‘One physical system’: Tansley’s ecosystem as Earth’s critical zone

Tansley review

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Summary

Integrative concepts of the biosphere, ecosystem, biogeocenosis and, recently, Earth’s critical zone embrace scientific disciplines that link matter, energy and organisms in a systems-level understanding of our remarkable planet. Here, we assert the congruence of Tansley’s (1935) venerable ecosystem concept of ‘one physical system’ with Earth science’s critical zone. Ecosystems and critical zones are congruent across spatial–temporal scales from vegetation-clad weathering profiles and hillslopes, small catchments, landscapes, river basins, continents, to Earth’s whole terrestrial surface. What may be less obvious is congruence in the vertical dimension. We use ecosystem metabolism to argue that full accounting of photosynthetically fixed carbon includes respiratory CO2 and carbonic acid that propagate to the base of the critical zone itself. Although a small fraction of respiration, the downward diffusion of CO2 helps determine rates of soil formation and, ultimately, ecosystem evolution and resilience. Because life in the upper portions of terrestrial ecosystems significantly affects biogeochemistry throughout weathering profiles, the lower boundaries of most terrestrial ecosystems have been demarcated at depths too shallow to permit a complete understanding of ecosystem structure and function. Opportunities abound to explore connections between upper and lower components of critical-zone ecosystems, between soils and streams in watersheds, and between plant-derived CO2 and deep microbial communities and mineral weathering.

I. Introduction

A remarkable congruence now exists in the core concepts of two scientific disciplines: ecology’s ecosystem and Earth science’s critical zone. This congruence becomes evident when we examine the perspectives of Tansley (1935), Lindeman (1942) and Hutchinson (1948), who defined ecosystems ‘in the sense of physics’ (quoting Tansley) as involving the study of ‘the living matter of the whole earth...a unit of higher order than the biome’ (Hutchinson, 1940). Here, we observe how these early ideas of the ecosystem...
compare with Earth’s critical zone, defined by Jordan et al. (2001) as the integrated and life-supporting systems of Earth’s surficial terrestrial processes. We critique the historical subdivision of terrestrial ecosystem science into above- and belowground branches, and argue that ecosystem metabolism can only be resolved by accounting for the full propagation of respiratory CO₂ and carbonic-acid weathering down through geologic substrata to the very base of the critical zone itself.

We assert that this larger perspective of the belowground ecosystem can help bridge above- and belowground ecology, and better connect the hydrology and biogeochemistry of the aboveground ecosystem and its soils with groundwater, streams, lakes and rivers. Given the congruence of the two concepts, scientists can reap major breakthroughs from coordinated investigations that engage the disciplines of hydrology, climatology, microbiology, geochemistry and biogeochemistry, pedology, ecology and geophysics. Such co-investigations will lead to more quantitative assessments of the evolution and resilience of critical-zone ecosystems (Chorover et al., 2011). In so doing, investigators will satisfy the concerns and scope of Tansley’s ecosystem and the recently conceived critical zone of Jordan et al. (2001).

II. Tansley’s ecosystem as ‘one physical system’

For decades, the term ‘ecosystem’ has enjoyed active use in the scientific and management literature. Although the term is used in a variety of ways, we promote the concept’s original scope set by its framer, Arthur Tansley (1935), who briefly but substantively defined the ecosystem to be the integrated biotic–abiotic complex:

the whole system (in the sense of physics), including not only the organism–complex, but also the whole complex of physical factors forming what we call the environment of the biome—the habitat factors in the widest sense.

Significantly, as if to emphasize what he meant by ‘the whole system’, Tansley (1935) added:

Though (as biologists) the organisms may claim our primary interest, when we are trying to think fundamentally we cannot separate them from their special environment, with which they form one physical system (italics ours).

Tansley (1935) took pains to frame the ecosystem concept, as is evident from his paper’s curious title, ‘The use and abuse of vegetational concepts and terms’, and from a number of historical details of the paper’s writing (Willis, 1997). But what is lasting about Tansley’s ecosystem concept is that he used ‘physics’ in the tradition of Aristotle, he opened the door to the ecosystem for scientists of many disciplines, and he calibrated the ecosystem to cross scales (Evans, 1956; Jenny, 1958). Although Tansley described ecosystems to fundamentally overlap, interlock and interact with one another over space and time, he was a practical scientist and foresaw that ecosystems, although overlapped and interlocking, could be studied as if in isolation.

