Boundaries in Miniature: Two Examples from Soil

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Transitions between atmosphere and soil, and between soil and roots, are two examples of small-scale boundaries across which the nutrient, water, and gas dynamics of ecosystems are modulated. Most atmospheric inputs to ecosystems have to pass through the soil; thus, the atmosphere–soil boundary influences the type and amount of materials and energy entering the soil. Belowground plant inputs occur through the rhizosphere, the zone of soil immediately adjacent to the root. This soil boundary layer affects root inputs to soil and root extraction of water and nutrients from soil. We discuss how water, carbon, nitrogen, and oxygen dynamics are affected by atmosphere–soil and soil–root boundaries and how light, soil pH, and dust are affected by the atmosphere–soil boundary. (We also examine pH with regard to the root–soil boundary, but not in a separate section.) We examine the linkages between these small-scale boundaries and landscape ecology and discuss how the understanding of small-scale boundaries can contribute to the emerging field of boundary theory.

Keywords: biological soil crusts, rhizosphere, nutrient cycles, nitrogen, carbon

Boundaries occur where steep gradients in physical environments directly affect ecosystem processes and the distribution of organisms (Gosz 1992). They have also been defined as locations where rates of ecological transfer change abruptly in comparison with the relatively homogenous units on either side of the boundary (Wiens et al. 1985). Naiman and colleagues (1988) suggested that boundaries often have emergent properties of their own rather than simply reflecting an average of the conditions on either side of the contact zone. Such emergent properties are a function both of the magnitude of the contrast between the resource patches on either side of the boundary and of the increased heterogeneity of patterns contained within the boundary (Gosz 1992). Boundaries can occur at any scale, depending on the question or phenomenon of interest. A boundary defined at one scale may not be apparent at a larger or smaller scale: A boundary for an ant, for example, may not be apparent to a deer (Wiens et al. 1985).

While the importance of hierarchical arrangements of landscape units and their associated boundaries is recognized (Cadenasso et al. 2003), the extension of ecological boundary concepts to small scales has generally entailed transects measured in units no smaller than meters (Fagan et al. 2003). Thus, studies of boundaries have mostly addressed biome or landscape scales. There are, however, many finer-scale boundaries that influence ecosystem fluxes and processes. Two such fine-scale boundaries (with dimensions in millimeters) that are important in ecosystem function are the interface between the atmosphere and soil surface and the transition between bulk soil and plant roots. The adjacent areas of atmosphere and soil and of soil and root have dramatically different physical environments, rates of ecological transfer, and distribution of organisms. Both of these interface zones have strong internal spatial and temporal heterogeneity, defined by the composition and density of biota that live within the zones and by the characteristics of the adjacent units (atmosphere–soil and soil–root). Like the riparian zones and estuaries discussed by Cadenasso and colleagues (2003), the atmosphere–soil and soil–root zones can be considered either as patches or as boundaries through which a variety of interactions occur. Both zones are three-dimensional volumes of soil, with time as an important fourth dimension. Considering these zones as boundaries facilitates the assessment of their function in the landscape.

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The zones between atmosphere and soil and between soil and root modulate flows of materials and energy between the neighboring air, soil, and root (figure 1). We discuss various examples in which the physical, chemical, and biotic characteristics of these two small-scale boundaries influence ecosystem characteristics and functions at the landscape scale. Enhanced rates of nitrogen (N) mineralization in the rhizosphere boundary layer increase availability of N to plants in N-limited temperate ecosystems, potentially increasing these ecosystems' net primary productivity. Nitrogen fixation by biological soil crusts can be a major N input to N-limited semiarid terrestrial ecosystems. The occurrence of anaerobic microsites associated with high carbon (C) availability in rhizosphere soil can account for a substantial portion of the N lost to terrestrial systems through denitrification. These anaerobic microsites can also account for the production of the atmospherically reactive trace gas nitrous oxide (N_2O). The temporal patterns of nutrient cycling and terrestrial carbon dioxide (CO_2) flux are controlled in part by water availability to microbes concentrated in rhizosphere soil; this makes these patterns highly sensitive to plant evapotranspiration and hydraulic redistribution. Soil surface stabilization resulting from crusts protects surface soils against loss of fine particles and nutrients.

Many characteristics of atmosphere–soil and soil–root boundaries have not been quantified or have been measured only in a limited number of habitat types (table 1). As with macroboundaries, the influence of these microboundaries on the materials and energy crossing them varies widely (Strayer et al. 2003); they can be absorptive (heat, moisture, N), transmissive (oxygen, water), reflective (water, light), transforming (nitrogen gas [N_2] to ammonium [NH_4], sugars to microbial biomass), or amplifying (light). As with macroboundaries, these microboundaries are variable in shape and composition (see figure 1 in Strayer et al. 2003). Although the scale of these boundaries is relatively small, their integrated impacts can be important at landscape and even global scales. In this article, we summarize the structure and function of atmosphere–soil and soil–root boundaries, how materials and energy crossing these boundaries are altered, and how their study can inform landscape ecology.

