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ECOSYSTEM SCIENCE: A NEW APPROACH IN THE ANALYSIS OF FUNCTIONAL PROCESSES IN NATURAL AND HUMAN TRANSFORMED TERRESTRIAL ECOSYSTEMS

LA CIENCIA DE LOS ECOSISTEMAS: UN NUEVO ENFOQUE EN EL ANÁLISIS DE LOS PROCESOS FUNCIONALES EN ECOSISTEMAS TERRESTRES NATURALES Y TRANSFORMADOS

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Abstract
Although Tansley originally proposed the ecosystem concept in 1935, ecosystem science underwent significant development in the last 20 years, as in this period it has been consolidated with concepts and methods arisen in convergent disciplines, such as ecosystem genetics, ecological stoichiometry, global ecology, and ecosystem services. The objective of this paper is to review new concepts and methods of water, energy, and nutrient dynamics research in terrestrial ecosystems to contribute to generate a new theoretical framework in the field of ecosystem science. From this review, a new conceptual definition of ecosystem is required based on three key issues: (a) the integration of functional processes at different spatial and temporal scales to understand the ecosystem dynamics in its environmental context; (b) the concept of resource (*i.e.*, water or nutrients) use efficiency as a key metric for ecosystem function; and (c) the role of biological species in ecosystem functioning, using the genetic framework. These new concepts and methods are necessary to advance in the research on ecosystem functioning and resilience in the context of the current environmental crisis that includes processes such as ecosystem degradation, biodiversity loss, and global climate change. Finally, this new conceptual definition must be linked to evolutionary theory and global ecology research.
Keywords: ecosystems, energy, functional biodiversity nutrients, resilience, resource use efficiency, water.

Resumen
A pesar de que el concepto de ecosistema fue propuesto por Tansley desde 1935, la ciencia de los ecosistemas ha tenido un desarrollo significativo en los últimos 20 años, ya que en este periodo se fortaleció con conceptos y métodos surgidos en disciplinas convergentes como la genética de ecosistemas, la ecología estequiométrica, la ecología global y los servicios ecosistémicos. El objetivo del presente trabajo es revisar los nuevos marcos conceptuales y metodológicos en los estudios de la dinámica del agua, energía y nutrientes en ecosistemas terrestres. De esta revisión, destacan tres aspectos relevantes: (a) la integración de los procesos funcionales a diferentes escalas espaciales y temporales para entender la dinámica de los ecosistemas en su contexto ambiental, (b) el concepto de eficiencia del uso de recursos (agua o nutrientes) como una medición clave en el funcionamiento de los ecosistemas, y (c) el papel de las especies biológicas en el funcionamiento de los ecosistemas en el contexto de la genética de los ecosistemas. Una nueva definición del concepto del ecosistema es necesaria considerando los avances de los marcos teóricos, y es necesario aplicar nuevas metodologías a los estudios de ecosistemas. Estos nuevos conceptos y herramientas son necesarias para mejorar la investigación sobre la resiliencia de los ecosistemas en la actual crisis ambiental que incluye la degradación de ecosistemas, la pérdida de la biodiversidad y el cambio climático global. Finalmente, esta nueva definición de ecosistema debe estar ligada con la teoría de la evolución y la investigación en ecología global.
Palabras clave: agua, biodiversidad funcional, ecosistemas, eficiencia de uso de recursos, energía, nutrientes, resiliencia.

Among the disciplines of ecology, ecosystem science is the most dynamic and has undergone the greatest development over the last 20 years. The term "ecosystem" was originally proposed by Tansley (1935), then Lindeman (1942) gave a framework to the ecosystem concept using the concept of trophic-dynamics of energy flow in lakes and, Odum (1969) integrated biodiversity, energy flow and nutrient dynamics into a conceptual model for ecosystem development. This conceptual model defined the ecosystem as a cybernetic system with a holistic approach (Margalef 1968, Odum 1969). However, this model had two main problems: the definition of ecosystem boundaries (Levin 1992) and the heterogeneity and scales, all of which were unclear within the *black-box* vision (Turner 1989, Pickett & Cadenasso 2002, Currie 2011, Carpenter & Turner 2017). Indeed, several contemporary ecosystem-level studies face these problems. In terrestrial ecosystems, the problem of boundaries was assumed to be a methodological issue encountered in the context of watersheds. The studies of Bormann & Likens (1979) and Swank & Crossley (1988) used small experimental watersheds for measuring water and nutrient budgets at the ecosystem level. Moreover, Bormann *et al.* (1974) proposed that forest ecosystems have the resilience capacity to cope with severe disturbances, such as complete deforestation; this study represented an important experiment to analyze the response of a forest ecosystem to disturbances. Although these studies do not solve the problem of boundaries, they address several conceptual and methodological problems for ecosystem science. O'Neill *et al.* (1986) suggested that the ecosystem is the highest hierarchical level of the components of a functional organization, and that the processes at the ecosystem level define the boundaries. However, this conceptual proposal is not fully accepted because of several limitations of the ecosystem concept as a closed biotic system (Currie 2011). The spatial heterogeneity and the integration of spatial and temporal scales have been addressed through landscape ecology (Turner 1989). All of these limitations of the ecosystem concept complicate the definition of ecosystem as an operational unit (Currie 2011). Ecosystem science thus requires convergent disciplines to overcome its limitations. Finally, in 1998, a scientific forum on ecosystem science was published in the *Ecosystems* journal (Carpenter & Turner 1998), that served to define a contemporary approach for ecosystem ecology research (Carpenter & Turner 2017).

