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The Influence of Soil Biodiversity on Hydrological Pathways and the Transfer of Materials between Terrestrial and Aquatic Ecosystems

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ABSTRACT

The boundaries between terrestrial and aquatic ecosystems, known as critical transition zones (CTZ), are dynamic interfaces for fluxes of water, sediment, solutes, and gases. Moreover, they often support unique or diverse biotas. Soils, especially those of riparian zones, have not been recognized as CTZ even though they play a critical role in regulating the hydrologic pathways of infiltration and leaching, or runoff and erosion, which can cumulatively affect biogeochemical processes and human livelihoods at landscape scales. In this review, we show how the processes that regulate hydrologic fluxes across and through soil CTZ are influenced by the activities of soil biota. Our message is fourfold. First, there are a variety of ways in which soil biodiversity, in terms of richness and dominance, can influence hydrological pathways in soil and thus the transfer of materials from terrestrial to aquatic ecosystems. Second, the influence of soil or-

ganisms on these hydrological pathways is very much interlinked with other environmental, soil biophysical, and vegetation factors that operate at different spatial and temporal scales. Third, we propose that the influence of soil biodiversity on hydrological pathways is most apparent (or identifiable), relative to other factors, in situations that lead to the dominance of certain organisms, such as larger fauna. Fourth, soils are buffered against environmental change by biophysical properties that have developed over long periods of time. Therefore, the effects of changes in soil biodiversity on hydrological processes at the ecosystem scale might be delayed and become most apparent in the long term.

Key Words: critical transition zones; soils; soil biodiversity; soil hydrological pathways; soil biophysical properties.

INTRODUCTION

The boundaries between terrestrial and aquatic ecosystems, known as critical transition zones (CTZ),

are dynamic interfaces for fluxes of water, sediment, solutes, and gases. Moreover, they often support unique or diverse biotas. Riparian zones, wetlands, estuaries, and littoral regions, which are at the interface between land and water or between freshwater and marine systems, are among the habitats most threatened by urbanization, industrial

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development, and farming/forestry activities (Naiman and Décamps 1997). They are also among the most ecologically important systems, not only in terms of their intrinsic conservation value, but also because of the ecosystem goods and services that they provide, including the regulation of hydrologic fluxes and the maintenance of water quality. Due to their functional importance and their current vulnerability, the study of CTZ has become a priority for all those concerned with global environmental change and was a major issue for the Rio Convention of Biological Diversity (1992).

Soils of riparian zones and those that facilitate groundwater-surface water exchanges and the transport of material into the riparian from surrounding uplands have not been recognized as CTZ, despite the fact that these interface soils (soil CTZ) play a role in regulating the hydrologic pathways of infiltration and nutrient leaching, or runoff and erosion, which can cumulatively affect biogeochemical processes and human livelihoods at landscape scales. Soil CTZ, especially those of riparian zones, possess an unusually high diversity of fauna and microflora (Ettema and others 1999, 2000). This biodiversity is maintained by a variety of disturbances (for example, periodic flooding, drought, freezing, abrasion, erosion, and occasionally toxic concentrations of nutrients) that create a spatial and temporal mosaic that has few parallels in other systems (Ettema and others 2000; Naiman and Décamps 1997). Although the activities of large burrowing mammals can greatly modify the heterogeneity of riparian soils and the distribution and cycling of nutrients within them (Naiman and Décamps 1997), there is a dearth of information about how other soil organisms and their interactions influence hydrological processes and ecosystem-scale processes of energy and material flow through soil CTZ.

In this paper, we consider from two perspectives how the processes regulating hydrologic fluxes across and through the soil CTZ are influenced by the soil biota. First, we establish the key hydrological pathways and abiotic controls of material transfers between terrestrial and aquatic ecosystems. Second, we identify how soil organisms and their interactions might influence these key pathways of material transfer and their stability. The role of soil biodiversity in maintaining the functional properties of soils has received increasing attention in relation to the impacts of land-use practices, global climate change, and the remediation of degraded land (Brussaard and other 1997; Bardgett and Cook 1998; Swift and others 1998; Wall and Moore 1999). Our goal here is to promote the recognition

of soils as CTZ and to stimulate thinking about whether changes in soil biodiversity will have far-reaching ecologically significant effects on material transfers from terrestrial to aquatic ecosystems.

HYDROLOGICAL PATHWAYS FROM TERRESTRIAL TO AQUATIC ECOSYSTEMS

The riparian zone is the main interface for the transfer of materials such as nutrients and pollutants from terrestrial to aquatic ecosystems. Riparian zones are among the most diverse, dynamic, and complex biophysical habitats on the terrestrial portion of the Earth (Naiman and Décamps 1997). Their spatial extent varies tremendously, depending largely on the size of the watercourse to which they belong. Central to material transfer through riparian zones, and from surface waters to groundwaters, are hydrological pathways that occur at two scales: the soil scale and the catchment (or hill-slope) scale (Heathwaite and Johnes 1996).