The atmosphere–soil boundary

Many ecosystem processes depend on atmospheric inputs of N_2, CO_2, nutrients, and water. With the exception of CO_2 and bedrock weathering, most inputs to terrestrial ecosystems occur by passing through the soil surface. Therefore, characteristics of the soil surface mediate the form and quantity of
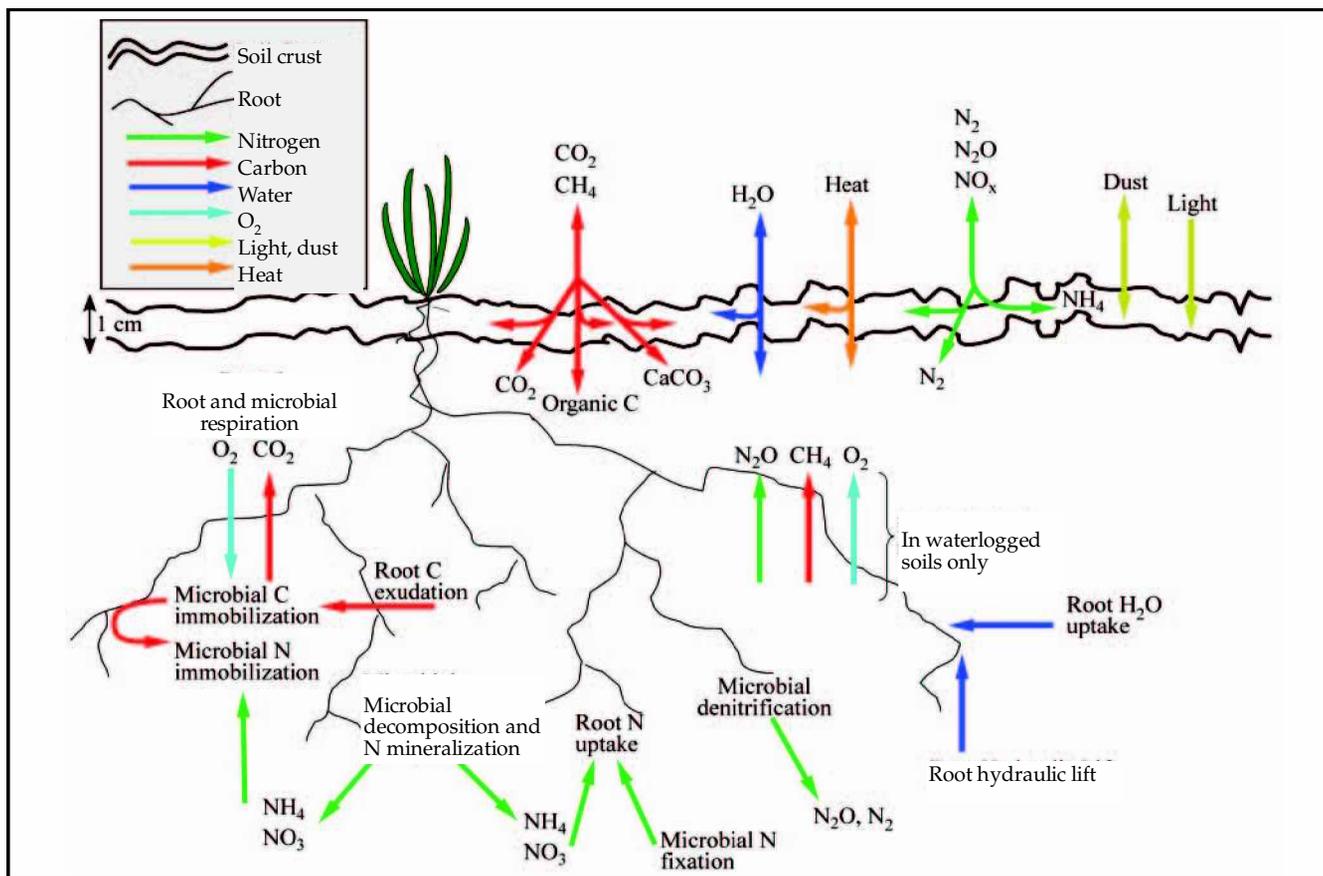
Figure 1. Diagram of the various types of materials and energy crossing the atmosphere–soil and soil–root boundaries. Each type of material or energy is depicted in a single color. C, carbon; $CaCO_3$, calcium carbonate; CH_4, methane; CO_2, carbon dioxide; H_2O, water; N, nitrogen; N_2, nitrogen gas; N_2O, nitrous oxide; NH_4, ammonium ion; NO_3, nitrate ion; NO_x, nitrogen oxide; and O_2, oxygen.

Table 1. Comparison of boundary and bulk pools and processes. Shown are the range of boundary to bulk soil ratios, where the boundary is the surface of soil or root, and the range of reported ratios for soil surfaces that have well-developed biological soil crusts (BSCs) compared with those that have poorly developed BSCs or none at all.

Flux	Lichen crust: Bare soil	Surface: Bulk	Rhizosphere: Bulk
Microorganism abundance	5.00–30.00[a]	—	2.40–1260.00[b]
Carbon processes			
Diffusion	—	—	—
Fixation	0.00–2.53	—	—
Exudation	—	—	—
Respiration	0.00–2.36	—	1.07–2.50[c]
Decomposition	—	—	—
Carbon pools			
Total carbon	—	1.84–2.48[d]	1.05–7.04[e] (TOC)
Nitrogen processes			
Fixation	0.00–6.68	—	1455–2555[f] (rice)
Mineralization	3.40–8.00[g]	1.23–7.40[h, i]	6.80–12.80
Nitrification	—	4.00–80.00[d]	0.00–1.00
Denitrification	0.42–1.36[j]	—	1.04–1.33[c]
Volatilization	0.42–0.67[j]	—	—
Nitrogen pools			
Nitrate	0.19–1.21[j]	0.81–1.63[d]	0.25–1.00[k]
Ammonium	0.46–1.14[j]	1.30–5.26[d]	1.56–12.73[e, h]
Organic nitrogen	1.85–22.29[j]	—	—
Water	0.98–1.11	1.08–1.60[h]	0.14–0.62[b]
Oxygen			
Consumption	—	—	3.30–16.50[k]
Concentration	1.21[l]	—	0.09–16.50[k]

Note: A ratio of 1 indicates no difference; greater than 1 indicates greater processing or larger pools at the boundary, and less than 1 indicates more processing or larger pools in bulk soil or poorly crusted surfaces. Blanks indicate processes or pools for which data were unavailable.

  a. Hawkes and Flechtner 2002.
  b. Kennedy 1998.
  c. Priha et al. 1999.
  d. Stark and Firestone 1996.
  e. Semenov et al. 1999.
  f. Rinaudo et al. 1971.
  g. R. Dave Evans, Washington State University, Pullman, WA, personal communication, 2001.
  h. Jackson et al. 1988.
  i. Norton and Firestone 1996.
  j. Nichole Barger, Colorado State University, Fort Collins, CO, personal communication, 2003.
 k. Sorensen 1997.
  l. Garcia-Pichel and Belnap 1996.

most inputs. There are many atmosphere–water–soil boundaries within the soil itself; however, we will address only the contact between the soil surface and the larger atmosphere.

In mesic systems, the soil surface is mostly covered by plants and plant litter, complicating the examination of this contact. In contrast, limited vascular plant cover in semiarid and arid regions means that most of the soil surface is in direct contact with the air. These regions make up almost 35% of US and global terrestrial ecosystems. Consequently, our examination of the atmosphere–soil boundary will focus on these large dry regions, where there is extensive contact between the atmosphere and the soil surface.