Over the last two and a half decades, several concepts and methods have arisen in different convergent disciplines, contributing to the consolidation of ecosystem science. These disciplines include ecosystem genetics (Whitham *et al.* 2006, Sardans *et al.* 2011, Peñuelas *et al.* 2013), ecological stoichiometry (Sterner & Elser 2002, Peñuelas *et al.* 2019), global ecology (Schimel *et al.* 2019, Schlesinger & Bernhardt 2020), and ecosystem services (Millennium Ecosystem Assessment 2003).

The role of biological species in ecosystem functioning has been a relevant subject for ecosystem science and several authors have proposed different models to understand the effect of species on ecosystem resilience (Peterson et al. 1998). However, the role of species in different ecosystem processes has been determined with the development of *omic* molecular methods, such as genomics, proteomics, and transcriptomics (Whitham *et al.* 2006, Sardans *et al.* 2011, Peñuelas *et al.* 2013). These *omic* methods were applied successfully to the understanding of the biological richness and their interactions in microbial and plant communities, allowing the development of a conceptual framework with which to understand the genomic basis of ecosystem processes (Whitham *et al.* 2006).

In the two last decades of the 20th century, several authors considered that specific ecosystems are limited mainly by a single nutrient; for example, temperate forests and deserts are mainly limited by nitrogen (N), while tropical forests are limited by phosphorus (P) (Vitousek 1984, Noy-Meir 1985, Vitousek & Sanford 1986, Aber & Melillo 1991). At present, the net primary productivity of ecosystems can be co-limited by carbon (C), N, and P; expressed as C:N, C:P and N:P ratios (Sterner & Elser 2002, Sinsabaugh *et al.* 2009, Tapia-Torres *et al.* 2015a). In order for biological species to maintain their C:N:P ratios, they must invest energy in nutrient acquisition, rather than in population growth (Sterner & Elser 2002). The conceptual framework of these processes is known as ecological stoichiometry (Sterner & Elser 2002, Peñuelas *et al.* 2019), and it serves to analyze nutrient uptake in relation to the metabolic efficiency of specific species or group of species (Sterner & Elser 2002, Peñuelas *et al.* 2019). This theoretical framework allows the study of nutrient dynamics in an evolutionary context. Wider aspects of these interactions across trophic levels and functional assemblages at different scales are expressed as eco-evolutionary dynamics (Brunner *et al.* 2019).

Global ecology is focused on the integrated study of ecosystems from regional to global scales including carbon and nutrient dynamics, water dynamics and global energy budgets (Schimel *et al.* 2019; Schlesinger & Bernhardt 2020, Yu *et al.* 2021). This discipline is based on the development of methods that allow measurements of processes at different scales, such as plant physiological (*i.e.*, photosynthesis and transpiration), soil (*i.e.*, respiration, C accumulation) and atmospheric (*i.e.*, turbulence, emissions) processes and their interactions. In this context, flux towers, remote sensing methods and isotopic ratios are fundamental tools in global ecology (Fry 2006, Schimel *et al.* 2019).

The human dimension as a key element for ecosystem functioning has been recognized since Odum (1969), but adoption of the concept of ecosystem services as a framework for research increased dramatically at the end of the 1990s (Costanza *et al.* 1997; Daily *et al*. 2000; Carpenter *et al.* 2009, Carpenter & Turner 2017). The advent of the Millennium Ecosystem Assessment synthesis (2005) clearly established the conceptual framework of ecosystem services and made it critical to current ecosystem management research. In addition, Currie (2011) and Yu *et al.* (2021) proposed ecosystem science as a tool for studying the effects of climate change and anthropic management on ecosystems, in terms of achieving sustainable development.

The objective of the present paper is to review novel concepts and methods of convergent disciplines that contributed to the theoretical framework of ecosystem science. In the two following sections, we review examples of concepts and methods relating to water, energy, and nutrient dynamics in terrestrial ecosystems. We then analyze how these new concepts and methods have influenced in the understanding of the ecosystem resilience processes.

Ecosystem water and energy dynamics

Water fluxes through soils, rocks, organisms, and the atmosphere essentially control all functional processes in terrestrial ecosystems (Biederman *et al.* 2016, Rodríguez-Robles *et al.* 2020). This circulation of water can be conceptualized and measured as energy and matter exchanges across ecosystem components that are central to the understanding of ecosystem processes. Given the close relationship between water fluxes and biological productivity, contemporary interdisciplinary fields such as ecohydrology have recently presented a research agenda to study ecosystem functions and applications (Newman *et al.* 2006). Ecohydrology embraces theory and methods from ecology and hydrology to identify couplings and feedbacks between organisms, populations and communities, as well as water-related processes across a broad range of spatial and temporal scales. This perspective has gained attention due to the significant impacts on ecosystems for the growing demand of ecosystem services (Sun *et al.* 2017) and climate change (Tague *et al.* 2020).