G. E. Hutchinson (1940, 1948), enthused by Vernadsky’s (1929, 1998) biosphere and by Tansley’s fusion of the biotic–abiotic complex, used metaphors of ‘circles’ and ‘cycles’ to describe the intimacy of interactions among ecosystem components. Hutchinson’s student Ray Lindeman (1942), in his brilliant essay on the ecosystem’s trophic energetics, explicitly emphasized how ecosystems were more than biological constructs. In Lindeman’s (1942) words,

the discrimination between living organisms as parts of the ‘biotic community’ and dead organisms and inorganic nutrients as part of the ‘environment’ seems arbitrary and unnatural. The difficulty in drawing clear-cut lines between the living community and the non-living environment is illustrated by the difficulty in determining the status of a slowing dying pondweed covered with periphytes, some of which are also continually dying... (M)uch of the non-living nascent ooze is rapidly reincorporated through “dissolved nutrients” back into the living “biotic community.” This constant organic-inorganic cycle of nutritive substance is so completely integrated that to consider such a unit as a lake primarily as a biotic community appears to force a “biological” emphasis upon a more basic functional organization.

It is important to understand that Lindeman could have substituted a terrestrial system into his text about lakes: for example, ‘to consider such a unit as a forest, a grassland, or a wetland primarily as a biotic community appears to force a “biological” emphasis upon a more basic functional organization.’ It is also notable that, in these early aquatic ecosystem studies, lake sediments were deeply cored sometimes to >10 m and deep sediment samples were central to analyses that explored ecosystem evolution back through the millennia (Deevey, 1939; Hutchinson & Wollack, 1940; Livingstone & Boykin, 1962).

Many of Tansley’s insights remain on target even though the science of ecosystems has grown in many directions and weathered a swirl of ideas about ecosystem stability, strategy, resilience and capacity for repair. The ecosystem concept is growing still (Table 1), with ecosystems today emphasized to be open, complex, non-linear, adaptive, unpredictable in temporal trajectory (O’Neill, 2001; Jørgensen & Sivitzcheg, 2004; Currie, 2011; Likens, 2013) and potentially operating far from equilibrium (Scheffer et al., 2001; Filotas et al., 2014). Although the soil component of ecosystems is widely recognized to be polygenetic (Richter & Yaalon, 2012), so too are ecosystems at large, that is, ecosystems are archival, time-dependent products derived from high-order interactions of external forcings and internal developments that ebb and flow over evolutionary and geologic time (Clark & Royall, 1996; Shugart, 1998). Although the scope and core of the concept can still be recognized in Tansley (1935), the science is advancing by many measures.

III. Earth’s critical zone

In 2001, Earth scientists outlined a new systems science of surficial geological processes writ large, an integrative, interdisciplinary study of terrestrial systems, a science of Earth’s ‘Critical Zone’. Critical zones (CZs) are energized by the sun that heats the Earth, powers plant photosynthesis and drives the planet’s great hydrologic and biogeochemical cycles. Led by Thomas Jordan and Gail Ashley (Jordan et al., 2001), the team marshaled the disciplines of hydrology, geomorphology, geology, geochemistry, geophysics,
pedology and ecology to explicitly frame an Earth systems science that included all activities of plants, microbes and animals, including human beings, as integral to and dependent on the planet’s diverse and numerous CZs. Over the long term, the functioning of CZs is supported by a richness in diversity, not only of biological organisms, but of soils, sediments and regoliths, dynamic and deep aquifers, biogeochemical weathering reactions and by geophysical preconditioning of the crustal substrates themselves. CZs were called ‘critical’ because of the fundamental dependence of life on CZ structures and functions, and on the gravity with which human activities are transforming most of Earth’s CZs (Vitousek et al., 1997). As a result, Jordan et al. (2001) emphasized the need for new integrative studies to coordinate measurements and modeling of CZs across space and time, all to accelerate an understanding of CZ change and management across human to geologic time scales.