Structure and characteristics of the atmosphere–soil boundary. Most desert soils are covered by a layer of photosynthetic organisms collectively referred to as biological soil crusts (BSCs). BSCs include cyanobacteria, lichens, mosses, and green algae (figure 2) that are concentrated within a few millimeters at and below the soil surface. Heterotrophic communities of microfungi and bacteria are associated with and supported by the photosynthetic layer. In arid and semiarid regions, these organisms often constitute more than 70% of the living cover. Because of the large areal extent of BSCs, most inputs to and losses from desert soils must pass through the boundary created by them.
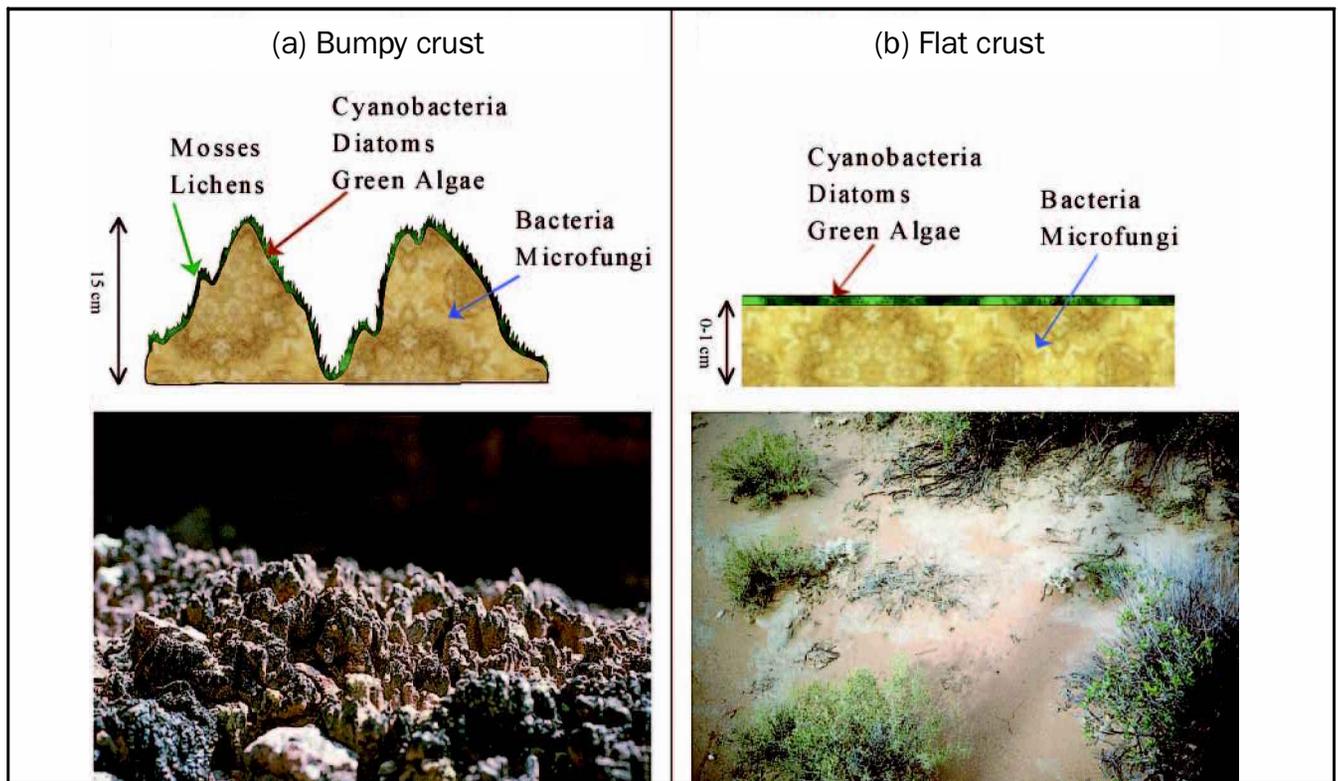
Figure 2. Different soil crust types. (a) Roughened crusts are found in relatively undisturbed areas. They have lichens, mosses, and high cyanobacterial biomass. Relative to flat crusts, they have greater nitrogen and carbon fixation, water interception, soil temperatures, and resistance to erosion. (b) Flat biological soil crusts are found after disturbance. They are lighter in color, as they lack mosses and lichens, and they have low cyanobacterial biomass.

Biological soil crusts play many ecosystem roles. They affect local hydrology; they contribute N and C to soils; they secrete plant growth–promoting factors (e.g., glycollate, vitamins, and auxin-like substances); and they secrete chelators critical to keeping essential plant nutrients available in high-pH desert soils. In addition, they excrete exopolymers that enhance microbial activity, create soil pore space, increase erosion resistance, and limit nutrient leaching losses.

The ways in which BSCs affect the flux of material or energy into and out of the soil are heavily influenced by their biomass, flora, and external morphology. These factors differ markedly with climatic factors. In hyperarid deserts where soils do not freeze (e.g., the Sahara), BSCs consist almost exclusively of cyanobacteria that smooth the soil surface relative to bare soil (figure 2). As moisture availability increases with latitude, the cover, diversity, and biomass of lichens and mosses also increase. Hot deserts (e.g., the Mojave and Sonoran Deserts) support small clumps of lichens and mosses (generally less than 10% cover) that slightly roughen the surface. In cool, mid-latitude deserts where soils freeze annually (e.g., the Colorado Plateau), the lichen–moss cover approaches 40%, and mounds form that are up to 15 centimeters high. In higher-latitude deserts (e.g., the Great Basin, the Arctic), lichen–moss cover can approach 100% of the soil surface. Soil disturbance reduces the biomass, surface roughness, and lichen– moss cover of BSCs; thus, time since disturbance also

influences BSC composition and morphology (Belnap and Eldridge 2003). In the following section, we discuss how energy and materials are influenced as they move from the atmosphere into soils, crossing the boundary whose characteristics are determined by BSCs.

Functions of the atmosphere–soil boundary. Characteristics of the atmosphere–soil boundary determine whether this boundary will transmit, reflect, or absorb materials or energy.

Water. Infiltration of water into the soil depends on water residence time and soil surface permeability. These characteristics, in turn, are influenced by factors such as soil surface roughness, wettability or repellancy, aggregate structure, and pore space. The types of BSC present affect all these boundary characteristics. In hot deserts where BSCs smooth the surface, water residence time and soil permeability are decreased. Thus, infiltration is decreased compared with bare soil. In cool deserts where BSCs increase soil aggregation, roughen soil surfaces, and themselves absorb moisture, the residence time of water and soil permeability is increased. Consequently, infiltration is increased compared with bare soil.