Early conceptual tools of ecohydrology, such as rain use efficiency (RUE), defined as the annual net primary production/mean annual precipitation ratio (Leith 1975, Le Houérou 1984), were widely used as basic process-integrators and to investigate environmental constraints on biological productivity (Lauenroth & Sala 1992, Paruelo *et al.* 1999). Since a fundamental relationship emerges when rainfall and biological production parameters are related, the role of water as a key driver for ecosystem function is clear. Indeed, when temperate or tropical-wet ecosystems experience water limitations, the slopes of rainfall and biological production converge to a common RUE (Huxman *et al.* 2004). This variation on the RUE slope indicates that the relationship itself is of interest, since RUE deviations in particular ecosystems, at specific times and under varying environmental conditions, could indicate ecophysiological adaptations (Plaut *et al.* 2012), organismic interactions (Rodríguez-Robles *et al.* 2020), constraints to nutrient availability (Porporato *et al.* 2003) and levels of ecosystem degradation (Ehleringer 2001).

When scaled to ecosystem level (Chapin III *et al.* 2006), photosynthesis (A) and gross primary production (GPP) express the CO_2 assimilation process in plants. This flux is therefore the main path for radiant energy and inorganic atmospheric compounds to be incorporated into ecosystems as organic matter. However, such a fundamental flux has an expensive water cost, since a water loss of two orders of magnitude occurs at leaf level for each CO_2 molecule fixed (Nobel 1999). This process led to the establishment of H_2O and CO_2 molecules as central currencies of matter and energy flow in studies addressing ecosystem function (Mooney 1972, Pearcy *et al.* 1989, Chapin III *et al.* 2002, Shuttleworth 2007).

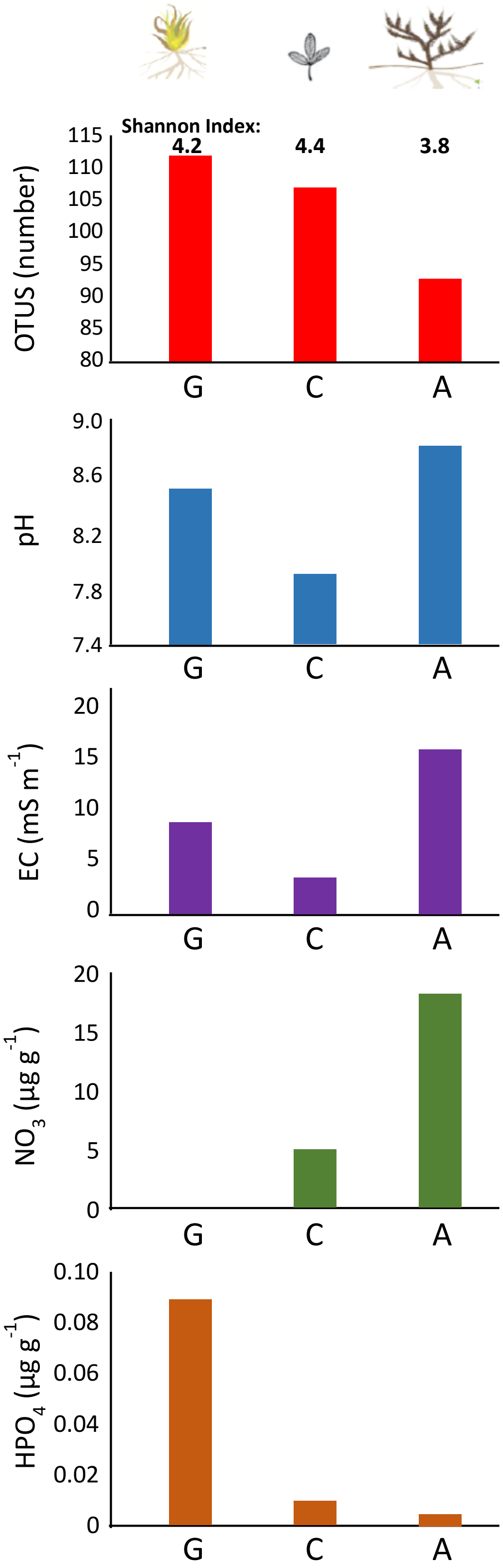

Figure 1. Soil bacteria OTUs, Shannon biodiversity index, and some soil characteristics (pH, EC: electrical conductivity, NO_3: nitrate concentration and HPO_4: available phosphate concentration) under three management conditions (G: natural desert grassland, C: cultivated plot with alfalfa, and A: abandoned plot) in the Cuatro Ciénegas Valley, Mexico. (Hernández-Becerra *et al.* 2016).

Theoretical approaches to assess the availability of water that controls biological productivity, and contemporary methods that rely on advanced technology capable of monitoring CO_2 and water fluxes in temporal and spatial scales to determine ecosystem function, are now central to ecosystem science research (Keenan & Williams 2018, Schimel *et al.* 2019, Baldocchi 2008, Yu *et al.* 2021). Careful tracing of H_2O and CO_2 fluxes across ecological scales of organization within an ecosystem has emerged as a powerful practical and conceptual tool with which to advance theory concerning ecosystem functioning (Tang *et al.* 2014), carbon cycle analysis (Vargas *et al.* 2012), as well as to consider ecosystems as natural climate solutions (NCS) in this age of chronic environmental climate change (Hemes *et al.* 2021).

