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Critical Zone and Ecosystem Dynamics

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The CZ as an Ecological Problem: How the Interplay of Biotic and Abiotic Actors Determines the Functioning of Earth's Living Skin

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1 An Emerging Recognition of the Critical Zone

Long before the term 'critical zone' (CZ) was coined by Ashley [82] to encompass Earth's biological and geological features from the top of the vegetative canopy to the depths of circulating groundwater, many scientists have recognized that both biotic and abiotic actors are centrally important for understanding many of Earth's most fundamental processes [141]. Scientists such as Alexander von Humboldt (1769–1859), Charles Darwin (1809–1882), Jacques-Joseph Ébelmen (1814–1852), Vasily Dokuchaev (1846–1903), Vladimir Vernadsky (1863–1945), Arthur Tansley (1871–1955), Hans Jenny (1899–1992), Robert Berner (1925–2015), and James

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Lovelock (1919–2022) worked across centuries and continents to demonstrate how momentary- and molecular-scale biotic actions (e.g., photosynthesis, respiration, production of organic acids, root growth) generate powerful chemical and physical forces that when scaled up govern environmental conditions of the planet. Indeed, it was a botanist familiar with plants' consumption of CO_2—Eunice Newton Foote—who first developed and published the concept of greenhouse gases warming the planet [53, 151], an idea developed as well by John Tyndall [165]. Today, we can recognize how these individuals and their colleagues integrated a diversity of ideas from biotic and abiotic processes into their work, a hallmark of today's CZ science.

Tansley's introduction of the ecosystem concept [159] offered an intellectual home for those interested in the systemic interaction of biota with the abiotic [130]. Ecosystem ecology, a particular branch of the broader field of ecology, is defined as the study of life as it interacts with the abiotic world [146]. In the nearly 100 years since the coinage of 'ecosystem' [159], this discipline has developed a literature, conceptual and mathematical models, and subdisciplines that have enhanced our understanding of how the biotic and abiotic interact on Earth's surface (e.g., [20, 74, 97, 103, 112, 118, 120, 122].

Concomitant with these developments, scientific institutions such as departmentally-organized universities and scientific societies, journals, and funding agencies also evolved, promoting more disciplinary approaches to science [131]. As a result, scientists began to face strong pressures to self-identify with particular disciplines. This development countered the ecosystem approach, which is defined by its interdisciplinarity. Perhaps because ecosystem ecology was linked by its name to other, purely biological subdisciplines of ecology (e.g., population and community ecology), it has often been assumed to be a fundamentally biological pursuit. Many contemporary ecosystem ecologists have been trained in and remain focused on biologically-focused areas such as photosynthesis, plant respiration, microbial cycling of organic matter, and plant–microbe interactions, and often lack training in the chemical, physical, and geologic dimensions of ecosystems. One manifestation of this problem is the superficial coverage of the belowground component of ecosystems [131, 109]. This feature was noted by Binkley [16], who highlighted that reviews of the ecological literature omit mention of soil, the very medium from which terrestrial ecosystems derive most of their required resources. Most ecological studies of soil focus on soil microbes and fauna interacting with each other or their organo-substrates, or on roots and their interactions with microbes—all important but largely biologically-focused endeavors (e.g., [5]).

This biological focus of many ecosystem-trained scientists and the institutions in which many function can limit our understanding of the interactive nature of many Earth surface processes. Multiple examples demonstrate this assertion. First, rock- and mineral-derived nutrients are critical factors driving biological activity in terrestrial systems [145]; with the exception of most N, even nutrients derived from organic matter recycling originally are released from mineral weathering. Second, the inherited geologic structures of bedrock strongly controls ecosystem water storage and transmission to groundwater and streams [93]. Third, landscape position and geomorphological characteristics constrain light availability [12]. These well-studied

phenomena demonstrate the degree to which an ecosystem's ability to capture nutrients, water, and light—and thus its productivity—is dictated by chemical and physical site characteristics.

A fourth phenomenon exemplifies an especially rapidly expanding branch of CZ science that, like the first three, clearly links biotic and abiotic processes. Multiple investigations reveal the importance of dust nutrient inputs to ecosystems as key promoters of ecosystem productivity. This feature of terrestrial ecosystem nutrition has been known for years (e.g., [32, 96, 150]), but recent CZ studies help expand this concept to more fully reveal the importance of dust-derived inputs to many ecosystems. Where highly weathered soils would otherwise promote relatively low productivity, dust can serve as an especially critical nutrient source [32, 59]. In addition to inoculating recipient sites with dust-bound microbial populations [101], dust can travel great distances [47, 184] to provide nutrients like P to biota [102, 170] at supply rates that can outpace that of bedrock itself in some systems [1]. Dust also can influence soil structure [42] and generate meaningful material thickness within soil profiles [95, 102]. Dust inputs are not an important source of nutrition in all systems (e.g., [166]), but the nutrient subsidies provided by dust in many may be sufficient to mitigate rock and mineral weathering that would otherwise supply nutrients. This echoes the hypothesis suggesting that OM-derived nutrients can mitigate rock and mineral weathering [25]. More broadly, evolution of dust-focused CZ literature rests within a concept central to ecosystem, and thus CZ, science—that nutrients are either obtained internally through de novo weathering or OM recycling, or from external sources, and that nutrient sources thus dictate weathering rates.

The interactive nature of many of Earth's CZ processes is further demonstrated by biological phenomena influencing multiple physical and chemical attributes of the CZ, going far beyond the role of vegetation as a key sink for atmospheric CO_2 and nutrients. Roots, for example, both help prevent erosion [153] on timescales of seasons to decades and help promote soil creep over longer timescales [22, 124]. Roots and the soil microbial communities they nurture generate organic acids and CO_2 that contribute to the weathering of soil minerals and bedrock [90, 104]. Roots and microbes are also capable of recycling organic matter-bound nutrients, mitigating subsequent weathering processes as nutrient demand is met partially by organic matter decay [69]. Holistic terrestrial ecosystem studies thus must embrace some combination of physical and chemical sciences (e.g., lithology, mineralogical weathering, physical geography, geomorphology, hydrology) along with the biological phenomena that interact with these features.

The emergence of the CZ paradigm [23, 82] promoted an interdisciplinarity already evident in the works of scientists such as Humboldt and Darwin [141, 132]. The explicit linkage of the bio- and geosciences in CZ studies provides the scaffolding needed to address environmental puzzles at a diversity of scales [15, 156, 185]. Realization of the CZ approach is hardly trivial: Implementing studies that integrate the bio- and geosciences requires collaboration among practitioners who represent disciplinary siloes, speak distinct vocabularies, and view scientific puzzles through separate lenses ([131]; Fig. 2.1). These traits can impede even well-intentioned

collaborations [174]. However, many lessons have emerged by bridging the bio- and geo-focused disciplines to examine the 'critical zone ecosystem' [130].