Within a decade of the framing of CZs by Jordan et al. (2001), international scientists and research managers, led by Drs Susan Brantley and Enriqueta Barrera, have helped launch an interdiscipli- nary network of Critical Zone Observatories (CZOs) in the USA, UK, Germany, France, China and other nations (Fig. 1). CZ scientists and research funders, affectionately called ‘critical zonists’ by Latour (2014), are ambitious to grow this new science of coordinated observation, experimenta- tion and modeling based at observatories world-wide, each wirelessly streaming real-time data that tie together the driving processes of the atmosphere, canopy-boundary layers, biota, soil and full weathering profiles that include deep aquifers. At a time when a Working Group of the International Commission on Stratigraphy is evaluating ‘the Anthropocene’ as a new, contemporary unit of geological time (Zalasiewicz et al., 2011, 2015; Haff, 2014; Waters et al., 2014; Edgeworth et al., 2015), how better to promote an understanding of the human forcings of the planet than by accelerating interdisciplinarity across the Earth sciences (Richter & Mobley, 2009)? Indeed, CZ science may become the science of the Anthropocene (Latour, 2014) and recent CZ literature demonstrates the great potential for collaborations among the disciplines that CZ science calls together (Table 2). Nevertheless, ambitious interdisciplinarity is not the only hallmark of CZ science; CZ science is notable for its congruence with the scope of ecosystem science conceived decades ago by Arthur Tansley (1935).

### IV. Historic developments in ecosystem science

1. **Above- and belowground**

Lindeman (1942) argued firmly that it was ‘arbitrary and unnatural’ to isolate plant producers from heterotrophic decomposers. Ecosystem science was, after all, about the system and the integration of its components and processes. As ecosystem science developed, however, many terrestrial ecologists divided into two camps: those who studied aboveground plant dynamics and those who focused on belowground processes. Literature and journals were created that rarely reference the other’s papers. Each developed terminologies and organized professional meetings. Given Lindeman’s (1942) powerful statement about the integral nature of production and decomposition (quoted above), it is tempting to envision him opposing such a rift between above- and belowground terrestrial ecology. How ironic that ecosystem science that was launched to integrate auto- and heterotrophic organisms and their environment would develop scientists who would display such guild-like behavior with regard to their expertise and interests with the above- or belowground ecosystem!

Such a critique of terrestrial ecosystem science is not new, and was in fact Wardle’s in writing his tour de force, Communities and Ecosystems (2002) that linked activities of aboveground plant producers with belowground heterotrophic decomposers. Binkley (2006) also critiqued the division between above- and belowground scientists and the lack of interaction between what he called ‘ecologists’ and ‘soil scientists.’ Binkley’s (2006) essay, entitled ‘Soils in ecology and ecology in soils’, attributed much of the problem to the disciplinary formation of ecology and soil science during the 20th century. Binkley (2006) characterized 19th century concepts of terrestrial science held by the likes of Darwin, Dokuchaev and Pasteur to be well-integrated, whole-system representations of the natural world, and he spiced his essay with a quote from Hans Jenny (Stewart, 1984), the noted pedologist and ecosystem scientist, who provocatively commented ‘Many ecologists glibly designate soil as the abiotic environment of plants, a phrase that gives me the creeps.’ Although Wardle (2002), Binkley (2006) and Jenny (1980) laid bare the historic divisions within

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terrestrial ecosystem science, here we emphasize the opportunities these estrangements create for more fully integrating above- and belowground components of terrestrial ecosystems.

2. The superficiality of belowground investigation

Before we can attend to the integration of above- and belowground ecology, we must examine the development of belowground terrestrial ecology itself. Like it or not, most belowground ecosystem science has been peculiarly superficial in its depth of exploration (Richter & Markewitz, 1995) and thus is limited in its expansiveness of interpretation. Relatively superficial understanding of belowground systems has had scientific and societal consequences. Although all may generically agree that ecosystems are open systems, the fundamental openness of ecosystems from below is practically unstudied. This is not an insignificant point, for if we characterize lower boundaries poorly, we may significantly misinterpret the evolution and resilience of terrestrial ecosystems, an idea we expand on below.

We present three examples to characterize how the lower boundaries of terrestrial ecosystems have been superficially studied. Our first example comes from two review papers that address the question of how land use change alters soil organic matter (Post & Kwon, 2000; West & Post, 2002). In the 360 studies of the two reviews, the median depth of soil sampling was 20 cm. About 90% of the 360 studies sampled the soil to 30 cm or less (Fig. 2). Although it is difficult to sample the belowground ecosystem, often composed of rocks, roots, and indurated and plastic clays, sampling

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difficulties only partly explain the sampling depths revealed in Fig. 2. The surficial sampling reflects the widely held assumption that the most important and dynamic soil layers for gains and losses of carbon and nutrients are those that are most surficial. The system below 20 or 30 cm is presumed to change at such slow rates that sampling is not required.