The same factors that influence infiltration can also influence soil water retention (George et al. 2003). The occupation of soil pores by BSC organisms reduces evaporative loss from the soil surface. Therefore, greater BSC biomass results in less water vapor loss than less-developed BSCs or bare soil. Species

composition also affects this process. Mosses and lichens cap the soil surface more effectively than cyanobacteria, whose thin filaments leave large open spaces through which water can evaporate.

Carbon. Carbon as CO_2 is transformed and its movement modulated as it crosses the BSC boundary (table 1). As BSCs fill soil pore space, passive diffusion of CO_2 in and out of the soil is reduced by the presence of BSC organisms relative to bare soil. As BSC biomass and lichen–moss cover increase with latitude, passive diffusion rates are expected to further decrease.

Atmospheric and soil-respired CO_2 can be used for photosynthesis or precipitated as carbonate when BSCs are present. The biomass and type of BSC organisms determine CO_2 transformation rates. Lichen–moss crusts have photosynthetic rates that can equal those of vascular plants (up to 11.5 micromoles CO_2 per square meter per second), with overall C balances estimated at 120 to 370 kilograms (kg) C per hectare (ha) per year in arid regions (Evans and Lange 2003). Photosynthetic rates of cyanobacterial crusts are lower, with C balances estimated at 4 to 23 kg C per ha per year. Given the low vascular plant productivity of arid lands, CO_2 transformation by BSCs contributes significantly to C budgets in these regions. Because BSCs are metabolically active only when wet, C transformations are dependent on the timing, amount, and intensity of precipitation. Most C gains occur during cool months, when soils are moist longer and temperatures are optimal for photosynthesis. Carbon deficits often occur during small summer precipitation events.

The cyanobacterial component of BSCs also transforms CO_2 into carbonates by utilizing bicarbonate (HCO_3^-) as a source of CO_2 for photosynthesis (Merz 1992). During the conversion of HCO_3^- to CO_2, hydroxyl ions are released and form carbonate ions within the sheath. These ions react with calcium adsorbed to the sheath to form calcium carbonate. Uptake of HCO_3^- is increased when CO_2 concentrations are low, light intensities are high, or pH levels are high, or when any of these three conditions are combined. Greater cyanobacterial biomass increases formation of carbonates at the soil surface both directly through photosynthesis and indirectly by decreasing soil CO_2 and increasing soil pH (discussed below).

Respiration of crust organisms and heterotrophic soil microbes releases CO_2 to the soils and the atmosphere. Crust components also secrete up to 50% of their fixed C within minutes to days of acquisition. When this secreted C is combined with the C contained in BSC tissue, BSCs can increase soil surface C by up to 300% (reviewed in Belnap et al. 2003). These additions stimulate the activity and CO_2 respiration of the often C-limited heterotrophic microbes in desert soil, increasing the CO_2 flux across the atmosphere–soil boundary. The rate and size of this flux is mediated by the type and biomass of the BSC organisms through which the respired CO_2 must flow. In addition, soil respiration rates are also regulated by soil temperature, moisture, C, N, phosphorus (P), porosity, and aeration (Keith et al. 1997), all of which are substantially influenced by BSC composition and biomass.

Nitrogen. As with CO_2, the atmosphere–soil boundary can be transmissive, reflective, or transformative for N gases. Nitrogen enters the soil through passive diffusion, fixation, or atmospheric deposition. Passive diffusion of N_2 into soil is highest in bare soils and declines as BSC biomass increases with latitude. As N_2 crosses the atmosphere–soil boundary, it is often transformed into NH_4 by N-fixing free-living (e.g., *Scytonema, Nostoc)* or lichenized (e.g., *Collema, Peltula)* cyanobacteria (Belnap 2003), a process lacking in bare soils. Rates of N transformation across the atmosphere–soil boundary are heavily dependent on the BSC species composition, as lichen BSCs fix much more N than cyanobacterial BSCs. No transformation takes place across the bare soil surface (table 1). Nitrogen fixation rates are also dependent on soil temperature and moisture, both of which are strongly influenced by the biomass and species composition of BSCs. Up to 88% of the newly fixed N is released to surrounding soils within minutes to hours and is available to associated organisms such as vascular plants and other microbes (Belnap 2003). Indeed, the fixed N from crust organisms can be a dominant source of N for desert ecosystems (Evans and Ehleringer 1993). Uptake of released N stimulates microbial activity, increasing respired soil CO_2 and gaseous N loss through denitrification.

Nitrogen entering the soil through atmospheric deposition must also pass across the BSC boundary. In nonurban regions of the United States, wet deposition can account for 1 to 6 kg N per ha per year (NADP 2000). Soil microbes quickly capture and immobilize most of this N, with some turnover to vascular plants within 15 days (Hawkes forthcoming). The rate and amount of N captured is influenced by the biomass and type of BSC organisms present (see the section on dust, below).

Gaseous N losses are determined by many factors that are influenced by BSC type and biomass (e.g., soil N, moisture, temperature, microbial populations; Belnap 2003). Estimates of N loss rates among deserts vary widely. Recent estimates in cool deserts range from 0.01 to 0.37 kg N per ha per year for cyanobacterial and lichen–moss crusts, respectively, with bare soil showing negligible losses (table 1).

Oxygen, pH, light, and dust. As with the other gases, the atmosphere–soil boundary can transmit, reflect, and transform oxygen gas (O_2). Greater moss–lichen cover and biomass decreases soil permeability relative to cyanobacteria or bare soil. BSC organisms transform O_2 during respiration and release it during photosynthesis, and the balance between these two processes is determined by the biomass and species composition of BSC organisms. Oxygen emitted from these organisms is concentrated in the top 0.5 millimeters of soil (figure 3), where most of the BSC organisms and maximum productivity occur (Garcia-Pichel and Belnap 1996). Worldwide, BSC activity typically increases soil surface pH from 8.0 to 10.5 (figure 3; Garcia-Pichel and Belnap 1996). Such changes in pH can profoundly alter transformation and weathering rates (e.g., carbonates, silicates) and the avail-

ability of many elements (e.g., P) at the atmosphere–soil boundary .