Here, we describe findings that emphasize how life, emphasizing vegetation and microbes, responds to and shapes the physical environment in which it persists, yielding feedbacks for Earth's climate, primarily through modifications to hydrologic functioning. We focus on the interactions of biota and the physical and chemical features of soil pedons and landscapes as they drive ecosystem-scale hydrologic fluxes. We acknowledge that the flowpaths for soil water are also the same conduits through which soil gases flow [83] and are thus key to understanding ecosystem functions (e.g., [67]). In the current work, we emphasize hydrologic flows due to their importance for vegetative water uptake and thus productivity, flows of soil organic C and nutrients, and soil weathering processes. These processes all reflect diverse disciplines that coalesce in Earth's soils (Fig. 2.1). We focus on hydrologically-relevant features because of the long history of individual disciplines telling us about the large-scale importance of these processes, and because of emerging research highlighting the importance of the intersection of these disciplines for projecting future
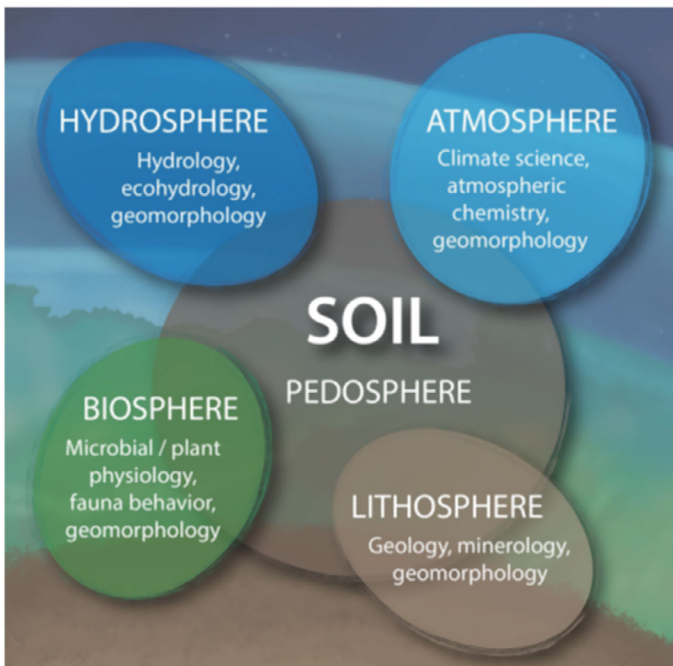
Fig. 2.1 Depiction of soil as representing the Earth science realms of the atmosphere, lithosphere, biosphere, and hydrosphere. Examples of scientific disciplines often associated with each realm are indicated. Note that all realms intersect with other realms as pairs (e.g., atmospheric chemistry interacts with plants to represent biosphere–atmosphere interactions), but soil is the salient feature of Earth's surface where all four realms intersect. Geomorphology is presented as a feature in multiple locations due to its influence on, and its capacity to be influenced by, multiple realms

ecosystem functioning on a rapidly changing Earth. The knowledge we spotlight reveals Earth's CZ as a fundamentally ecological problem.

2 Soil and Landscape Constraints on CZ Hydrologic Functioning

Within a given climate regime, hydrologic function is strongly influenced by the properties of and interactions between biotic and abiotic components of the CZ ([7, 39], Fig. 2.2). Here we adopt a physically-oriented, catchment-scale definition for hydrologic function as the partitioning, storage, and discharge of water [171, 181]. Although different locations within the CZ contain both biotic and abiotic components, it is the interaction between these components in the soil environment that exerts a strong control on hydrologic function through its effect on soil hydraulic properties. This near-surface soil environment is subject to steep and dynamic energy and soil moisture gradients that drive the relatively rapid flux of water and the temporal variations in the direction and velocity of this flow [176]. As soil biota (e.g., microorganisms, plant roots, and macrofauna) respond to these variable near-surfaces fluxes of water, they shape the organization of soil particles and pores [156] and thus influence the development of soil horizons especially within shallow depths where the soil biological activity is concentrated. This modification happens primarily through the production of soil organic C (SOC), the formation and stabilization of soil aggregates, and the direct and indirect creation of macropores that perforate the soil. However, the ability of biota to modify the soil environment is constrained by the physical and rheological properties of the material, which are largely controlled by soil texture.

Soil texture is important to the hydrologic functioning of the CZ because it directly affects the relative surface area of the soil and the soil pore-size distribution. Pore size (i.e., effective pore diameter) and relative surface area control the affinity of water to the soil matrix and impart a potential energy to the soil water (i.e., matric potential; [71]). Matric potential, in combination with components such as gravitational and hydrostatic pressure potential, governs the total potential energy of the soil water. Differences in the total potential energy state drive infiltration and the movement of water through the CZ. Thus, texture strongly affects water flux through soil by governing potential energy gradients. Soil texture also affects the ability of the soil to conduct water because of its control over surface area and the porosity of the soil matrix (especially, pore size and tortuosity). That is, as the soil particle-size distribution becomes finer, so do the pores between those particles, reducing the hydraulic conductivity of the soil. As the soil dries, air is introduced, bounding the soil water between the air–water interface and surfaces of the soil particles, this modifies the lengths and tortuosity of the paths that the water must follow to move through the soil, further reducing the hydraulic conductivity [83]. Therefore, soil texture—both on its own and in conjunction with degree of saturation of the soil—is
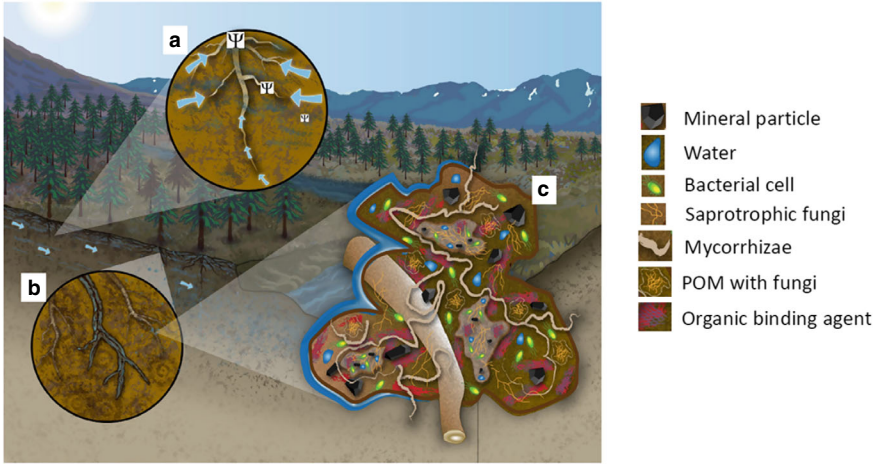
Fig. 2.2 Schematic describing examples of belowground features of the critical zone (CZ). (1) At the landscape, catena, and pedon scale, water flows down potential energy gradients (arrows) and through relatively large soil pores (water depicted near roots in **a**). Larger ψ symbols indicate more negative water potentials. Where soil profiles have distinct boundaries, water flows can change abruptly. (2) Roots are opportunistic drivers of hydrologic functioning. Roots take up water primarily from surficial horizons and to a lesser extent from deeper in the soil profile (**a**). Where roots can reach the water table, productivity tends to be higher. (3) Because roots and microbes influence soil structure, within a given climate region they shape their own water availability. Roots must perforate the soil to grow, creating channels for flow (**b**). When they die, shrink, and eventually decay (larger channel in **b**), these channels become more open, becoming reinforced as preferential flow paths. Microbes and roots also govern soil structure by exuding soil binding agents. When microbes die, their necromass appears to have an especially outsized role in serving as "sticky" binding agents. Binding agents, no matter their source, help to form soil aggregates (**c**), and it is those aggregates that dictate where the voids are in soil through which water can flow and be stored. The relatively large pores surrounding macroaggregates are especially important for water flow. The mineralogy, particle texture, and capacity of clay minerals to bind with organic matter all influence aggregate characteristics. Within macroaggregates (**c**), microaggregates harbor their own microbial communities, stores of organic matter and minerals, water, and gases (visible as outlined shapes containing these features, within the macroaggregate). POM, particulate organic matter