Although organic carbon inputs and outputs are most rapid in surficial layers of soil, the relative balance of organic carbon inputs and outputs in surface layers may contrast with that at depth (Trumbore et al., 1995; Richter et al., 1999; Gaudinski et al., 2001; Mobley et al., 2014). Temporal changes in subsoil organic carbon have not been well addressed (Jenkinson et al., 2008; Rumpel & Kögel-Knabner, 2011; Mobley et al., 2014) and yet they may be highly significant to local and global carbon cycles. Relatively small changes in organic carbon concentrations in large volumes of subsoil may be hard to detect, but may still amount to substantial changes in carbon content. For example, over a century, a gain or loss of 0.1% soil organic carbon (SOC) in 100 cm of subsoil would be difficult to detect, but the content of that SOC would be the same order of magnitude as the rates of change in SOC contents estimated by Post & Kwon (2000) and West & Post (2002) in the upper 20–30 cm of soil. This point was recently quantified by Mobley et al. (2014) who documented no net change in SOC in repeated samplings of the surficial 60 cm of mineral soil in 16 plots that were undergoing 50 yr of reforestation following long-term cultivation. Remarkably, no net change in SOC across 60 cm was the net result of significant increases in organic carbon at 0–7.5 cm and concurrent significant decreases in carbon at 35–60 cm.

A second example of belowground sampling practices is from the International Biological Program (IBP) conducted in the 1970s in 36 ecosystems in Europe, Asia and North America (Reichle, 1981; Coleman, 2010). The objectives were to estimate fluxes and inventories of carbon and nutrients across a broad range of the world’s terrestrial ecosystems. For the time, the IBP data were invaluable in their detail, revealing contents and dynamics of chemical elements of foliage, branches and boles of forest trees and understory plants, and of the forest floor and mineral soil. Depth of sampling belowground varied among the 36 ecosystems, with the belowground sample generally conceived to represent the root zone. Although the data accumulated in the IBP ecosystems were a landmark in the history of ecosystem science, belowground contents of carbon and nutrients were reported with little to no indication of the depth of sampling. Cole & Rapp (1981) noted:

There are many assumptions, some of them perhaps unacceptable, built into these calculations, but the major difficulty derives from lack of information regarding below-ground processes. Very few studies included any root information, and none had annual elemental increment information for the root system. Consequently it was not possible to include roots in any flux calculations.

Thus, even by the 1970s and 1980s, quantitative data describing terrestrial ecosystems continued to be confined largely to above-ground components. It was during the IBP project that fine roots were discovered to be highly ephemeral structures and that their rapid turnover rivaled the fluxes of carbon and nutrients in the annual turnover of leaf fall (Harris et al., 1980). The continuing controversy surrounding rates of fine root turnover and their contribution to fluxes of the carbon and nutrients of terrestrial ecosystems (Gaudinski et al., 2001; Matamala et al., 2003; Pregitzer et al., 2008) underscores the point that belowground processes are relatively poorly and superficially characterized.

A third example is an international project of the late 1980s and 1990s, the Integrated Forest Study (IFS). This project was organized to investigate how industrial air pollution and resultant acid deposition were acidifying the environment, diminishing the availability of soil nutrients and influencing productivity and long-term functioning of terrestrial ecosystems. The IFS was organized in part as an updated version of the IBP and included 17 sites across North America and Europe. The depths of belowground sampling were conceptually taken to be rooting depths, but in contrast with IBP, the IFS sampling depths were precisely quantified, ranging from 41 to >120 cm, with the median depth of sampling of c. 60 cm. Johnson & Lindberg (1992) were well aware that: sampling depths and lower boundaries of the belowground ecosystems greatly affected interpretations of the vulnerability of ecosystems to acidic deposition, and belowground ecosystem data had large uncertainties. A major conclusion of the IFS project was that deep soil processes, such as nutrient release via mineral weathering and deep root uptake, were in much need of research (April & Newton, 1992).

These three examples demonstrate the historic, unresolved nature of lower boundary conditions of terrestrial ecosystems, and point directly to underlying boundaries being an important focus of contemporary belowground studies. Recent and on-going research demonstrates that lower ecosystem boundaries are deeper and more open, diffuse, heterogeneous and temporally variable than we have often assumed in the past (Richter & Yaalon, 2012). Deep cores and excavations are revealing that subsoil nutrient and organic matter supplies, even in rocky terrain, can be quantitatively and ecologically substantial down through several meters (Jobbágy & Jackson, 2001; Harrison et al., 2003, 2011; James et al., 2014). Deep underlying bedrock chemistry can impart substantial effects...
on vegetative productivity and ecosystem evolution itself (Hahm et al., 2014), and the geochemical importance of underlying bedrock has even been extended to nitrogen (Morford et al., 2011). The phenomenon of hydraulic lift (Caldwell et al., 1998) demonstrates the remarkable ability of deep roots to extend hydrologic rooting depths, with roots efficiently taking up deep water via diurnal cycles based on water potential differences of plant cells and soil. Lastly, mycorrhizal research continues to expand our appreciation of the ecological significance of deep subsoils. Mycorrhizas are observed to tunnel through feldspars and hornblends, presumably via organic acid dissolution, releasing rock-bound nutrients for biotic uptake (Hoffland et al., 2003). Although tree roots in deep C horizons and regolith may be physically excluded from the regolith matrix and confined to bedrock fractures, their ectomycorrhizal hyphae can proliferate throughout the regolith’s microporosity, enabling ecosystems to cycle water and nutrients from, in one case, a 4-m-deep rooting zone (Bornyasz et al., 2005).