Carbon dioxide and water measurements taken at the ecosystem scale with the eddy covariance technique have provided key metrics (Chapin III *et al.* 2006), such as evapotranspiration (ET), gross primary production (GPP), net ecosystem exchange (NEE), net ecosystem production (NEP) and ecosystem-level water use efficiency (EWUE), with which to assess ecosystem functioning across continents (Baldocchi 2008, Tang *et al.* 2014, Baldocchi *et al.* 2018, Keenan & Williams 2018, Delgado-Balbuena *et al.* 2019, Tarin *et al.* 2020, Kang & Cho 2021, Heiskanen *et al.* 2022). One example of these applications in the semiarid region of western North America comes from an integration of ecosystem water and CO_2 measurements in combination with remote sensing tools (Biederman *et al.* 2016, 2017), to use time by space substitutions to explore the relationships of rainfall and ET to the NEP and GPP, and to compare the carbon sink potential and controls of arid and forested ecosystems. Taking advantage of the RUE-like criteria (see above), the authors invoked "fast" (*i.e.*, weather, soil moisture, leaf area, microbial communities) and "slow" (*i.e.*, climate, atmospheric CO_2 concentration, soil development, biogeochemical pools, plant community) factors as differential controls of ecosystem processes across sites. Since most of the unexplained NEP variability was related to site-specific functions, further research is necessary to obtain more conclusive evidence regarding how slow factors drive carbon and water relations in ecosystems (Biederman *et al.* 2016, Baldocchi *et al.* 2018). However, since common temporal and spatial sensitivity to interannual environmental changes can be extrapolated to predict fundamental water controls on CO_2 exchanges and biological productivity over long-term temporal scales, an important tool emerges to improve our understanding of ecosystem resilience in the context of climate change and human pressures (Yu *et al.* 2021).

Moreover, when disaggregated ecosystem fluxes are related among themselves (*i.e.*, ET and GPP), there is a clearer biological response to the environmental drivers. For instance, the RUE slope for widespread ecosystems is asymptotic, while an ET vs. GPP relationship is linear (Biederman *et al.* 2016). As part of understanding these differences, the issue of temporal and spatial scales is unavoidable, but this also presents a challenge to ecosystem science regarding how to implement means to separate ecosystem fluxes into their fundamental components; for example, ET into transpiration (T) and evaporation (E), or NEP into GPP and ecosystem respiration (Reco), such that more in-depth explorations of the biological responses to environmental drivers can be made at ecosystem scales, while obtaining mechanistic information pertaining to ecosystem processes (Yepez *et al.* 2007, Stoy *et al.* 2019).

To confront this challenge, a combination of tools, including leaf cuvettes, porometer techniques, sap flow probes, soil chambers, lysimeters, and *in situ* spectral tools, has traditionally been employed. However, the propagation of error when scaling these methods up to an entire ecosystem is substantial (Wilson *et al.* 2001, Kool *et al.* 2014). A partial solution is provided by the eddy covariance technique (EC), which provides a direct and continuous estimate of aggregated fluxes, such as ET and NEE (NEE = NEP), within an ecosystem. In combination with modeling, data assimilation techniques and ancillary measurements have provided evidence of the capacities of these approaches to partition fluxes. Recently, Zhou *et al.* (2016) and Scanlon & Kustas (2010) were able to employ a water-use efficiency criterion to partition ET as the ratio of GPP and ET, simply by using the eddy covariance method, providing promising results. Although this approach is appealing, considerable uncertainties remain regarding the estimation of GPP with these criteria, since GPP is not a directly measured variable in EC operations but rather one that is modeled (Reichstein *et al.* 2005). Nevertheless, there is a promising future for disentangling spatial and temporal NEP variation with the application of remote sensing techniques (*i.e.*, drones, microsatellite clouds, satellites, and space stations), relying on the spectral properties of surfaces, combined with numerical assimilation schemes that can offer greatly enhanced spatial resolution to detect functional traits and temporal dynamic changes in ecosystems (Schimel *et al.* 2019).

Fundamentally, the aim of separating water and carbon flux components demands a combination of temporal and spatial congruent techniques (Yepez *et al.* 2007, Stoy *et al.* 2019). Combining EC and stable isotope techniques constitutes an alternative that allows flux partitioning at the ecosystem scale (Good *et al.* 2012). This is possible since the stable isotopes of water and carbon can be used as tracers of hydrological and carbon cycles, because of their different fractionation processes (Yakir & Sternberg 2000).

Implementation of a concise scheme of combined methods, for incorporation into long-term monitoring programs to generate baselines of ecosystem functions responding to environmental variation at different scales, will undoubtedly contribute to the identification of effects of climate change on ecosystems and to the provision of ecosystem management strategies as options for natural climate solutions in the context of chronic climate change.

Ecosystem nutrient dynamics

The ecosystem nutrient dynamics (END) is broadly defined as the manner in which nutrients are taken up, retained, transferred, and recycled over time and space in an ecosystem (Allan & Castillo 2007). END is an emerging property of ecosystems, which, like the other biogeochemical processes, is the result of a convergence of geological, pedological, and ecological processes, each of which depends on the spatial and temporal scales at which they are observed (Berhe & Kleber 2013, Berhe *et al.* 2018). In most terrestrial ecosystems, END not only depends on the rate of input from extreme boundaries (*i.e.*, atmospheric deposition, weathering) but also, and more importantly, from internal cycles, where soil organic matter is the main source of inorganic nutrients through its decomposition by the soil microbial community (Schlesinger *et al.* 2011, Banwart *et al.* 2019). In general, three stages help to summarize END: (a) absorption and allocation of inorganic nutrients by plant roots, (b) reabsorption of nutrients from senescent tissues and return of nutrients by litterfall and abscission of fine roots, and (c) release of inorganic nutrients from organic matter to the soil solution through microbial metabolism (mineralization).