critical for understanding the retention and flux of water in the CZ due to its influence on both the total potential energy gradient driving flow and the conductivity of the soil through which the water moves.

Macroporosity of the soil is another important determinant of fluxes of water through the CZ. Although there are different classifications of macropores that depend on their origin and shape, here we restrict our discussion to macropores that are large (often greater than a few hundred micrometers), planar or tubular, and continuous; these macropores function as potential pathways for the preferential transmission of water ([64, 78], Fig. 2.2). Macropores of this type result from either biotic or abiotic processes in the soil. Abiotic processes include the drying and concomitant shrinkage of the soil matrix especially in fine-textured materials, the formation of aggregated structural units (e.g., clay tactoids, clusters of clay and silt

domains, and subsurface peds like angular blocks and prisms) due to the cohesion of the soil particles or precipitation of inorganic cements (e.g., $CaCO_3$, opaline Si, or Fe-oxides), and the reinforcement of preferential pathways by the development of surface coatings [78, 161]. This latter process is largely due to the illuviation of clay (e.g., argillans, expanded on below) or the reorientation of the soil fabric at the pore surface from mechanical pressures (e.g., fabric hypocoatings, [154]). Biotic processes responsible for the formation of macropores include the activity of fossorial fauna [126], the growth and subsequent decay of roots [64], and the formation of stable aggregates through, for instance, the egestion of soil particles by earthworms [81], enmeshing of particles by mycorrhizal fungi and fine roots [79, 135], and secretion by soil microorganisms of extracellular polymeric substances (EPS) that glue soil particles together [36].

Macropores created through the processes outlined above typically make up only a minor fraction of the soil volume, but have an inordinate effect on water flux through the soil in saturated and even unsaturated conditions [113, 175]. The reason for this phenomenon is that volumetric flow through a pore is proportional to the fourth power of its radius (i.e., Poiseuille's law). Watson and Luxmoore [175] demonstrated this principle by reporting that, under ponded conditions, macropores may be responsible for 96% of the water flow though only accounting for 0.32% of the soil's volume. Where these macropores intersect the land surface (e.g., open biopores or aggregated surface soil horizons), they are important for the infiltration of water into the soil and the potential for runoff generation, and, thus, the loss of sediments and nutrients through erosion [10, 92, 149]. Recent findings have shown that soil macropores are sensitive to shifts in climate, likely driven by soil biota [30, 73]. Given the large control over water flow that macropores exhibit, even small changes to these pores in response to climate is likely to affect the water cycle and the hydrologic function of the CZ via changes to infiltration, aquifer recharge, and the lateral redistribution of water by runoff [73].

As soils form in response to the addition, loss, transformation, and translocation of mass and energy, soil horizons develop that are distinguished from each other, in part, on the basis of macromorphological properties exhibited as color, consistence, texture, structure, and porosity [140, 164]. Differences between vertically adjacent soil horizons in the expression of these latter properties create layered conditions that are important for water flow through the vadose zone. This is because the boundaries between horizons, especially if they are abrupt, can represent significant discontinuities in soil hydraulic conductivity and water content [71]. The discontinuities—for example, a coarse-textured A horizon above a clay-enriched Bt horizon—act to retard the rate of soil water infiltration due to the reduced saturated hydraulic conductivity of the lower compared to the upper layer [127]. However, even in cases where fine-textured layers or horizons with concentrated organic matter overlie more conductive, coarse-textured materials (e.g., an O horizon directly over an E horizon, or a clay-rich horizon over a sandy horizon), the boundary between these horizons forms an obstacle (often temporary) to the wetting front that reduces infiltration. This is due to the differences in potential energy of the soil water across the boundary of the two layers with the fine-textured material imparting a sufficiently lower total potential

energy compared to the underlying layer [127]. The water hangs at this boundary until the saturated zone behind the leading edge of the wetting front increases sufficiently for the added hydrostatic pressure to overcome the matric forces holding the water. In addition to effects on infiltration, differences in soil hydraulic properties through and across horizons strongly influence the generation of preferential flow [46].

At a broader scale, ecosystems, soils, and landforms coevolve to shape the soil-geomorphic properties of the landscape [182]. For example, slope curvature affects soil thickness and the concentration/dispersion of surface water (e.g., [123]), and elevation controls snow accumulation, rainfall, and evapotranspiration (e.g., [178]). These features and the soil properties discussed above all constrain the hydrologic functioning of the CZ by driving the lateral redistribution of water and sediments along topographic gradients from ridges to valleys and by controlling the radiative conditions, and, thus, the soil temperature, effective moisture, and ecological properties corresponding to land-surface aspect [48]. The lateral fluxes of water along topographic gradients occur both at the land surface and within the subsurface, controlling the vertical distribution of plant-available water and, therefore, plant rooting depth across the landscape [50]. Milne's [106] concept of the soil catena that was used in part to explain different drainage classes along a hillslope [182] is especially useful for understanding this relationship. A catena is a chain of adjacent and geomorphologically-related soils along a hillslope, from summit to base, perpendicularly transecting the topographic contours [140]. Within this framework, soil morphological differences at different hillslope positions are explained by the lateral and vertical fluxes of surface water, groundwater, and sediments. Indeed, catenas can be conceptualized as hillsheds that undergo soil creep [26]. The movement of soil material and redistribution of water from steeply sloping positions to the base of hillslopes give rise to textural differences on the landscape that control CZ hydrologic functioning such as soil water retention (Fig. 2.3).