The soil scale is of the order of millimeters to meters; it is concerned primarily with the flow of water through and across the soil physical domain of the riparian and into watercourses and/or groundwaters. The catchment scale is from meters to hectares; it concerns major pathways of water flow through and across riparian soils and the flow of water into the riparian zone from the surrounding uplands. An understanding of these pathways and the physical, chemical, and biological mechanisms of material flow within them is urgently needed so that we can control material transfer between terrestrial and aquatic ecosystems and hence mitigate water pollution. Because much of this information is available elsewhere, we will provide only a brief comment on the key pathways and material transfers from terrestrial to aquatic ecosystems.

Precipitation in the form of rain, snow, and dew, and its subsequent pathways in the soil, is the main vehicle for material transfer through riparian zones and from surface waters to groundwaters. Water reaching the soil surface as incident precipitation or throughfall is partitioned into different pathways. At the catchment scale, the key pathways of water movement are: (a) the infiltration and/or surface runoff of water; (b) the interflow of water below the soil surface; (c) evaporation and the uptake and evapotranspiration of water by plants; and (d) deep percolation to groundwater. These fluxes can be related to such distal environmental variables as vegetation cover, slope, soil type, and the intensity of land management (for example tillage, applications of fertilizers, tree-felling) and to natural dis-

turbances (for example fire, weather events). The proximate determinants, however, involve finer controls at the soil scale that are influenced directly by soil organisms and their interactions with plant cover and the mineral matrix (Anderson 1988). The presence of plant litter protecting the soil surface, aggregate stability and capping by microphyte crusts, infiltration through macropores, and preferential flow pathways in soil are not determined solely by the soil biota; instead, their specific functions emerge as higher-order biophysical determinants of these fluxes.

THE ROLE OF SOIL BIODIVERSITY IN HYDROLOGICAL PATHWAYS

Soil organisms and their interactions are fundamental to processes of soil structural formation and in the transformation of materials in soil CTZ. It is therefore very difficult, if not impossible, to distinguish any definitive, direct roles for soil organisms in the transfer of materials from terrestrial to aquatic ecosystems, whether they are through riparian soils or soils that facilitate groundwater-surface water exchanges. However, in this section, we attempt to identify examples of situations where the activities and interactions of organisms that live in soil CTZ substantially alter the hydrological pathways and thus have an indirect influence (alongside physical and chemical factors) on the transfer of materials from terrestrial to aquatic ecosystems. Many of the examples that we use are taken from studies that did not explicitly set out to demonstrate the role of soil organisms in soil CTZ; however, they serve to highlight the potential for changes in soil biodiversity to influence material transfers from terrestrial to aquatic ecosystems. A summary of the role of soil organisms in these soil CTZ hydrological pathways is given in Figure 1.

Mechanisms and Key Functional Groups of Organisms Involved in Hydrological Pathways

Infiltration of water through the soil surface. In a structurally homogeneous soil, rain falling on the soil surface is drawn into soil pores under the influence of suction and gravity (White 1997). True soil organisms and those occurring on the soil surface can have both direct and indirect effects on infiltration rates through soil CTZ of the riparian zone and the surrounding catchment. Direct effects occur when organisms provide a physical barrier to water infiltration, leading to surface runoff of water. Examples of such mechanisms that influence material transfer from land to water are the black

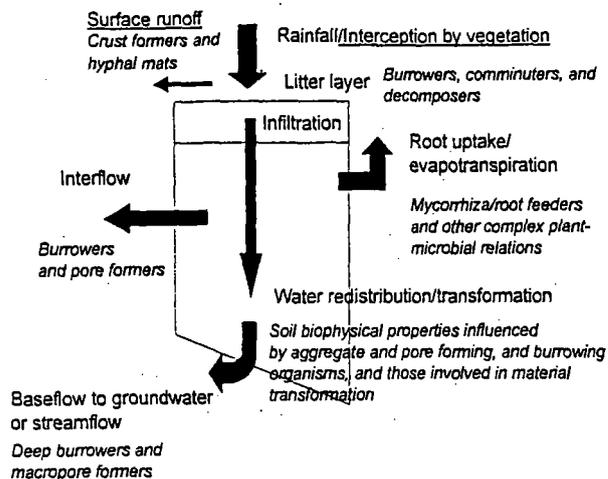


Figure 1. Conceptual model of the role of soil biodiversity in hydrological pathways in soil.