Light is also mediated across the atmosphere–soil boundary. Whereas light is slightly amplified at the surface, it is rapidly extinguished with depth in the soil (figure 3). Rates of extinguishment are dependent on the type and number of BSC organisms that reflect or absorb incoming radiation and on the nature of the soil particles (Garcia-Pichel and Belnap 1996). For example, a quartz-containing soil without BSCs will allow deeper penetration for a greater range of wavelengths than a fine-textured soil with BSCs.

Dust is a critical source of nutrients and water-holding capacity for many desert soils. Biological soil crusts secrete sticky exopolymers and roughen soil surfaces, greatly enhancing dust capture and creating a nutrient-rich zone directly at the atmosphere–soil interface (Verrecchia et al. 1995, Reynolds et al. 2001).
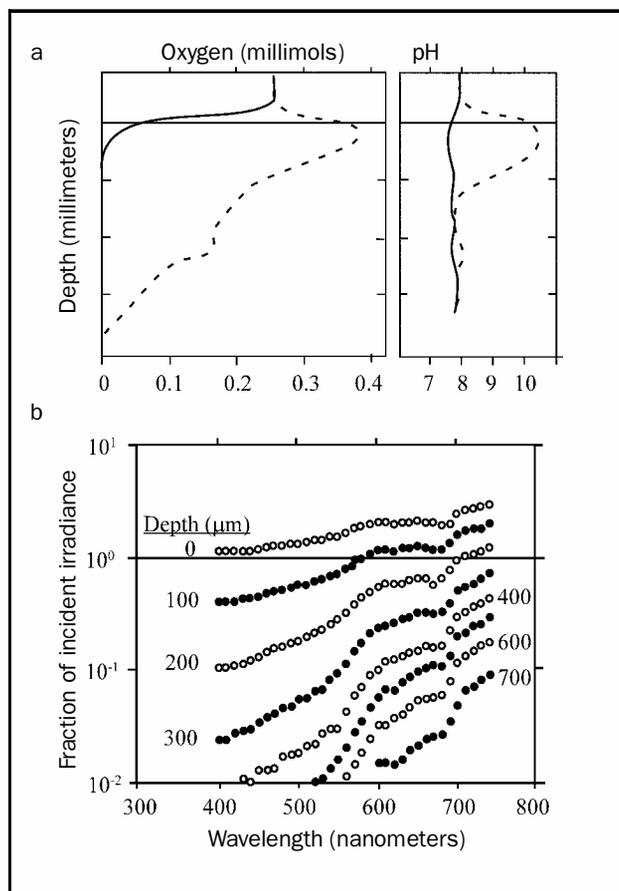
Figure 3. Oxygen concentration, pH, and spectral attenuation of light across the atmosphere–soil boundary in the presence of biological soil crusts. (a) Oxygen and pH. Solid lines represent measurements made in the dark; dashed lines represent measurements made in the light. (b) Spectral attenuation. Each spectrum shows the fraction of incident radiation in the soil at various depths (given in micrometers). Filled and empty circles alternate to aid in reading the figure. (Adapted from Garcia-Pichel and Belnap 1996.)

The soil–root boundary

Many ecological studies assume that soil is a homogenous system (figure 4a), but belowground fluxes are not spatially homogenous. The zone of soil influenced by roots, the rhizosphere, is delineated on one side by the surface of the root. The other side of this zone is less clearly delineated and grades into surrounding bulk soil. The rhizosphere is a fine-scale boundary, with transects from the root to bulk soil generally measured in single-digit millimeter units. Through this zone, roots exchange energy and matter with surrounding soil, the atmosphere, and water (table 1), resulting in substantially greater fluxes in the rhizosphere boundary zone than in neighboring patches of soil.

While roots do not affect every property of soil (e.g., figure 4b), the physical environment of the rhizosphere differs dramatically from that of bulk soils. Many process rates are elevated in rhizosphere soil, and pool sizes can be increased or decreased (table 1). Plant roots exude a complex array of organic compounds into the nearby soil in large quantities (Kennedy 1998). The bulk density of soil is commonly higher in rhizosphere soil because of the roots pushing their way through the solid matrix. Compared with bulk soil, solution pH values can be different in the rhizosphere, and soil water potentials can vary dramatically near the root surface (Kennedy 1998). Active transpiration by plants reduces soil water content and moves water from bulk soil through the rhizosphere, carrying nutrient and nonnutrient salts. This flux of soluble salts into the rhizosphere can result in salt concentrations that are 15 times greater in the rhizosphere than in bulk soil. Rhizosphere soil is an environment of substantially elevated CO_2 concentration because of active root and microbial respiration (table 1; figure 4c). Conversely, nutrient ion uptake by roots drives diffusional movement and creates zones of nutrient depletion (e.g., NH_4, nitrate [NO_3^-], and phosphate in rhizosphere soil; figure 4d.

The soluble carbohydrates produced by roots are a source of energy for free-living bacteria and fungi in the rhizosphere. As a result, bacterial, fungal, and protozoal numbers are orders of magnitude higher in rhizosphere soil than in bulk soil (table 1; Kennedy 1998). Bacteria are commonly the most numerous organisms found in the rhizosphere, with as many as a billion cells per gram of soil (Kennedy 1998). Rhizosphere communities are known to have different metabolic profiles, greater microbial activity, and distinct microbial species compared with bulk soil communities (e.g., Sorensen 1997). The activity of the microbial community in the rhizosphere is of particular interest, as it drives many of the fluxes in that zone.

Fluxes in the rhizosphere. Flows of materials and energy can be modulated or unaffected by passage through the rhizosphere boundary. Movement of water, carbon, nitrogen, and oxygen provide useful examples.

Water. The rhizosphere boundary is primarily transmissive with respect to water, but net movement has the potential to be either toward or away from the root (figure 1). An actively

transpiring plant removes huge quantities of water from the soil solution. Depending in part on the rate of water supply from the surrounding soil to the rhizosphere, the water potential in rhizosphere soil can be much lower than in the surrounding soil (Papendick and Campbell 1975). In the daytime, rhizosphere soil is commonly drier than bulk soil. In some terrestrial ecosystems, the situation can be reversed at night through hydraulic redistribution (Caldwell and Richards 1989). This process is most common in arid and semiarid ecosystems, where deeply taprooted plants move groundwater to surface soils through their root systems. In these systems the flux of water from roots out into the rhizosphere can increase nighttime water availability in soil.