In the first stage of END, nutrient absorption by the roots depends on the characteristics of the nutrients themselves, such as solubility, diffusion speed, and concentration. For example, N, P, and K, in the forms of HPO_4^{2-} and H_2PO^{4-}, K^+ and $NH_4{}^+$, diffuse slowly due to the strong affinity with other components of the soil, cations in the case of P and clays in the case of K^+ and NH_4^+, while NO_3^- is highly mobile and diffuses rapidly in the soil solution (Sparks 2019). One of the most common approaches to estimate the consequence of nutrient absorption in biomass production is through nutrient use efficiency (NUE), which is defined as the quantity of biomass production per unit of nutrient acquired. However, this does not allow direct measurement of the flow of nutrients to the plant (Silla & Escudero 2003, Chapin III *et al.* 2011). Once the roots acquire the nutrients, these are distributed through the different tissues. These requirements determine the demand for acquired nutrients and ultimately define their limitation (Peñuelas *et al.* 2019). The distribution of nutrients in plants is determined by their destination, including structural molecules, tissues with high metabolic activity such as photosynthetic organs, chemical defenses, or other defense structures. In general, three factors govern the allocation of nutrients in plants: (1) the genetic structure of the plant species community, (2) the environmental conditions in which the plants grow, and (3) the seasonal program of resource allocation (Hartmann *et al.* 2020).

In the second stage of END, leaves and fine roots have higher concentrations of nutrients (mainly N and P) than other tissues since both of these organs are physiologically active. Likewise, these structures are continually replaced due to depletion of their physiological function but, prior to detachment from the plant, they go through a process of preparation or deciduous senescence in which some nutrients are recovered and reabsorbed before abscission, then transported and stored in branches, stem or structural roots where they remain available for the formation of new functional or reproductive structures in the following phenological cycle (Leopold 1961, Killingbeck 1996, Cartaxana & Catarino 2002). Translocation or reabsorption of nutrients from senescent leaves has been recognized as an efficient mechanism for conservation of nutrients in several plant species (Killingbeck 1996) since it allows them to be less dependent on the availability of N and P in the soil (Aksekili *et al.* 2007). It has been calculated that between 50 and 80 % of foliar N and P can be reabsorbed, and that there are differences between these and other nutrients, (*e.g.*, the cations), for which translocation is less efficient (Killingbeck & Costigan 1988, Rentería *et al.* 2005, Hagen-Thorn *et al.* 2006, Covelo *et al.* 2008b). One of the more commonly accepted metrics to calculate nutrient reabsorption is reabsorption efficiency, defined as the percentage of the nutrient that has been reabsorbed, based on the nutrient content in living leaves and the nutrient content in senescent leaves (Killingbeck 1996, Vergutz *et al.* 2012).

Multiple factors can define nutrient reabsorption patterns, including soil nutrient availability, foliar nutrient concentration, senescence time, air temperature, water stress, and factors associated with the physiological characteristics of each species (Hagen-Thorn *et al.* 2006). For example, it has been reported that between 1,300 and 1,900 genes are activated in *Arabidopsis thaliana* when senescence begins (Zentgraf *et al.* 2004). However, it is not known how many of these genes are directly related to nutrient resorption (Jones 2004). Studies have been carried out for different tree species, aiming to define their reabsorption patterns compared to other taxa (Killingbeck & Costigan 1988, Hagen-Thorn *et al.* 2006), considering the effect of forest management (Covelo *et al.* 2008b), and with climatic conditions such as a water gradient (Del Arco *et al.* 1991, Zhao *et al.* 2017). Moreover, studies have analyzed the effect of spatial patterns (Covelo *et al*. 2008a) and the foliar phenological strategies of different species (Huang *et al*. 2007, Brant & Chen 2015) on foliar nutrient resorption. In general, it has been determined that deciduous species have higher reabsorption efficiencies than perennials and, even within the same phenology, species with a longer leaf life-span present lower reabsorption efficiencies (Huang *et al*. 2007, Vergutz *et al.* 2012, Chavez-Vergara *et al.* 2014). It is widely accepted that nutrient reabsorption efficiency has an important genetic component at population level (Allan *et al.* 2012, Whitham *et al.* 2012) or at different taxonomic levels (Chávez-Vergara *et al.* 2015). The effect of physiological plant traits with a genetic basis on the chemical composition of the plant-derived material that returns to the soil is considered a part of ecosystem genetics, since these physiological traits can be analyzed within an evolutionary framework (Whitham *et al.* 2006, Peñuelas *et al.* 2013).