algal crusts that developed on recently deglaciated terrain in Glacier Bay, Alaska, (Chapin and others 1994) and the microphyte crusts that affect runoff and interception zones in arid areas of western Queensland and determine patch dynamics of the vegetation at landscape scales (Tongway and others 1989). Larger organisms such as earthworms and termites, which exploit plant litter at the soil surface, can substantially increase infiltration rates through soil CTZ by creating macropores and channels as a consequence of their feeding and burrowing activities (Peterson and Dixon 1971; Wilkinson 1975; Carter and others 1982) and reduce sediment losses in surface runoff (Edwards and others 1990). Conversely, the elimination of earthworms from pasture through the use of pesticides has been shown to decrease water infiltration by up to 93% (Sharpley and others 1979; Clements 1982). The effects of earthworms, especially deep-burrowing species, on infiltration can result in increased leaching of nutrients from the soil to groundwaters. In studies of grain-crop agrosystems (Subler and others 1997), the inoculation of soils with earthworms produced a four- to 12-fold increase in leachate volumes and a 10-fold increase in nitrogen. Similarly, the inoculation of earthworms (*Aporrectodea caliginosa*) into limed coniferous forest soils produced a 50-fold increase in the concentration of nitrate and cations in soil solution (Robinson and others 1992, 1996). The quantity of nutrients lost to groundwater or to plant uptake is unknown.

Nests of soil-nesting ants provide extensive macroporosity to the soil, which affects infiltration and percolation rates. Bulk flow along nest galleries also represents an important route of recharge of

deep soil moisture in arid and semi-arid environments. For example, in semi-arid Western Australia, ant biopores transmitted water down the soil profile when the soil was saturated and water was ponding on the surface (Lobry de Bruyn and Conacher 1994). Similarly, water infiltration on soils with nest entrances of funnel ants (*Aphaenogaster barbigula*), which can reach densities of up to 88,000 ha⁻¹, averaged 23.3 mm min⁻¹, but it was only 5.9 mm · min⁻¹ in nest-entrance-free soil (Eldridge 1993). On the red earth soil of the semi-arid woodlands of eastern Australia, ponded steady-state infiltration averaged 1026 mm h⁻¹ on soil with nest entrances of *A. barbigula*, but it was only 120 mm h⁻¹ on soils without nest entrances (Eldridge 1994). Although they have not been quantified, the effects of ants on water infiltration are likely to have a significant effect on the transfer of water to groundwaters, as well as the movement of water from the wider catchment to the riparian zone.

Various organisms are also likely to have indirect effects on water infiltration through soil CTZ by causing changes in the nature of a surface litter layer or organic horizon. These changes can greatly alter the initial infiltration rate and thus the potential for either downward flow, adsorption, or surface runoff of water. The presence and character of surface litter or an organic layer is related to the balance between biological decomposition and primary productivity, which are ultimately determined by climatic and/or other environmental factors. Soil organisms and their activities are key determinants of decomposition rates. Thus, they provide a clear example of soil biodiversity indirectly influencing the transfer of material between land and water. There are numerous examples of changes in the abundance of keystone decomposers (through predation, migration, or a change in environment) substantially altering the nature of the surface soil organic matter and thus the hydrological character of soils. The experimental elimination of small populations of the termite *Gnathamitermes* in the Chihuahuan Desert resulted in long-term increases in the encroachment of grass patches by shrubs as a consequence of changes in the patterns of surface runoff and infiltration at the catchment scale (Elkins and others 1986). A further example comes from sub-Antarctic Marion Island, where the soil-borne larvae of a flightless moth, *Pringleohaga marioni*, process some 1.5 kg plant litter or peat m⁻² an⁻¹, thereby stimulating nitrogen (N) and phosphorus (P) mineralization 10-fold and threefold, respectively (Smith and Steenkamp 1990). Recently, the house mouse (*Mus musculus*) was intro-

duced onto the island. It feeds on the moth larvae, thereby reducing annual litter turnover by some 60% of that originally processed by the moth (Smith and Steenkamp 1990). According to Smith and Steenkamp (1990), if the number of mice continues to increase, the rate of peat accumulation will also increase, dramatically altering the hydrological regime and vegetation of the island. Conversely, excluding a single species of omnivorous land crab from areas of rainforest allowed a buildup of litter cover on the soil surface that was atypical of the normal seasonal dynamics of decomposition processes (Green and others 1999).