All of these soil and landscape physical constraints on CZ hydrologic functioning are both the product of, and influence, biotic functioning. Soil geomorphic properties of landforms, and the soil properties of soil profiles, strongly affect the lateral and vertical distribution of water and, thus, the distribution of vegetation across the landscape and the distribution of roots within a profile. However, the influence of vegetation on both surface and subsurface hydrology significantly affects landform evolution and soil formation as well (e.g., [33, 179]). Indeed, rooting depths appear sensitive to the different vertical distributions of soil moisture that result from hillslope-driven fluxes [48] and the properties of a given profile. In well-drained summit positions, for instance, the pool of plant-available water is largely contained at relatively shallow depths (i.e., from the infiltration of rainwater) with the water table too deep for plant roots to access; this is in contrast to poorly-drained toeslope positions that favor wetland species due to the creation of permanent water-logged conditions from a water table that is near or above the land surface at the base of the hillslope [48]. Between these two ends of the hillslope, plant-rooting distributions are affected by the relative positions of infiltration-controlled soil moisture and the capillary fringe above the water table, with plant roots sensitive to the
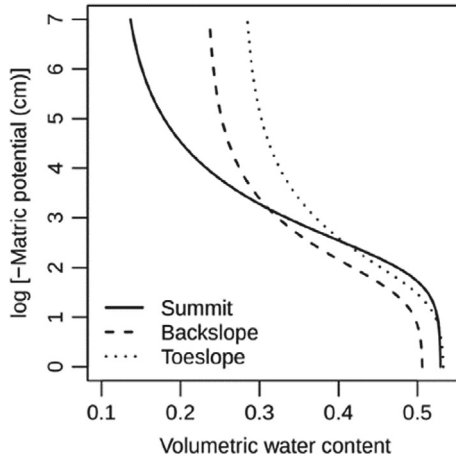
Fig. 2.3 Soil water retention curves relating soil volumetric water content to the energy at which that water is held in the soil (matric potential) plotted for three surface A horizons representing different hillslope positions along a catena in the Fitch Natural History Reservation at the University of Kansas Field Station near Lawrence, KS, USA depicting the soil and landscape constraints on hydrologic functioning of the CZ. Soils on the broad, relatively-level summit position of this hillslope have developed within the fine-textured loess parent material without significant lateral additions or losses of soil material. The texture of the A horizon has coarsened naturally in this position through the vertical translocation of fines (silt and clay) to deeper subsurface (B) horizons, yielding a surface horizon water retention curve with a steeper slope (i.e., greater change in water content with unit change in matric potential) in the plant-available water range (i.e., y-axis approximately between 2.5 and 4.2). The steeper slope translates to soil water that would be released relatively easily in response to increasing root-water demand. By contrast, soils in the steeply sloping backslope position have developed under conditions of frequent erosion of material to lower-lying toeslope positions where surface A horizons inherit properties of the exhumed clay-rich subsurface layers. The higher clay content of these surface horizons in both the backslope and the more distal toeslope positions that have received inputs from movement along the catena create a greater proportion of very fine pores that retain more water in the soil even under low matric potentials (i.e., a relatively shallow slope in the plant-available water range) and a greater amount of residual water content which can be seen as high water content even under extremely low matric potentials (6–7). Material moved to the surface horizon of the backslope is likely to have been derived immediately upslope from a higher position along the backslope. The curves were assumed to follow a [168] water retention function with the parameters of the function predicted from sand, silt, clay, bulk density, and the volumetric water contents at 33 and 1,500 kPa using the Rosetta3 pedotransfer function [186]. Although the water retention curves in this figure are plot with matric potential on the y-axis and water content on the x-axis, they are often plot with these axes switched. We note that these two equally-accepted conventions of plotting the water retention curve stems from the lack of matric potential and water content in being a clear response variable

seasonal changes in water table depth in upper backslope and footslope positions [48]. Thus, without a transdisciplinary knowledge base embracing geomorphology, soil science, and vegetation water uptake patterns, CZ water balance would remain poorly understood.

3   Roots as Direct, Biotic Drivers of CZ Hydrologic Functioning

3.1   Ecohydrological Considerations

Discerning root water uptake patterns must be informed by root biology and the soil and landscape constraints on soil physical properties described above. Historically, root water uptake has been the purview of ecophysiologists and ecosystem ecologists with training in ecophysiology, and to a certain extent soil physicists. However, plant water availability and root water uptake impose cascading influences on whole-CZ structure and function. It has long been recognized that the physical and biogeochemical changes that occur with changes in species composition and root architecture co-evolve with topography, geology, soil, and climate to control the trajectory of catchment hydrology (e.g., [65]). Understanding such connections and non-linear feedbacks is particularly important as we confront the need to forecast Earth system evolution in the face of accelerating climate change and human perturbations [155]. Thus, in addition to the role of landscape position influencing system hydrology discussed above, we must also emphasize that vegetation plays a role in governing water flows as well.

With ample nutrient availability, vegetative growth tends to be optimized where water availability is balanced by evaporative demand [136]. Though at the largest scale this is governed by the overall climate, within each climate zone, the local CZ (e.g., the landscape features discussed above) exerts strong governance over water abundance and depth to the water table. If rooting networks are able to access this groundwater, plants can flourish in what might otherwise be sub-optimal conditions [49]. This action can result in an altered position of the water table, even in low landscape positions, as plants meet their evaporative demands [157]. The depth of this drawdown is a function of the soil's water holding capacity, which can be impacted by plant-induced clogging of pores, or perhaps pore generation [158]. Thus, the relationship between vegetation and groundwater or water table position, and factors that possibly alter water availability and position, can have significant impacts on how the CZ-ecosystem functions.

An additional layer of complexity in ecohydrologic processes has been hinted at for decades and is emphasized in recent, explicitly CZ-focused work. In multiple ecosystems, rock water extraction by vegetation has been observed [2, 21, 152]. More recently, neutron probe data from the mountainous western U.S. demonstrate a meaningful reliance of some vegetation on deep rock moisture—water retained in the weathered rock vadose zone [108, 129]. Given that rates of root growth into the subsurface can outpace rates of soil loss from erosion, roots thus not only influence water storage in these zones, but also govern the detachment of bedrock and the initiation of soil formation [137], factors that feedback to govern the generation of porosity and thus water storage. In the Anthropocene, rates of forest harvesting may be outpacing the rate at which root growth by trees impart their ability to fracture or detach bedrock in working forests [137].