In the third stage of the END, the return of nutrients to the soil via organic residues follows different routes, such as canopy leaching (throughfall), litterfall, root death and root exudates. Litterfall quantity is regulated by primary productivity and seasonality by phenology, which is influenced by the availability of water, temperatures during the

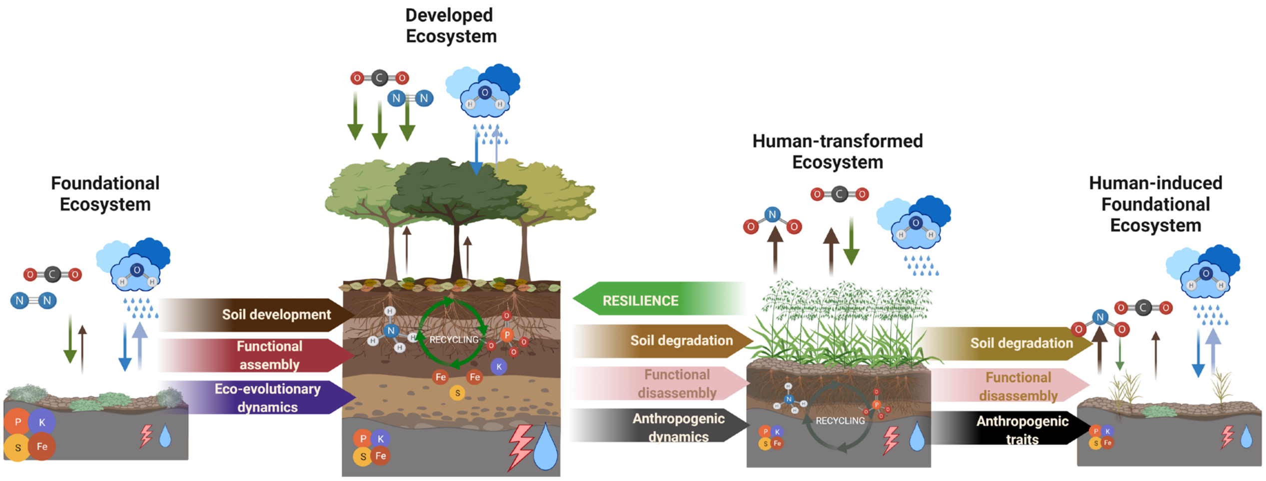

Figure 2. Functional and ecological processes involved in the evolutionary stages of *foundational*, *developed*, *human-transformed* and *human-induced foundational* ecosystems. Created with BioRender.com

growing season, and the canopy morphology (Brant & Chen 2015). In forest ecosystems, the contribution from litterfall is dominated by the tree stratum, which represents 95 % of the litter mass that falls to the soil surface (Kögel-Knabner 2002). Of this percentage, about 80 % corresponds to foliar biomass (Rapp *et al.* 1999; Santa Regina & Tarazona 2001). The concentration of nutrients in the leaves that fall to the ground is regulated by the processes of nutrient resorption, environmental conditions, and plant physiological responses, while the intrinsic characteristics of the species themselves determine the quantity and chemical composition of the organic residues (Chavez-Vergara *et al.* 2014). Another way to return nutrients to the soil is through the abscission of fine roots, but very little is known about this process due to the difficulty of collecting samples. Nevertheless, in some cases, it can be as important as litter fall in terms of the mass and concentration of nutrients returned to the soil (*e.g.*, in tropical dry forests) (Martinez-Yrizar *et al.* 1996).

Before organic residues can be transformed, they must be suspended or dissolved in the soil solution, when they become known as dissolved organic matter (DOM) and must be smaller than 0.45 µm (von Lützow *et al.* 2007). Some chemical characteristics that can hinder their decomposition include hydrophobicity, since they will tend to form micelles that are difficult to break, a high C:N ratio, non-polarity of the molecules, the presence of carbon covalent bonds (C-quaternary), functional groups with poorly hydrolyzable bonds (ester, phenyl, cyano), nitrogen heterocyclic (pyrrole, pyridine) and long hydrocarbon chains (Kiikkilä *et al.* 2005, van Hees *et al.* 2005, Roberts *et al.* 2009; Kiikkilä et al. 2011, Glanville *et al.* 2012, Jones *et al.* 2012). The use of solid-state ^{13}C NMR and ^{31}P NMR allows the definition of the molecular structure of soil organic C and P molecules and thus indicates their susceptibility to degradation (Almendros *et al.* 2000, Turner *et al.* 2003, 2007, Noack *et al.* 2012, Bonanomi *et al.* 2013, Merino *et al.* 2015, García-Oliva *et al.* 2018, Merino *et al.* 2021).