V. The metabolism of ecosystems and critical zones

Unresolved lower boundaries of ecosystems are perhaps best explored by considering ecosystem metabolism, the biological–physical–chemical process of energy flow through ecosystems and CZs. In this section, we first consider why the study of ecosystem metabolism accelerated first in the 1940s in aquatic ecosystems, decades before that in terrestrial systems. Terrestrial science finally coalesced around common approaches to metabolism in the 1960s, but even today we maintain that our understanding of terrestrial metabolism is limited by incomplete belowground data. We use the propagation (Reiners & Driese, 2004) of belowground respiratory CO₂ to help define the lower boundary of the ecosystem, and therefore the congruence of the ecosystem and CZ concepts.

1. Metabolism in aquatic and terrestrial ecosystems

Energy flow through ecosystems has excited scientists throughout the history of ecosystem ecology and biogeochemistry (Lindeman, 1942; Odum, 1956; Gosz et al., 1978; Enquist et al., 2003; DeLucia et al., 2005; Cole, 2013). Odum (1968) called eco-energetics ‘the core of ecosystem analysis’ and Hutchinson (1940) and his students helped initiate ecosystem science with studies of the metabolism of aquatic systems (Lindeman, 1942; Odum, 1956).

In the 1940s and 1950s, ecosystem metabolism was documented in lakes, ponds, reefs, streams and rivers (Hagen, 1992), in part because aquatic systems have characteristics that make them amenable to metabolic studies. Specifically, aquatic systems have relatively rapid and thorough mixing rates, the water column is relatively easy to sample (Fig. 3), many aquatic organisms have small sizes and, despite great abundance, can be efficiently sampled, and the gas–liquid phase boundary strongly constrains gas diffusion between the aqueous and atmosphere systems. In addition, by the 1930s, analytical instrumentation was available to estimate aquatic ecosystem photosynthesis and respiration.

Following sanitary engineers, such as Harold Streeter and Earle Phelps, who for decades had estimated heterotrophic oxidation of pollutant organic matter in river stretches (Vesilind et al., 2010), aquatic ecologists measured diurnal variations of aqueous oxygen to estimate ecosystem photosynthesis and respiration (Odum, 1956). What was new was that ecosystem scientists quantified energy flow throughout the whole physical system. Odum’s (1956) classic illustration (Fig. 4) of stream metabolism depicts the ecosystem approach, showing photosynthetic inputs (‘P’) of organic reductants and respiration (‘R’) of the various organisms. In Fig. 4, P is less than R because the stream respired a sizeable amount of allochthonous detritus (‘imports’), a clear demonstration of what Tansley (1935) had referred to as the overlapping and interlocking of ecosystems.

By the 1960s and 1970s, metabolism data had become sufficient to make first-order estimates of terrestrial energy flows in forests, grasslands and other terrestrial systems. Gases, water and solids of terrestrial ecosystems are not as well mixed as they are in aquatic systems, and metabolic rates range by many orders of magnitude across plant and animal biomass, organic detritus, the decomposers themselves, soil and underlying substrata. Gases and water flow through complex networks that include vascular tissues, mycorrhizal hyphae and tortuous interconnections of pores within soil, regolith and the weathering bedrock itself with its fractures and heterogeneous weathering zones. As a result of this complexity, metabolism measurements in terrestrial ecosystems proved to be a daunting task, with much work left to be accomplished even today.

