactions be strongly localized such that natural selection among local ecosystems can occur.

Evolution of organisms and ecosystems is important, as it can teach us about how our systems of production could (and maybe should) *also* evolve—as analogies, and as dynamic systems that are truly embedded within their dynamic environments.

<sup>53</sup> Although outside of the scope of this paper, for a more comprehensive understanding of any ecosystem, *synchronic* frameworks (or contextual ones, such as these) should be supported with *diachronic* frameworks (historical studies across time), which will help explain how these relationships change over time. Beyond frameworks, such as the *Five Kingdoms of Life*, that help explain the evolution of life in a pedagogic way, *seasonal cycles* – and even *diurnal cycles*—are important for understanding how relationships and assemblies of communities change over time.