The human influence in the Anthropocene is also evident via shifting rooting depth and/or rooting function at a diversity of scales. Given the role of roots as soil architects, human activities that modify root activities are likely altering the physical structure of the subsurface. Within a given biome, changes in environmental conditions that shift the amount and timing of plant water use (e.g., via changes in plant water use efficiency, the depth to which water is extracted, or the frequency with which soils may undergo wetting and drying) may alter aggregate formation and stability, and thus soil structure [27, 35, 40, 41, 121]. Where permafrost thaws or alpine tundra warms, more deeply rooted, woody vegetation can develop [180]. Woody encroachment of deeply-rooted shrubs into grasslands in warmer climates is also accelerating [139]. Globally, estimates suggest that an additional ~19,200 km^3 of soil have become rooted in regions experiencing root deepening in the Anthropocene ([68]; Fig. 2.4). These root-deepening phenomena have the potential to sculpt the subsurface in ways that influence water flow through the subsurface [156]. Root shallowing also is an important Anthropocene phenomenon; roots are absent from an estimated 30,100 km^3 of soil today compared to soil volumes rooted by potential vegetation [68]. Roots have been removed from an estimated 13,700 km^3 of this volume where perennial systems have been replaced with annual agriculture, a landscape feature expected to expand in the future ([68]; Fig. 2.4).

The net effect of human activities in the Anthropocene thus has been a shallowing of roots, and a decline in the soil volume directly mined by roots for water and nutrients [68]. This feature prompts the question of how soil formation processes are transformed as root shallowing limits the production of weathering agents, particularly given the long time periods over which root regeneration occurs [13]. More generally, this phenomenon highlights the fundamental role of an ecological consideration—rooting depth—as an agent of soil engineering at depth and thus of CZ functioning.

3.2 Ecophysiological Considerations

The water uptake patterns permitted by local climate and physical landscape- and pedon-scale features, described above, are the scaled-up result of processes occurring at the momentary and cellular temporal and spatial scales, respectively. The dynamics of plant water uptake and loss are rapid. Indeed, while water accounts for up to 95% of the fresh weight of herbaceous plants, the majority of water absorbed by most plant species (~98%) is lost to the atmosphere via transpiration within minutes of being absorbed from the soil. Thus, plants need enormous amounts of water to offset transpiration losses and facilitate C uptake (and photosynthesis). While some species can absorb a significant portion of water through leaf pores (as dew or vapor) [9, 70], the vast majority of plant species rely on root uptake to meet water demands. Roots provide several key functions for plants, including anchorage to the terrestrial surface, but the functional consequences of water and nutrient absorption from the
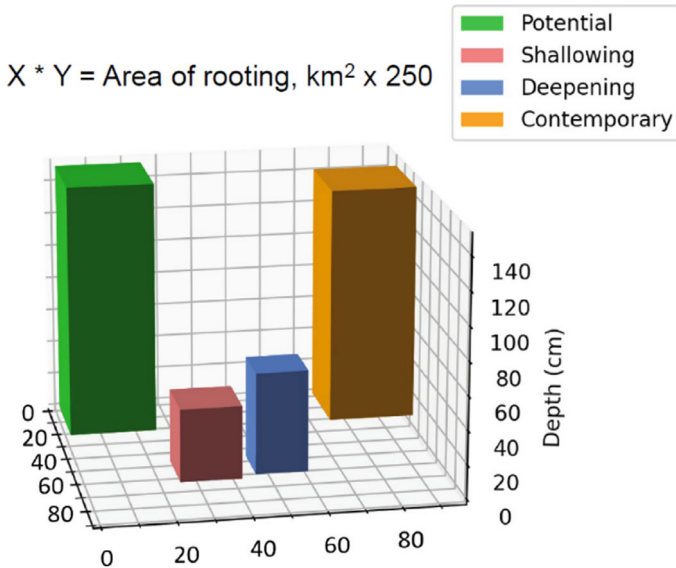
Fig. 2.4 Scaled depiction of estimates of the volume of Earth's rooted soil rooted with potential vegetation (green) versus actual contemporary vegetative cover (orange), and the two competing changes driving that difference. The red bar represents the volume of soil where roots are absent now that contemporary vegetation has replaced potential vegetation (~30,100 km3), largely due to agricultural clearing. The blue bar represents the volume of soil now experiencing rooting that, prior to the Anthropocene, was not rooted (~19,200 km3); this is largely due to woody encroachment. The top of each bar is scaled to reflect the area represented by the data. Hence, the top of the green and orange bars are of equal area to reflect all of Earth's vegetated surface; the red bar's top area is larger than the blue bar to reflect the larger area over which roots are shallower in the Anthropocene compared to potential vegetation. The depth axis reflects the average depth to which roots extended globally prior to the Anthropocene (green) and today (orange), and the average depth to which roots in regions experiencing shallowing (red) and deepening (blue) extend. In all cases, 'depth' refers to the depth of 99% of root biomass. Data derived from maps of potential vegetation, remote sensing-derived estimates of current vegetation, and biome-specific rooting depth distributions in the literature; for details see Hauser et al. [68]

soil are key determinants of nutrient, C, and water recycling within ecosystems and serve as a link between belowground and aboveground physiological processes [77].

Plant roots absorb water from the soil based on the hydrostatic pressure gradients established from soil matric to leaf water potentials. Water flows down this potential energy gradient as long as the potential energy in the leaf that is established by water lost via transpiration is lower than that in the soil. As the soil dries, the potential energy gradient from soil to leaf declines, resulting in less plant-available water. In this situation, plants: (1) close leaf stomata to reduce the water potential gradient, (2) lower the leaf water potential (by increasing transpiration) to re-establish a larger pressure gradient from soil to leaf allowing for greater potential extraction of water from soil spaces, or (3) utilize water from potentially wetter zones of the soil. The degree of leaf stomatal control used to regulate transpiration flux has been

commonly described as isohydric or anisohydric [105, 160]. Isohydry refers to a strategy of stomatal regulation to maintain a constant water potential prior to wilting and prior to the establishment of air embolisms and cavitation in the xylem vasculature. Thus, isohydric strategies reduce transpiration to minimize the chance of wilting and hydraulic failure, but with a cost of reduced C assimilation and growth. Plant species that utilize anisohydric strategies regulate transpiration at the expense of potential hydraulic failure to maintain the hydrostatic pressure gradient as soils dry and water is less available. Thus, anisohydric species are able to maintain C assimilation but at greater risk of desiccation. Strategies of isohydry or anisohydry vary by species and genotypes according to changes in soil water availability, which in turn vary across catenas and landscapes (Fig. 2.5). While these strategies present dichotomous endpoints of acclimation to low water availability, most plant species exhibit aspects of each, with examples of isohydric behavior during specific periods of growth or portions of a season and anisohydric behavior during others [87].
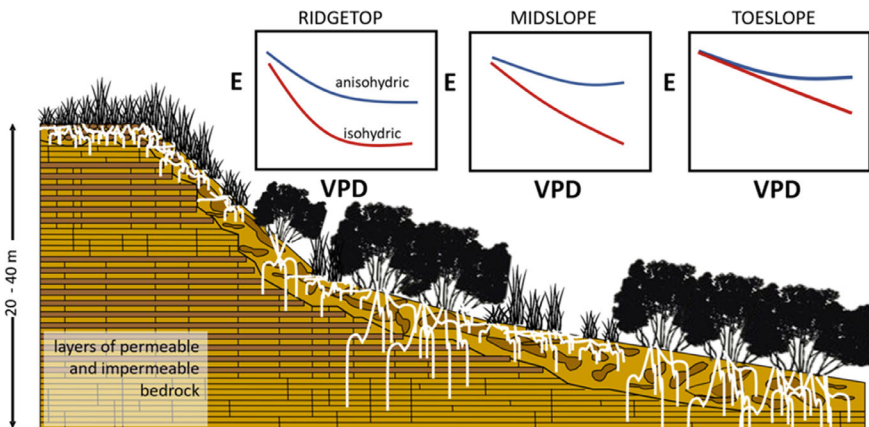