In spite of these challenges, terrestrial primary productivity was quantified in a number of ecosystems by the 1960s (Ovington, 1957; Rodin & Bazilevich, 1965; Woodwell & Whittaker, 1968). In the 1970s, Lieth (1975) and Lieth & Whittaker (1975) compiled terrestrial carbon data and weighted them by area of the world’s...
major terrestrial ecosystems to make the first global estimates of terrestrial ecosystem metabolism. Globally, gross primary productivity, net primary productivity and soil respiration were estimated to be responsible for carbon fluxes of \(1.20 \times 10^{15}, 6.0 \times 10^{15}\) and \(6.0 \times 10^{15}\) g C yr\(^{-1}\), remarkably large fractions of the total CO2 of the atmosphere \((c. 800 \times 10^{15}\) g C yr\(^{-1}\)). Most notably, after nearly 40 yr of additional research of ecosystem carbon exchange from the tundra to the tropics in field-based and remote sensing research, these initial estimates of global terrestrial metabolism have proven to be robust.

By the 1990s, some of the most important ecosystem studies tested the response of terrestrial metabolism to the rising CO2 of the global atmosphere in Free Air Carbon Exchange (FACE) experiments. In FACE experiments in deserts, croplands and forests, ecosystem metabolism has exhibited a strong dependence on CO2 concentrations in the aboveground atmosphere (Fig. 5), with metabolic effects highly significant belowground. Responses of the young temperate zone pine forest in Fig. 5 included soil CO2 effluxes (\(R_h\)), changes in activity of different microbial groups dependent on soil carbon as an energy source (Billings & Ziegler, 2008) and depth-dependent concentrations and carbon-isotope gradients of CO2 down to 200 cm (Andrews & Schlesinger, 2001; Oh & Richter, 2004; Bernhardt et al., 2006; Oh et al., 2005, 2007; Jackson et al., 2009).

2. Towards a systems perspective of belowground respiratory CO2

From the earliest estimates of terrestrial primary production in the 1950s to the most recent FACE studies, terrestrial ecosystem metabolism is largely understood to be an ecological process of land-to-atmosphere exchange. Although most photosynthetically fixed carbon exchanges rapidly with the atmosphere, little attention has been paid to the propagation of CO2 downwards throughout soil and deep bedrock substrata. These fluxes of deep CO2 are
examples of the propagation of ecosystem effects by Reiners & Driese (2004) and of Tansley’s ‘overlapping and interlocking’ of ecosystems. We assert that the downward propagation of respiratory CO\textsubscript{2} and its biological, chemical and physical effects are integral to the functioning of terrestrial ecosystems and CZs, and are key to understanding the congruence of the two concepts.

At the Calhoun CZO in the warm temperate zone of North America’s Southern Piedmont, forest respiration rates are highest in surficial O and A horizons, even though O and A horizon CO\textsubscript{2} concentrations are the lowest of the entire soil and weathering profile (Richter & Markewitz, 2001). The soil’s A horizon, home to the most densely rooted and most biologically active volumes of the mineral soil’s decomposition system, has well-developed macroporosity that allows respired CO\textsubscript{2} to rapidly diffuse and escape to the aboveground atmosphere. At deeper depths, however, although respiration rates are diminished, concentrations of CO\textsubscript{2} increase by orders of magnitude as a result of pore network tortuosity, which decreases gas diffusivity and greatly increases CO\textsubscript{2} residence time. From the Calhoun soil surface to c. 4–6 m, the apparent depth of maximum CO\textsubscript{2} concentrations (called here Z_{\text{max}}), CO\textsubscript{2} increases by c. 100-fold (Fig. 6a).

Despite a large and rich literature devoted to belowground CO\textsubscript{2} production, diffusion and fluxes, there are only the beginnings of research into CO\textsubscript{2} dynamics above and below Z_{\text{max}} (e.g. Oh et al., 2005; Johnson et al., 2008). Oh et al. (2005) modeled belowground CO\textsubscript{2} concentrations in the upper 10 m of soil (Fig. 7) using physical and biological properties corresponding generally to Calhoun soil profiles, whose CO\textsubscript{2} observations are illustrated in Fig. 6. In the upper meters of soil above Z_{\text{max}} modeled [CO\textsubscript{2}] closely tracked observed concentrations (Figs 6, 7). From 6 to 10 m and presumably all the way down to 30 m, where the weathering profiles meet unweathered granite, modeled patterns of declining [CO\textsubscript{2}] depict a downward propagation of CO\textsubscript{2}. Although not yet measured, such a dynamic would represent highly significant biogeochemistry that is yet to be much discussed in the ecosystem, soil or CZ literature.