Carbon. The rhizosphere soil is primarily a transforming boundary in which organic C originating from the root is transformed into microbial bodies and CO_2. As mentioned above, roots contribute substantial amounts of C to adjacent soil. The quantity and quality of this rhizodeposition varies with plant species, age, root morphology, soil organisms, and water availability (Curl and Truelove 1986). The variety of C compounds changes with location along the root (Jaeger et al. 1999). Root cap cells and mucilages (carbohydrates) constitute the bulk of C input near the root tip. Near the zone of root extension, exudates, secretions, and lysates generally reflect the composition of root cell contents. In rhizosphere soil near older sections of roots, C inputs commonly reflect their origin from root cell turnover and include both structural components of roots and lysate materials. The rhizosphere boundary is thus a zone of high organic C availability, compositionally heterogeneous in space and time, and characterized by high rates of microbial utilization and transformation.

Root respiration and enhanced microbial respiration release large amounts of CO_2 into the rhizosphere soil pores (figure 1). The elevated concentrations of CO_2 in this zone of soil can alter the pH of the rhizosphere soil solution.

Nitrogen. Rhizosphere soil can transmit incoming inorganic N ions to the root, transform the oxidation state of inorganic species, convert organic N and N_2 to NH_4, and convert organic and inorganic forms of N to microbial biomass (figure 1). All transformations of N in this boundary are under microbiological control.

The fluxes of N in rhizosphere soil are driven by root uptake of water, NO_3^-, and NH_4, as well as by microbial utilization and transformation. The rhizosphere has long been known to be a zone of high microbial activity, and recent work has shown the gross rates of N mineralization in rhizosphere soil to be about 10 times those of bulk soil (table 1). Rates of nitrification are potentially controlled by plant utilization of NH_4. In soil adjacent to zones of active root NH_4 uptake, rates of gross nitrification approach zero; in contrast, rates of nitrification in rhizosphere soil near root tips are similar to those in bulk soil (table 1). Denitrification activity in rhizosphere soil can be enhanced by O_2 depletion and high C availability or, alternatively, reduced because of uptake of NO_3^- and water by roots. When denitrification is concentrated
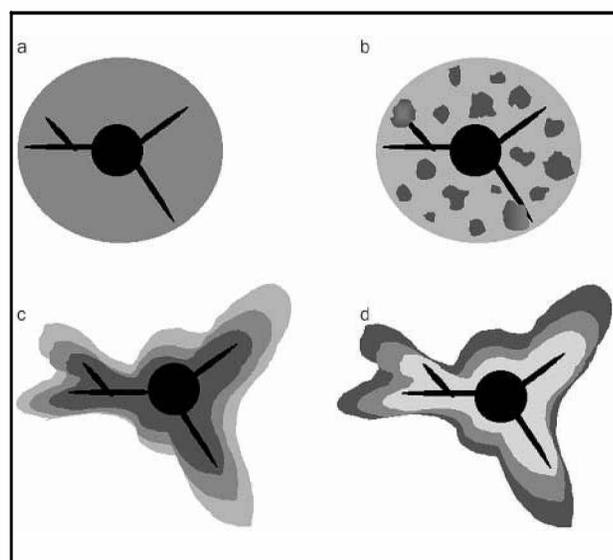
Figure 4. Idealized distribution patterns in rhizosphere soil near root. (a) No effect of root on homogenous distribution (e.g., sand, silt, or clay); (b) no effect of root on heterogeneous distribution (e.g., soil organic matter); (c) gradient of increasing concentration approaching root (e.g., carbon dioxide); and (d) gradient of decreasing concentration approaching root (e.g., ammonium).

in rhizosphere soil, this zone can be a major source of the atmospherically reactive trace gas N_2O (Firestone and Davidson 1989).

Oxygen. The flux of O_2 from the surrounding biosphere into plant roots passes through and is modulated by rhizosphere soil. Rhizosphere soil can function as an absorptive or transmissive boundary with respect to O_2 movement in soil. While this flux is generally dominated by diffusive movement toward the root, the rhizosphere provides an interesting example of a boundary in which the direction of flux can be opposite in different environments. Concentrations of O_2 in rhizosphere soils can be substantially different from those of the surrounding soil. Rates of O_2 consumption are elevated in the rhizosphere zone because of root respiration and microbial respiration (the latter fueled by enhanced C availability) (table 1). Depending on the rate of O_2 resupply, high rates of O_2 consumption can result in zones of lowered concentrations, including anaerobiosis (figure 4d). Diffusional resupply of O_2 is highly dependent on soil water content, with water-filled pores retarding movement of O_2. Conversely, if water removal by plant transpiration reduces the water content of soil pores in the rhizosphere, then enhanced resupply of O_2 from the atmosphere can result in higher availability or higher concentration of O_2 in this soil zone.

In habitually saturated soils where O_2 diffusion and availability is much reduced, the flux of O_2 can be in the opposite direction, flowing from the root into the surrounding soil. Plants common to waterlogged soils typically have specialized cells (e.g., aerenchyma) and structures (e.g., pneumatophores) that allow movement of O_2 to the root system. As O_2 is sup-

plied to root cells, some O_2 makes its way to the soil surrounding the roots; as a result, aerobic microbial processes and microbial respiration of NO_3 and iron are common to the rhizosphere soil of plants indigenous to submerged soils. In this case, the flux of O_2 is from the surface of the root out into the surrounding soil. Depending on the plant and soils present, the flux of O_2 may be toward the rhizosphere and root or away from the root. While the flux may potentially occur in either direction, high rates of O_2 flux are characteristic of the rhizosphere boundary .

The mycorrhizosphere. Mycorrhizal fungi infect the roots of more than 80% of plant species worldwide, with representatives in almost every habitat and plant family. The mycorrhizosphere is an extension of the rhizosphere boundary formed by the association of roots with mycorrhizal fungi (figure 5). Though the mycorrhizosphere is similar in many ways to the rhizosphere boundary, flux of matter and energy across the mycorrhizosphere is likely to differ in magnitude. Mycorrhizal fungi obtain C from plants and in turn typically provide the plants some benefit, such as increased nutrient uptake, improved drought resistance, or protection from pathogens (Newsham et al. 1995). Fluxes in the rhizosphere are certain to be affected by the interactions of mycorrhizae with roots and other root-associated microorganisms. For example, mycorrhizae have the potential to affect soil C and N cycling in the mycorrhizosphere through changes to plant C exudation (Schwab et al. 1984), through enhanced decomposition of complex organic material (Hodge et al. 2001), through retention of C and nutrients in recalcitrant fungal tissues (Rillig, et al. 2001), and through increased transfer of nutrients to plants (Ibijbijen et al. 1996). Mycorrhizal fungi may also indirectly affect soil C and N cycling through impacts on the soil microbial community (Hodge et al. 2001).