Fig. 2.5 Plant functional types and rooting depths change across complex landscapes with varying soil depths and varying layers of permeable and impermeable bedrock. For example, in regions where grasses can proliferate, fibrous-rooted grasses dominate in shallow soils associated with ridgetops, with surficial bedrock penetration. These soils often exhibit periods of high and low soil moisture, with low soil moisture often accompanying seasonally high vapor pressure deficit (VPD). Isohydric species show high transpiration (E) when surface moisture is high (and VPD is low) but illustrate greater stomatal regulation in dry soils during periods when atmospheric demand (i.e., VPD) is high; this response to VPD is similar but muted for anisohydric species. At midslope locations, deeper soil layers facilitate species with fibrous and tap-roots that utilize soil moisture across relatively large depth intervals. Penetration of bedrock by tap-rooted species is possible. Anisohydric species at midslope positions exhibit markedly reduced declines in E across a range of VPD, supported by decreased stomatal regulation and the larger soil moisture storage capacity of the soil and rock layers. Soil depth tends to be greatest at toeslope locations, resulting in relatively few differences between isohydric and anisohydric species in E across a range of VPD. In all locations, isohydric species employ drought tolerance strategies (anatomical, physiological) to maximize E across a range of VPD

Root traits have long been examined to try to understand plant, and thus ecosystem, functions. The root trait most frequently reported as a predictor of ecosystem function has been maximum rooting depth, which has been reported for a diversity of species and varies with biogeography [142, 143, 153, 163]. However, if we want to improve our ability to predict how species coexist within ecosystems or how global environmental changes may impact communities in space and time, other characteristics of root systems beyond maximum rooting depth require consideration [88, 114]. For example, not all roots are created equal. Angiosperm species can be tap-rooted or fibrous, with branching tap-roots more common in eudicots, and dense fibrous root systems more common in monocots [17]. Fibrous and tap-rooted species have inherently different morphologies, with different root densities within a given layer of the soil, varying depth distributions of roots, and varying root diameters within depth distributions of the soil [76, 107]. Species with tap roots tend to have roots of larger diameter, with a deeper maximum rooting depth but reduced fine root density at any particular depth compared to fibrous root systems [76]. Species with fibrous root systems tend to be more efficient at absorbing water, can typically resist lower water potentials [37], and have higher root turnover (lower longevity). Even within species (and genotypes), these root morphological traits have high variability [34, 89], highlighting the need for greater investigation of what drives this variability in root morphological traits.

In addition to differences in root system morphology, the functional attributes (i.e., physiology, including water absorption) of roots vary among species, locations, and temporal periods of the growing season. Using stable isotopes as natural tracers of resource uptake, plant scientists have discovered that root presence at a particular soil depth does not equate to water uptake (root function) from roots that exist within a particular depth [31, 38, 115]. This result implies that just because a plant species has roots within a particular zone of the soil it does not mean that water is being absorbed from that soil zone. Interestingly, this outcome has been documented for many plant species that have roots in portions of the soil profile with plant-available water. For many herbaceous species, deep roots typically contribute very little to the overall plant water budget despite roots being present at depth. It remains unclear why plants possessing roots in zones of the soil with available water may not use that reservoir. As previously described, water moves primarily by mass flow to roots and root hairs down a pressure potential gradient. Following absorption, water can move towards the vascular cylinder via apoplastic (between cells) and symplastic (from cell to cell across membranes) movement pathways. However, once water reaches the endodermis, only symplastic transport is possible across the Casparian Strip (CS) [62]. Plant biochemists still have a limited understanding of how water movement is regulated across the CS, but transport across this barrier can be turned on and off [6, 62]. Thus, vascular plants have the ability to regulate water transport through cellular mechanisms associated with transport across the endodermis. Finally, the microanatomical features of roots vary within an individual based on root order, depth in the soil, and phenological stage [116]. For herbaceous species, this typically means reduced hydraulic conductivity (and reduced rates of water transport) from deeper soil depths [116, 119]. To better understand how, when, and where root functionality

occurs requires a greater understanding of the variability in root micro-anatomical features.

Microanatomy is a historically overlooked aspect of plant roots that links physiology and whole-root system morphology—and thus to CZ-ecosystem functioning. The microanatomical characteristics provide insights into the larger functional contexts of root systems. Root traits like the ratio of cortex to stele, vessel size, vessel number, xylem wall thickness, and hydraulic conductance, all provide clues towards understanding the investment in safety versus efficiency of water transport through root systems [51]. In the seminal work by [172], the authors used root microanatomical traits (e.g., cross sectional area, number of xylem, xylem wall thickness) with aboveground processes like relative growth rate. This work illustrated tradeoffs in safety versus efficiency of water transport in root microanatomy that predicted whole plant growth traits for perennial grasses [172]. Based on these observations, subsequent studies have highlighted how the internal root structure sets a foundation for the whole root system function [116, 173, 119]. Relationships between root microanatomy and aboveground physiology / growth vary by within communities [119], plant functional type [173] and phylogeny [167] and are an active topic of investigation. Because microanatomical images of roots require more preparation time than whole root systems, they have been utilized much less than other traits. For this reason, there is much remaining to discover with regard to linking the internal anatomy of roots to the broader water and nutrient uptake patterns of plant species and communities [56].

As described so far, plant roots vary in both morphology (whole-plant and microanatomical) and physiology among plant types, species, and ecosystems, and the biological focus of this knowledge base is clear. Unsurprisingly, these root differences translate to variability in resource uptake, subsurface porosity, and weathering within the soil profile in space and time. For these reasons, inferring root functional processes (e.g., water uptake) is rarely as intuitive as measuring maximum rooting depth, or root biomass and yet has great importance for projecting whole CZ-ecosystem functioning. Improving linkages between root physiology and CZ-ecosystem properties requires better measurements of root longevity, associating roots to species (in mixed-species environments), quantifying growth rates and biomass by depth through time, and linking these features to the dynamic physical and chemical properties of the soil. Resolving these biologically-focused frontiers in the context of the abiotic constraints on CZ hydrology will undoubtedly assist with linking root presence and activities with ecosystem modification, and further our understanding of how root structure and function regulate pools of water and nutrients and fluxes of water, C, and nutrients in the CZ [22, 39]. Specifically, such efforts are necessary for understanding how ecological processes feedback to CZ hydrologic functioning.