The dominant molecular size in dissolved organic matter is greater than 10 kDa, but most microorganisms can only assimilate small molecules (< 1 kDa) and the soil microbial community therefore requires a mechanism with which to cleave them (Neff & Asner 2001, Jones *et al.* 2012). This mechanism of depolymerization is primarily extracellular and carried out by ecoenzymes (exoenzymes). These are protein catalysts secreted into the soil solution and are essential for breaking the chemical bonds of organic molecules (Sinsabaugh 1994, Baldrian 2009, Bai *et al.* 2021). The enzyme can be produced if the genes that code for it are present in microbial community (Starke *et al.* 2021). For example, it is known that ascomycetes fungi have a greater specialization for the degradation of polysaccharides, while basidiomycetes, in addition to their capacity for polysaccharide degradation, are specialized in the degradation of lignin, polyphenols, and other aromatic compounds (Baldrian *et al.* 2011b, Culleton *et al.* 2013). The composition of the soil microbial community, as well as its genetic diversity, is therefore critical for soil organic matter decomposition, providing other example of the importance of genetic diversity to ecosystem functioning (Whitham *et al.* 2006, Sardans *et al.* 2011, Peñuelas *et al.* 2013). Likewise, to produce exoenzymes, a stimulus that generates the gene expression that produces the enzyme must be present (Ekschmitt *et al.* 2005, Baldrian *et al.* 2011a, Voříšková *et al.* 2011). For example, a high availability of nitrogen in the soil can reduce the production of exoenzymes associated with the depolymerization of nitrogenous molecules, while a low availability of nitrogen can stimulate the production of ecoenzymes, such as proteases, chitinases, and laccases. This suggests that microorganisms do not invest in producing these enzymes if they have access to available nutrients in the soil (Šnajdr *et al.* 2011, Glanville *et al.* 2012). Consequently, the soil microbial community must invest more energy in different ecoenzymes to acquire the limited element rather than growing the population (Sterner & Elser 2002, Sinsabaugh *et al.* 2009). However, the investment of energy in nutrient acquisition must be related to the C:N:P ratios of the soil microbial community. For example, Cleveland & Liptzin (2007) reported that the soil microbial community presents a relatively constant C:N:P ratio (60:7:1) in several terrestrial ecosystems. Furthermore, Sinsabaugh *et al.* (2009) reported an ecoenzymatic stoichiometry of 1:1 for C-N and C-P ecoenzymes in a different ecosystem, suggesting a strong relationship among ecoenzymatic activities. All of these results suggest that the C:N:P ratios are key indicators for understanding the integrated dynamic of nutrients in ecosystems, the conceptual framework of which is known as ecological stoichiometry (Sterner & Elser 2002, Sinsabaugh *et al.* 2009, Tapia-Torres *et al.* 2015a, Peñuelas *et al.* 2019).

Ecosystem resilience

In the two previous sections, we reviewed new theoretical frameworks and methods by which to understand the water, energy, and nutrient dynamics in terrestrial ecosystems, and which have served to consolidate ecosystem science. From this review, we highlighted three key issues: (a) the requirement for integration of functional processes at different spatial and temporal scales (*e.g.*, from genomic based processes to global fluxes) to understand the dynamics of an ecosystem in its environmental context; (b) the resource use efficiency (energy, water or nutrients) as a key metric for ecosystem function; and (c) the role of biological species in ecosystems functioning using the genetic framework. As stated above, the development of new methodologies (*i.e.*, eddy covariance, remote sensing, stable isotope, solid-state ^{13}C NMR and ^{31}P NMR, and the *omic* molecular methods) has allowed the three issues mentioned above to be adequately addressed.

One of the main problems of human well-being is related to the current environmental crisis, mainly through the problems derived from ecosystem degradation and global climate change (Millennium Ecosystem Assessment 2005, IPCC 2013). In 2005, one quarter of the continental area worldwide was converted to cultivated systems and approximately 60 % of the ecosystem services were degraded (Millennium Ecosystem Assessment 2005). Moreover, the last decade was the warmest since 1850 as a result of greenhouse gas emissions by human activities increasing the frequency of extreme climatic events (IPCC 2021) and disturbing several components and processes of ecosystems. For example, genetic diversity decreased globally (Millennium Ecosystem Assessment 2005), along with the capacity of soils to sequester carbon (Hoffmann *et al.* 2012, Albaladejo *et al.* 2013). Under this current scenario of environmental crisis, it is very important to understand the factors that determine the resilience capacity of ecosystems and find means by which to implement natural climate solutions (Griscom *et al.* 2017). Resilience is defined as the capacity of an ecosystem to return to the functional and structural condition it presented prior to perturbation (Holling 1973, Pimm 1984, Dell *et al.* 1986). López *et al.* (2011) then defined ecosystem resilience as how and to what extent the ecosystem condition changes between the different states prior to disturbance, in a model of different structural-functional states that includes threshold values of degradation that define the resilience capacity of an ecosystem for changing functional states. This definition considered that the ecosystem function has several equilibrium states, some of which could be far removed from its original condition. This latter definition therefore incorporates a dynamic concept of ecosystem resilience. Most of the papers related to ecosystem resilience analyzed changes of biological diversity following disturbance (MacGillivray et al. 1995, Tilman 1996, Griffiths et al. 2000, Wardle et al. 2000), but a few studies analyzed the recovery of functional processes (Herbert et al. 1999, Orwin & Wardle 2004, Hernández-Becerra *et al.* 2016). In addition, some authors proposed a quantitative index of ecosystem resilience (Herbert *et al.* 1999, Griffiths *et al.* 2001, Orwin & Wardle 2004).