Boundary dynamics
The structure and function of the atmosphere–soil and soil–root boundaries change over time and space. Changes in BSC composition and morphology occur during natural succession as biomass increases and new species colonize. Disturbance can also induce succession. Changes in BSC species composition alter many characteristics and functions of the atmosphere–soil boundary. Lichens and mosses are more susceptible to soil surface disturbance and slower to colonize than cyanobacteria. Removal of the dark-colored lichens and mosses increases soil albedo by approximately 40 watts per square meter, decreasing soil temperatures by up to 14 °C (Belnap and Eldridge 2003). Lichens have higher C and N fixation rates per unit soil surface area than cyanobacteria (Lange 2003); thus, loss of these organisms reduces levels of C and N in plants and soils (Evans and Belnap 1999, Belnap and Eldridge 2003). Compressional disturbance also reduces soil aggregate structure and flattens soil surfaces, thereby decreasing resistance to wind and water erosion (Belnap and Eldridge 2003). Moving sediment can also bury nearby soil crusts, resulting in the death of photosynthetic organisms.

Thus, the removal of biological soil crusts can have varied and profound consequences for a given ecosystem.

Roots also change through space and time. As roots grow through soil and age, the characteristics of the rhizosphere boundary change. Different sections of the root will vary in C exudation, in rates of respiration, and in the ability to take up water and nutrients. In general, activity decreases in older sections of root. The variety of C compounds released from roots changes with location along the root (Jaeger et al. 1999). Disturbances such as soil turnover or belowground root herbivory can change the proportion of old to new roots in soil as established roots are severed from the plant and new ones are grown. Rhizosphere processes are also highly dependent on plant productivity and, in some cases, on specific plant species.

The rhizosphere is the primary interface for plant–soil interactions. This zone mediates changes to plant communities or to soil environments. Thus, the structure and function of the rhizosphere boundary will be critical in defining terrestrial ecosystem responses to environmental change.

Interactions between atmosphere–soil and soil–root boundaries
Flux across the atmosphere–soil boundary affects flux in the rhizosphere. As discussed above, microbes at the soil surface (e.g., in BSCs) capture, transform, or deflect atmospheric inputs (e.g., Hawkes forthcoming), changing the amount and rate of arrival in the soil–root boundary zone. The total resource flux across the atmosphere–soil boundary and the soil–root boundary depends on many simultaneous interactions of organisms and conditions in both zones. Plant roots may directly take up the N generated in or captured by BSCs, but to do so, roots and associated mycorrhizae must compete with heterotrophic microbes in the BSCs (Hawkes forthcoming). The presence of BSCs can also affect root infection by mycorrhizal fungi (Harper and Pendleton 1993) and whether mycorrhizae have a positive or negative effect on plant growth and nutrient uptake. These two small-scale soil boundaries provide experimentally accessible examples of interaction between spatially distinct boundary zones.

Links to landscape ecology
A landscape perspective can be informative for the study of small-scale boundaries. The concepts and models developed for discussion and study of landscape boundaries provide novel, revealing perspectives on microboundary zones. By thinking of the rhizosphere and the soil surface as ecotones or boundaries, we can better understand their role in a broader context. The simple recognition that microboundary zones can be characterized as absorptive, transmissive, reflective, transforming, or amplifying more clearly defines the varied roles played by these boundaries in terrestrial system function. The soil surface and rhizosphere are dynamic boundaries, the extent of which can differ temporally (both daily and seasonally) and spatially (along the root and in different soil patches). Both boundary zones involve alterations
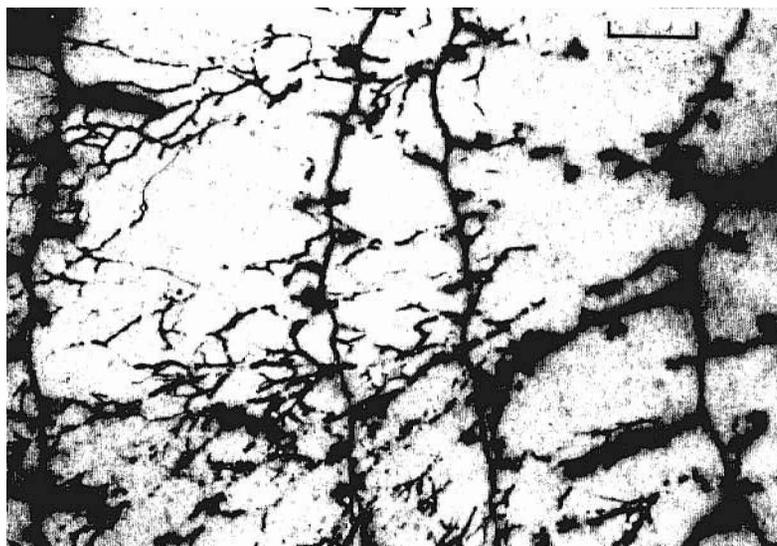
Figure 5. Autoradiograph of Ponderosa pine roots and ectomycorrhizae (from Norton et al. 1990). The soil–root boundary changes as roots grow through soil and become infected with mycorrhizae. Without identifying information, it is difficult for the viewer to determine whether this is an image of microscale root–soil boundaries or macroscale stream networks.

in the rates of processes (e.g., water versus C cycling), the density of microbiota, and the characteristics of the relevant microhabitat. The characteristics and controls of flows into and across these fine-scale boundaries can be characterized and measured in many of the same ways as the flows across boundaries at coarser scales. Yet these microscale boundaries have not commonly been characterized or measured in terms of their shape, area, rates of change, contrasts between patches on either side (rhizosphere versus bulk soil, air versus bulk soil), and smoothness of transition. The definitions of the edges of these microboundaries will be flux specific (Cadenasso et al. 2003). The flows of materials and energy are directional and nonrandom, with microorganisms acting as biotic vectors. Microbial behavior, density, and response to the environment can dramatically affect flows into and across the rhizosphere and soil surface. In the rhizosphere, the root itself acts as both a source and a sink; thus, diffusion as well as bulk flow can be bidirectional. The rhizosphere is highly permeable to most substances entering the zone through mass flow or diffusion, but it acts as a filter for some organisms and substances.