Two factors can drive the reversal of [CO\textsubscript{2}] below Z_{\text{max}} (Fig. 7). First, soil respiration rates diminish to near insignificance below Z_{\text{max}}. Second, silicate mineral weathering becomes a sink for CO\textsubscript{2} below Z_{\text{max}} and this sink drives diffusion of CO\textsubscript{2} downwards. At the Calhoun CZO, a 70-m-deep core through a zero-order interfluve (Bacon et al., 2012; Brecheisen & Richter, 2014) traversed 30 m of soil and saprolite, and 40 m of unweathered granite bedrock. The solid core materials had strongly depth-dependent pH, exchangeable cations, \tau Na	extsubscript{Na} and \tau Ca	extsubscript{Ca}, all of which demonstrated advanced weathering to >10 m depths. At Calhoun, the CO\textsubscript{2} sink at >10 m can be represented with equations that describe how CO\textsubscript{2} consumption is tied to the weathering dissolution of albite (Na\textsubscript{Al}Si\textsubscript{O}_\textsubscript{4}), with reaction products being kaolinite [Al\textsubscript{2}Si\textsubscript{3}O\textsubscript{5}(OH)\textsubscript{4}], soluble sodium bicarbonate and silica:

\[
\text{CO}_2 + \text{H}_2\text{O} \leftrightarrow \text{H}_2\text{CO}_3
\]

\[
2\text{HCO}_3^- + 2\text{Na}^+ \rightarrow \text{Na}_2\text{CO}_3 + \text{H}_2\text{O}
\]

\[
\text{Al}_2\text{Si}_3\text{O}_5(\text{OH})_4 + 2\text{Na}^+ + 2\text{HCO}_3^- + 4\text{SiO}_2
\]

In Calhoun’s deep weathering profile, the pH ranges from 3.7 to 4.2 (in 0.01 M CaCl\textsubscript{2}) in all samples from 0 to 10 m, but gradually increases to pH 5.5 in samples taken from 16.8 to 18.3 m (Bacon et al., 2012). The chemistry of soil water collected from within this profile tells a similar story (Markewitz et al., 1998; Richter & Markewitz, 2001). Throughout the upper 6 m of soil, soil water is dilute and marked with low HCO\textsubscript{3}\textsuperscript{−} alkalinity (33 \textmu mol l\textsuperscript{−1} at a depth of 6 m). The Calhoun soil is an advanced weathering stage soil with no weatherable minerals to react with carbonic acid, despite high concentrations of CO\textsubscript{2} (Fig. 5). However, water collected from c. 25 m below the soil surface from a deep groundwater seep was >15-fold more concentrated in HCO\textsubscript{3}\textsuperscript{−} (Fig. 8). The increases in alkalinity were balanced by increases mainly in Na\textsuperscript{+} and Ca\textsuperscript{2+}, but also in Mg\textsuperscript{2+} (Stumm & Morgan, 2012). Respiratory CO\textsubscript{2} propagated deeply into this profile thus
No weatherable minerals exist in the upper 10 m of these highly weathered Ultisols and thus, despite elevated CO$_2$, HCO$_3^-$ alkalinity is very low until deep in the weathering profile (c. 25 m below the soil surface and containing > 10-fold the alkalinity as that of the water collected throughout 0–6 m). Reproduced with permission from Cambridge University Press.

driving carbonic-acid weathering of Na-, Ca- and Mg-bearing minerals in the saprolite below $Z_{\text{max}}$ (Richter & Markewitz, 2001; Bacon et al., 2012).

Diffusion of CO$_2$ downwards in the profile may account for a relatively small fraction of the total CO$_2$ that diffuses upwards through the soils and into the aboveground atmosphere (Fig. 7). Andrews & Schlesinger (2001) estimated the leaching of alkalinity from the FACE pine forest (Fig. 5) to be only c. 1% of total soil respiration. Nevertheless, plant life in the aboveground ecosystem drives weathering reactions in the lowest reaches of the ecosystem by the biophysical magnification of CO$_2$ partial pressures (Figs 6, 7), with strong seasonal and depth-dependent waves of [CO$_2$] propagating deeply through the belowground ecosystem (Richter & Markewitz, 1995; Baldocchi et al., 2006; Johnson et al., 2008; Jackson et al., 2009). The biogeochemical result is carbonic acid weathering of rock-derived minerals that releases soluble nutrients to deep roots and drainage waters and – critically – produces soil from the bottom up (Heimsath et al., 1997). Thus, the small fraction of the system’s total respiration that diffuses downwards can have an enormous influence on ecosystem structure and function by helping to generate the soil that ultimately supports the ecosystem itself. We submit that, although the lower boundary of the terrestrial ecosystem may be diffuse, heterogeneous and open, the metabolism of the terrestrial ecosystem demonstrates that the ecosystem’s lower boundary is the bottom of the CZ itself, the depth to which biogeochemical signals penetrate the Earth’s surface.