4   Roots and Microbes as Indirect Biotic Drivers of CZ Hydrologic Functioning

In addition to the direct effect of roots on water uptake throughout soil profiles and across landscapes, roots are active sculptors of the subsurface (Fig. 2.6). As such, they represent key agents linking the biotic to the abiotic realms within a CZ. Roots have significant impacts on the depth to which water can infiltrate and the position of the water table. Specifically, roots promote flow. Macropores, acknowledged above as a soil constraint on hydrologic functioning, are often formed via root growth [3, 99, 185] and reinforced via deposition and accumulation of clay films [147]. After root shrinkage, saturated films on root surfaces or along pore walls provide evidence of flow in these pores [16]. Where roots persist at depth, development of preferential flow paths is thought to trigger a positive feedback by enhancing the water drainage to depth [44, 125, 169]. Not only do roots generate pores, but their growth can both build and destroy soil aggregates through enmeshing small particles or cleaving apart big aggregates [123], a process that alters the size and distribution of macropores. Because roots control soil-hydraulic properties and the generation of preferential flow, small changes in rooting depth distributions can alter water flow significantly [11, 117]. Indeed, given that roots transform far more soil volume than rhizosphere dimensions might initially suggest [134], extant aggregate size distributions and pore networks likely represent the legacy of past generations of roots.

Root growth also imparts an important impact on the translocation of clay minerals and clay-sized particles, a process that influences both soil water flows and storage. Though clay-rich horizons can develop as clay forms within the horizon, in many locations clay accumulates in a horizon with illuviation from upper horizons [29,
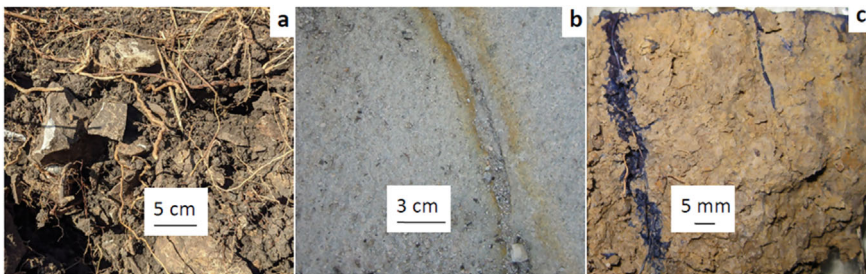

Fig. 2.6 Visual evidence of the role of roots as soil structural architects and their interaction with rocks and minerals is offered by **a** roots in surface horizons of Mollisols in Kansas, U.S., in intimate contact with limestone cobbles which experience dissolution upon exposure to the increased acidity imposed by root and microbial activities; **b** pine roots penetrating granite underlying well-developed Ultisolsin the southeastern U.S., resulting in enhanced porosity and thus oxygen flow, oxidation of organic reductants in the rhizosphere, and subsequent reduction of Fe^{3+} which diffuses away from the rhizosphere and undergoes reoxidization; and **c** methylene blue dye revealing a large, tubular pore likely formed via root growth and now serving as a preferential flow path in a Mollisol from the University of Kansas Field Station, Kansas, U.S. Photo credits: **a** J. Nippert; **b** D. Richter; **c** D. Hirmas

176]. The downward movement of clay-sized particles and clay minerals is linked to climate, occurring where effective precipitation is sufficient to promote downward movement of particles through the profile [57, 58, 91] and likely facilitated by seasonal wetting and drying. However, the downward transport of clay across horizons also is governed by the generation of flow paths through which clay illuviation can proceed [128]. The resulting clay-rich horizons influence profile water dynamics via lower saturated hydraulic conductivity and thus enhanced water storage, and depth-dependent hydraulic conductivity due to the textural discontinuities with neighboring soil horizons [133], Fig. 2.7). Clay-rich horizons also can result in a layer of soil difficult for roots to penetrate [61]. In this indirect way, then, roots govern their own hydrologic environment.

Microbes, too, sculpt the soil. Soil microbes exude compounds that can serve as binding agents [162]. The complex mix of exudation compounds (e.g., polysaccharides, organic acids, enzymes, diverse waste products, often referred to collectively as EPS (see above)) is composed of materials critical for soil aggregate formation and preservation [79]. Microbial necromass is emerging as an important feature for
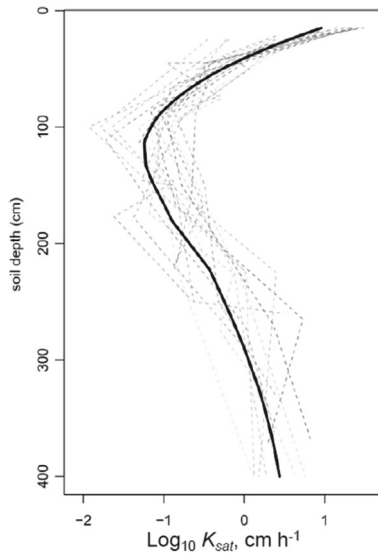

Fig. 2.7 Depth dependence of log10-transformed saturated hydraulic conductivity (K_{sat}) in cm h^{-1}. Data derived from measurements made at 21 locations within the Calhoun Critical Zone Observatory from 2017 to 2019. Each dashed line corresponds to one of the 21 profiles. For each profile, repeated K_{sat} measurements at the same soil depths were averaged within the 21 locations and a rolling mean of K_{sat} was calculated for each profile (window width = 3) across depths. The solid bold line is a LOESS fit (Local Polynomial Regression Fitting) of all 21 soil profiles for which K_{sat} was measured. All sites exhibit a Bt horizon, typically between ~40 cm and ~150 cm depth, that results from climate and biota promoting vertical clay movement via infiltrating soil moisture (i.e., lessivage). The accumulation and concentration of fine clay particles in these Bt horizons results in diminished K_{sat} relative to the coarser textured soils above and below

aggregate formation and preservation. The remnants of dead soil microbes appear to persist in soil far longer than some plant-derived compounds [94], potentially serving as glue and adhering mineral and organic particles together into aggregates [28]; the observation that microaggregates tend to harbor relatively old organic C [138] suggests that smaller aggregates may retain microbial necromass to a greater extent than in larger aggregates. Thus, necromass and the exudates of living microbes govern soil void geometries by influencing soil aggregate formation and durability. Like all soil microbial activities, these processes are especially prevalent in and around the rhizosphere, but any such microbial actions whether in bulk or rhizosphere soil can be important for structural change.