Most studies are focused on a few variables, limiting the conclusions that can be made regarding the resilience capacity of ecosystems. For illustrative purposes, we present a resilience study conducted in a desert ecosystem in northern Mexico published by Hernández-Becerra *et al.* (2016). These authors analyzed soil microbial composition and soil nutrient dynamics in three plots with different management conditions (natural desert grassland, plot cultivated with alfalfa and plot abandoned for over 30 years) in the Cuatro Ciénegas Basin in northern Mexico. Briefly, the management consisted of cultivation of alfalfa (*Medicago sativa* L.) by flooding the fields and introducing large quantities of fertilizer, but the agriculture plots were abandoned because of soil degradation, mainly salinization (Hernández-Becerra *et al.* 2016, Tapia-Torres *et al.* 2018). Figure 1 shows the variables with the greatest differences among the three plots. The number of OTUs of soil bacteria and the Shannon diversity index decreased from the grassland to the abandoned plot, suggesting a reduction in the number of bacterial species as a result of the agricultural management. Soil pH and electrical conductivity were both reduced in the alfalfa plot, but these variables both increased dramatically in the abandoned plots. Soil pH is considered as a strong filter of several soil bacterial species (Delgado-Baquerizo *et al.* 2018, Malik *et al.* 2018). The bacterial species were therefore affected by two strong soil pH changes; one during the cultivation of alfalfa and the other after the agriculture activities were abandoned. The strongest changes in the bacterial community composition were observed during cultivation, in which the proportion of protobacteria decreased from 50 to 35 % in both the native grassland and alfalfa plot, and the species of cyanobacteria and chloroflexi bacteria were not observed in the latter plot. Finally, the available soil NO_3 and HPO_4 concentrations increased and decreased, respectively, in the abandoned plot. These two variables also had the lowest resilience index values among all the variables measured. These results suggest that nitrification increased with cultivation and soil P occlusion increased along with pH in the abandoned plots. Soil vulnerability to N loss therefore increased (Tapia-Torres *et al.* 2015b), as well as the soil capacity for geochemical occlusion of P (Perroni *et al.* 2014), and the soil processes that reduce the availability of N and P are therefore enhanced. These results suggest that the loss of bacterial species strongly affects the mechanisms of soil nutrient availability. The effect of the management could be worse than that of global climate change in this site, since the frequency of extreme climatic events had increased over the last decade (Montiel-González *et al.* 2021). In conclusion, soil bacterial composition is the key factor that controls the resilience of soil nutrient dynamics in this desert ecosystem. However, it is necessary to study the changes of expression of functional genes of bacteria that are related to nutrient dynamics. With this information, it is possible to design soil restoration or degradation mitigation methods, for example, by incorporating the functional bacterial species which were lost during the agriculture activities.

According to the global ecology perspective, one future challenge is the development of simple but integrative metrics with which to assess the resilience capacity of ecosystems at large scales. As an exploratory tool with which to assess ecosystem response to disturbances, space for time substitutions in resource use efficiencies (*i.e.*, RUE) can be used to measure resilience (*i.e.*, as disturbance increases, the slope of RUE decreases, and *vice versa*, as ecosystems recover the slope RUE increases) (Ehleringer 2001). To develop these powerful metrics for the assessment of ecosystem function responding to disturbance, we first require the baseline information that only long-term monitoring schemes combining techniques at the appropriate scales can provide.

Integration of resource use efficiency, species functions, and ecosystems processes is critical for understanding changes in the resilience capacity of an ecosystem. Unfortunately, no studies have integrated these three components to date. Figure 2 shows the main processes driving ecosystem changes in four evolutionary stages. Prior to soil development in the *foundational ecosystem stage*, the parent material has a high concentration of mineral-derived nutrients but with low incorporation of organic matter, resulting in a low capacity for accumulating energy and water. Primary succession then occurs, promoting ecological interactions among the species with their eco-evolutionary dynamics, while the soils develop at the same time. In the *developed ecosystem stage*, the ecosystem shows a high water and energy storage capacity in the soils and biomass compared to the previous stages. In this stage, the availability of resources is strongly regulated by internal recycling mediated by the metabolic capacity of the organisms. This capacity depends on the species composition of the communities, where the resource use efficiency of species, defined by the genetic composition of species, could be an important driver of community composition. Incorporation of anthropic management into the ecological processes modifies the ecosystem function (*human-transformed ecosystem stage*), disrupting the feedback among ecological components and leading to soil degradation. In this condition, the storage capacity of energy and water is reduced due to the decline in functional, metabolic, and biodiversity. However, if the effect of anthropic management does not irreversibly deplete the biodiversity, it is possible for the ecosystem to return to its condition prior to management, depending on its resilience capacity. However, if the biodiversity is strongly depleted, a new *human-induced foundational ecosystem stage* is reached. This new stage is strongly limited by nutrients, energy, and water, with highly adverse physical and chemical conditions, representing a strongly degraded ecosystem.

Final remarks

In the last two and half decades, several concepts and methodologies from different convergent disciplines have contributed to the consolidation of ecosystem science. From these, three key issues emerge: (a) the requirement for integration of functional processes at different spatial and temporal scales to understand the dynamics of the ecosystem in its environmental context, (b) the concept of resource use efficiency (*i.e.*, water or nutrients) as a key metric for ecosystem function, and (c) the role of biological species in ecosystem functioning, using a genetic framework. However, a new conceptual definition of the ecosystem is required in the context of the advance in theoretical bases, and it is necessary to apply these new methods to ecosystem studies. These new concepts and tools are necessary for improving ecosystem resilience research in the context of the current environmental crisis (*i.e.*, ecosystem degradation, biodiversity erosion and global climate change). Finally, the new conceptual definition must be linked to evolution theory and global ecology research.

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