VI. Towards a more active biogeoscience

We began this review with the assertion that terrestrial ecosystems and Earth science’s CZ were congruent across spatial and temporal scales of vegetation-clad weathering profiles and hillslopes to small catchments, landscapes, river basins, continents and the terrestrial Earth itself. We asserted that the congruence of concepts is most readily apparent viewed from Tansley’s ecosystem as ‘one physical system’ and Lindeman’s and Hutchinson’s conviction of the inseparability of the biotic–abiotic complex. From this perspective, it is evident that terrestrial ecosystem scientists have important unfinished business in the study of ecosystem metabolism, specifically in quantifying the propagation and biogeochemical effects of plant-derived respiratory CO$_2$ that diffuses throughout soils and deeply into weathering geologic substrata. Although these metabolic processes may account for a relatively small fraction of total respiration belowground, they are fundamental for the biogeochemical effects that follow: the microbiological recycling of CO$_2$ and the carbonic acid weathering that helps to produce the very soil on which the ecosystem depends (Richter & Markewitz, 1995).

Two implications follow from this congruence in concepts. First, given that ecosystems are open, three-dimensional systems, the ecosystem is cut short if it includes too little of the belowground environment. Ecosystem resilience and sustainability cannot be accurately gaged, nor can Tansley’s ecosystem vision be realized, if lower boundary conditions are not carefully evaluated. Today, opportunities abound to explore connections between upper and lower components of CZ ecosystems, between soils and streams in watersheds, and between CO$_2$ derived from plants and deep microbial communities, all to better resolve ecosystem and CZ evolution and resilience. The biological and geological arms of the national science foundations of many nations now support

Fig. 7 A model simulation of soil CO$_2$ using system properties and fluxes comparable with those at the Calhoun pine forest illustrated in Fig. 6 (Oh et al., 2005). The figure is an excellent illustration of an ecosystem propagation as in Reiners & Driese’s (2004) propagation of ecosystem influence (CO$_2$ and carbonic acid) throughout the belowground ecosystem and down into the weathering bedrock. Here, the depth of maximum CO$_2$ concentration ($Z_{\text{max}}$) is modeled to be seasonally dependent and between 3 and 6 m.

Fig. 8 Soil and seep water chemistry at Calhoun’s long-term soil experiment site illustrated in Fig. 6 and modeled in Fig. 7 (Richter & Markewitz, 2001). No weatherable minerals exist in the upper 10 m of these highly weathered Ultisols and thus, despite elevated CO$_2$, HCO$_3^-$ alkalinity is very low until deep in the weathering profile (< 50 µeq l$^{-1}$), with groundwater collected from a seep c. 25 m below the soil surface and containing > 10-fold the alkalinity as that of the water collected throughout 0–6 m. Reproduced with permission from Cambridge University Press.
programs, such as the International Long-Term Ecological Research Program (ILTER), the international CZO programs (Fig. 1), and in the USA the National Ecological Observatory Network (NEON), each of which can greatly benefit from the recognition of the congruence of the ecosystem and CZ concepts. For example, although we expect much significant and timely data to soon flow from the USA’s NEON program, the explicit 2-m-deep limit of belowground sampling (Loescher et al., 2014) terminates belowground ecological processes at a depth far too shallow for many ecosystems. Given the tens of thousands of sensors and samplers being installed in the 60 NEON sites across the USA, a relatively small number of additional sensors and samplers at > 2 m depth can be installed to monitor moisture, temperature and biogeochemistry, and thereby extend the ecosystem to the full depth and volume of the CZ. The results would almost certainly transform how we understand ecosystem dynamics and evolution, and have major benefits for CZ science, given the extensive and careful placement of NEON sites across North America’s climatic and vegetative gradients.

The second implication that follows the conceptual congruence is that we who study Earth’s terrestrial environments, whether our core expertise be plants, animals, microbes, soils, hydrology, geomorphology, geological processes, social sciences or the humanities, need to redouble the breadth of our professional interactions and become involved in more integrative studies. We need to more actively follow the interdisciplinary leads of Tansley (1935) and Jordan et al. (2001). Our individual disciplines give us skills, laboratories, literature and insights, but disciplinarity also limits the wider vision of our planet and distracts us from the richness of what can only be gained from the pooling of ideas, data and expertise from across the disciplines.

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References


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