Can study of small-scale boundaries be informative for landscape ecology? The two boundaries discussed here, the atmosphere–soil and soil–root boundaries, provide interesting model systems for the study of boundaries and ecotones. All landscapes are created by mosaics of patches that are delineated by boundaries. A terrestrial ecosystem may be described as a mosaic of rhizosphere patches or as soil and plant patches delineated by the rhizosphere boundary. In either case, processes and pools in the rhizosphere drive large-scale patterns and fluxes. The soil surface is a boundary at all

scales, though the variability in any given flux will depend on the scale of observation, since the characteristics of the atmosphere–soil boundary are spatially patchy.

Integrating a hierarchical view of the landscape with models of spatial patch dynamics may be an effective way of dealing with scale and complexity in a landscape (Wu and David 2002). We expect fluxes in most systems to be driven by a combination of top-down and bottom-up forces. Lower levels of hierarchy provide an understanding of embedded mechanisms and the initiating conditions for higher levels. We have explained how the atmosphere–soil and soil–root boundary zones drive fluxes that are important at larger scales. Incorporating the characters of these local interactions into landscape and global dynamics may or may not improve understanding and prediction.

Examining boundaries in fine-scale systems may facilitate the advancement of boundary theory, especially for biochemical and biophysical processes. Applicability of generalized principles found at these finer scales can then be tested on larger-scale boundary systems. As with any system, however, researchers applying principles developed at one scale to different scales may encounter problems with discontinuities of scaling.

Some models that have been developed for fine-scale processes can be applied to coarser scales. Decades before the development of landscape-scale models, analyses of small-scale diffusion–reaction problems were developed by researchers (Thiele 1939, Aris 1965) who were interested in predicting rates of reactions controlled by diffusion or rate kinetics. For systems that could be approximated by kinetic reaction rates and constant diffusivities, these early models captured critical relations between the scale of diffusional distance (patch size), diffusivity, and process rate. These reaction–diffusion models, using diffusionally controlled arrival of species and kinetically based processing of materials and energy, may be conceptually and mathematically similar for all boundaries.

Reaction–diffusion models have been successfully applied to studies of N processes in heterogeneous soil aggregates (Myrold and Tiedje 1985) to explain the occurrence of an anaerobic process (denitrification) within generally aerobic soils. These models have also been applied to nutrient uptake by growing roots (Barber and Silberbush 1984). Microsite models provide examples of how transport processes, ecological processes, and characteristic dimensions are strongly coupled with the evolution of environmental heterogeneity in structured habitats. Moreover, microsite models can be generalized and coupled to heterogeneous flow and transport across boundaries at landscape scales, effectively describing spatially complex patterns of reactants in terrestrial environments.

The soil surface and rhizosphere may also provide useful experimental systems. Both systems include sharp transi-

tions (e.g., the atmosphere–soil interface) and gradual transitions (e.g., organic C concentration grading from rhizosphere to bulk soil), biotic and abiotic vectors, and processes that occur at a variety of scales. Small-scale environments can be replicated in ways that are not feasible for biomes and landscapes. In an experimental setting, the rhizosphere and its adjacent root and soil patches can also be manipulated. Factors that can be controlled in the root boundary include the plant genotype, the microbial and mycorrhizal communities, the number of boundaries per unit area (and therefore the probability of boundary encounter), and the permeability and nutrient status of the bulk soil environment. The same is true of the soil surface, where manipulations not only of soil but also of atmosphere are possible.

There are a number of examples in which the effects of boundary manipulation on function have been studied and quantified for both the rhizosphere and soil surface. Many researchers have addressed the effects of root inoculation with arbuscular mycorrhizal fungi on rhizosphere processes. Mycorrhizae can have dramatic effects on structure and function in the rhizosphere, but this effect is highly dependent on the combination of plant and fungal species used. Thus, the quantity and number of labile C compounds exuded in the rhizosphere have been shown to increase (Schwab et al. 1984), decrease (Bansal and Mukerji 1994, Marschner et al. 1997), and remain the same (Azaizeh et al. 1995, Marschner et al. 1997) in response to mycorrhizal infection. Mycorrhizal inoculation of roots can also increase rhizosphere N_2 fixation by *Rhizobium* bacteria and increase nutrient uptake by roots (and therefore increase nutrient flow through the boundary zone) compared with uninoculated controls (Ibijbijen et al. 1996). The species composition of BSCs has also been manipulated through various disturbances. As discussed in the section above on boundary dynamics, disturbance to soil crusts results in a number of changes in the boundary zone, including reduced C and N fixation, water infiltration, and soil aggregation, and increased nutrient loss.

Conclusion

Although small in scale, the functions of the atmosphere–soil and soil–root boundaries can have a profound influence on the structure and function of ecosystems at landscape, regional, and global scales. Like those of macroboundaries, the characteristics of these microboundaries vary in time, in space, and in their influence on the materials and energy that cross them. Indeed, it is somewhat surprising to recognize that there are no fundamental differences between fine- and coarse-scale boundaries other than units of measure and methods for study. For instance, the autoradiograph of pine roots and mycorrhizae shown in figure 5 is largely indistinguishable from a satellite image of a stream network across a landscape.

Atmosphere–soil and soil–root boundaries are found in all terrestrial landscapes. They are microscale zones of significant material and energy flow that are affected by and affect broader characteristics of ecosystems. For example, inter-

actions between atmospheric concentrations of CO_2 and C exudation from roots will be important to microbial mediation of N availability to plants as well as to the ecosystem C cycle.

In considering the characteristics of these two small-scale boundaries, the importance of soil microbial communities in mediating and modulating fluxes becomes clear. The microbial community of the soil surface forms a living skin that covers most of Earth's terrestrial surfaces and moderates most inputs into soils. The interactions of vascular plants with their soil environment are modulated by a diffuse net of microbes interfacing the root with the surrounding soil. Anthropogenic disturbance to the soil microbial community at the atmosphere–soil boundary or at the soil–root boundary can alter the way in which the terrestrial system functions. An improved understanding of how soil microbes, their functions, their redundancy, and their responses to climate change affect the energy and material crossing these boundaries may significantly increase our understanding of how landscapes will respond to future human disturbance.

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