Additional microbial actions further can drive soil structure. Soil microbes induce soil organic matter (SOM) decay via exo-enzymes, and transform some of the C into CO_2 and released nutrients and C into biomass. As SOM is transformed from a solid into a solute, and then into either a gaseous or microbial form, soil aggregates can collapse [27]. The fate of the non-decayed SOM that had resided within collapsed aggregates is unclear, though it is presumed that the removal of aggregate structural protection [148] means that any remaining SOM experiences a greater probability of undergoing decay. Whether aggregate collapse associated with SOM decay promotes a loss or a gain in soil porosity is a matter of some debate. Over broad spatial scales, higher concentrations of SOM generally correlate with greater porosity [54]. However, the transformation of a solid material into a gaseous or solute form results in the presence of small pores in the space where that solid material previously existed. The net effect of SOM mineralization within an aggregate on soil aggregate stability and size distribution is unclear, though some studies suggest that pore opening dominates (X. Zhang, P. Sullivan, S. Billings, et al., unpublished data). Discerning the conditions under which SOM decay induces porosity gains or losses is a current research focus.

Another mechanism by which both soil microbes and roots can influence soil structure is via the exudation of organic acids and CO_2. Organic acids release nutrients from minerals [4, 84, 100], often via ligand exchange [60, 66, 84]. Carbon dioxide, once dissolved into the carbonic acid system, can also induce acid-promoted rock and mineral transformations (e.g., [85]). Acid transformations of rock are a key feature of long-term soil development [24, 43, 154]. Indeed, over long timescales, such momentary-scale processes can enhance soil porosity in the regolith and bedrock itself, and ultimately promote soil production from rock. Thus, microbial and root acid losses can be important determinants of soil structure over diverse timescales.

Because roots and microbes influence soil structure, and because soil microbes tend to proliferate near roots, any change in rooting depth distributions has the potential to alter soil aggregate and void arrangement, and thus CZ functioning (Fig. 2.2). Recent work highlighting the role of humans during the Anthropocene in regionally-dependent deepening or shallowing of roots indicates the massive scale at which these phenomena are occurring [68]. Ecosystem process models, reactive transport models, and continental-scale models of biosphere–atmosphere exchanges of energy and water offer the opportunity to test hypotheses probing the effects of modified abundances of deep root influences on soil structure [156]. Modeling efforts like

these will further strengthen the intellectual ties among ecosystem ecologists and the diversity of investigators working on CZ problems.

5   Conclusion

Understanding the CZ as an ecological problem and designing research that invokes the CZ paradigm offers us a way forward as we attempt to project future environmental processes in the Anthropocene. In this chapter, we provide examples of biotic-abiotic processes across a diversity of scales that govern CZ functioning and that are impossible to understand and predict without the use of the CZ paradigm. We specifically focus on hydrologic functioning given water's importance in both the biotic and abiotic realms.

By describing the influence of soil texture and macroporosity on hydrologic flow patterns, we highlight how fundamental CZ constraints ([52]; here, the particle surface area present in a soil profile and the capacity of that soil to move water with relatively little tension) can govern the storage and fluxes of a critical resource—water. In turn, water fluxes through a soil profile influence the extent and pace of soil horizonization, which can result in varied capacity of soil at a given depth to store and release water (Fig. 2.7). Roots also contribute to soil development in numerous ways (Fig. 2.6), among them their capacity for perforating soil and thus generating pores through which fluids can flow. Of course, roots also drive water loss from soils. Combined, these actions—root growth and water uptake—promote movement of soil particles at small (~nm to cm) scales, further modifying the soil pore networks through which liquids and gases flow. Widespread changes in rooting depth in the Anthropocene (Fig. 2.4) likely have modified pore networks in meaningful but unquantified ways. Microbes further contribute to these dynamics, in multiple ways. One salient role of soil microbes is their mineralization of soil organic C into CO_2. This mineralization removes a structural agent from the soil, and likely can induce the collapse of soil structural features that may protect soil organic matter from microbial attack (Fig. 2.2). Microbes and roots also generate acids that impose structural change to the regolith and bedrock via rock and mineral transformations. These root and microbial actions, and associated flows of water and soil particles, only sometimes scale up in a predictable way. However, at a landscape scale, we can expect spatial variability in soil capacity to retain water (Fig. 2.3) and plant adaptations to varied water availability (Fig. 2.5) that reflect water's tendency to flow towards more negative water potentials. Scaling the flows of fluids and solids, and patterns of root water uptake and soil microbial mineralization, across watersheds and landscapes remains a challenge important to address given spatially-varied responses of water availability to a changing climate. This challenge cannot be met without appreciating both the biotic and abiotic characteristics of the soil profile or landscape in question.

A multitude of biotic-abiotic interactions not addressed in this work but that govern CZ functioning also require a transdisciplinary, CZ approach to develop a predictive understanding of the processes at large. Consider, for example, how within-canopy

air currents govern system energy and water dynamics throughout the CZ [19, 111]. Linkages among soil structural attributes and hydrologic flows and resulting soil C and nutrient pools and fluxes are well-established [176, 133]. Other examples of biotic-abiotic interactions include the generation of channels by soil fauna through which gases and solutes flow [126], and how SOM flows across landscapes with erosion [8, 43] result in a redistribution of this key agent of soil structure and a source of CO_2 and organically-bound nutrients [14]. All of these processes participate in the complex interplay of the biota with the abiotic that structure the physical and chemical conditions in which life persists.

We emphasize that the biotic responses to land use, temperature, precipitation patterns, and atmospheric CO_2 concentrations—often explored in ecosystem ecology—can be rapid. Because biota influence soil structure, rapid responses of biota to environmental conditions may prompt rapid changes in the structure and function of the CZ, and thus impart meaningful alterations to CZ-climate feedbacks [156]. It is no longer possible to examine these environmental puzzles effectively from the perspective of a single or even a pair of disciplines. The knowledge bases required to understand these processes emerge from a diversity of disciplines, including geomorphology, soil science, ecohydrology, plant physiology, and ecosystem ecology. It is no coincidence that biotic-abiotic interactions all revolve around soil; soil is where the lithosphere, biosphere, atmosphere, and hydrosphere interact to form Earth's living skin, and is perhaps the most intuitive location within the CZ where biotic and abiotic processes come to govern the functioning of the CZ ecosystem (Fig. 2.1). Integrating knowledge from these realms has offered CZ scientists the opportunity to gain new insights about the functioning at Earth's surface, which in turn allows the community to project Earth's future functioning via both empirical and modeling studies. Taking our cues from the likes of Humboldt, Foote, Tansley, and Berner, we can continue to contribute to the rich history of the science of the CZ ecosystem, and move forward with greater confidence in our ability to project future CZ functioning.

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