Changes in the aboveground environment can also substantially alter the nature of decomposition processes, either indirectly through changes in substrate supply to organisms or directly through changes in the abundance/dominance of individual species or groups of organisms. For example, studies of peat soils in the UK suggest that atmospheric warming will increase the abundance of the enchytraeid worm (*Cognettia sphagnetorum*), a keystone comminutor in peat soils, leading to increased rates of organic matter decomposition and nutrient mineralization, as well as changes in the hydrological character of the peat. Taken together, these changes, have been shown to result in an increased transfer of nutrients, especially dissolved organic carbon (DOC), from soil to drainage water (Briones and others 1998). Changes in plant species composition may also have profound influences on the quality of plant litter and hence have strong "after-life" effects on soil biodiversity and decomposition. For example, studies of herbivory show that browsing of vegetation forces a selection toward plant species that are unpalatable (Pastor and others 1988). These plant traits are then transferred to the litter, reducing food-web complexity and rates of litter decomposition (Grime and others 1996; Bardgett and others 1998). Again, these changes could ultimately influence soil CTZ hydrological pathways, especially at the catchment scale, as well as transfers of material between the land and the water and from the catchment to the riparian zone.

These studies all point to the importance of single dominant keystone organisms in determining the rates of litter turnover and therefore altering soil CTZ hydrological pathways. In contrast, there are also examples showing that changes in the diversity of functional groups of organisms influence decomposition rates. For example, in a microcosm study of montane peat soils, Bardgett and Chan (1999) showed that rates of surface organic matter decomposition and nutrient leaching (N and P) were higher in the presence of more complex faunal

communities, composed of different functional groups of Collembola and nematodes, than they were when these organisms were acting alone. As we have already noted, soils of the riparian zone tend to possess an unusually high diversity of organisms (Ettema and others 2000). Currently, there is a dearth of information on both the effects of such high diversity and the effects of changes to the microbial and invertebrate community structure on the processes of decomposition and water infiltration in the riparian. We intend to make this issue a research priority in the future.

Redistribution of soil water. The percolation of water through soil is largely dependent on porosity, which in turn is dependent on soil texture and the formation and stabilization of soil aggregates and peds (White 1997). Soil organisms are critical to the formation and stabilization of aggregates and peds; they also create burrows and macropores that greatly facilitate the movement of water and material in the soil (Anderson 1988). Numerous studies have shown that earthworms contribute to soil aggregation through the production of casts, which can make up the majority of structural aggregates in the surface soil (see Edwards and Bohlen 1996). Earthworms also improve soil porosity and drainage through their burrowing activities. One of the main effects of earthworms on soil porosity is to increase the proportion of macropores and channels (Edwards and Lofty 1982; Knight and others 1992; Lavelle and others 1997). Those formed by larger deep-burrowing earthworms, such as *Lumbricus terrestris*, may act as pathways for the preferential flow of water that bypasses the soil matrix and moves solutes directly to groundwater or streamflow (Edwards and others 1988; Bouma 1991).

Individual species of worms have markedly different effects on aggregation and pore formation. Different species of worms produce aggregates that differ in their size and stability (Guild 1955), and different functional groups produce burrows that differ in their ability to conduct water (Edwards and Bohlen 1996). Changes in the dominance of competing earthworms,—for example, through invasion—can have a negative effect on the structural properties of the soil. Chauvel and others (1999) showed that the conversion of Amazonian forest to pasture reduced the original soil macrofaunal community by 68% and led to invasion by the earthworm *Pontoscolex corethrurus*, an aggressive exotic colonist. The particular pattern of burrowing and casting by this species actually reduced soil macroporosity by half (from 3 to 1.6 cm³/100 g).

Soil macrofauna can have local effects on the physical structure of litter and soil that significantly

affect soil CTZ hydrologic pathways, both within the catchment and the riparian zone. However, it is difficult to relate community composition to processes operating at hillslope or catchment scales because we would first need to link the spatial and temporal scales (or domains) at which specific organisms operate with those at which fluxes are measured (Anderson 2000). Hence, most of our understanding of these effects comes from examples, such as those considered above, in which a single species dominates a functionally important group over significant areas of the system. With increasing numbers of species, which by definition are likely to have slightly different functional attributes, it becomes progressively more difficult to separate the "diversity signal" from the "community noise." This is particularly true for microbial communities that are characterized by very high diversity at small spatial scales.

Microorganisms also contribute to the formation and stabilization of aggregates. It is generally accepted that an increase in microbial biomass and the associated production of extracellular polysaccharides increases the stability of soil aggregates (Lynch 1983). It is also evident that different species of microorganisms (bacteria and fungi) have markedly different effects, both positive and negative, on aggregate stability (Aspiras and others 1971a, b). Hence, establishing the effects of soil microbial diversity on water infiltration involves similar issues of scaling and dominance. Caution should be employed regarding simplistic statements about the importance of diversity or, conversely, its redundancy.

It would appear, therefore, that the activities of both microbes and fauna contribute significantly to the formation of a soil matrix that favors efficient water movement through the soil CTZ. Improvements in porosity and aggregation can increase the soil's ability to retain moisture by allowing plant roots to proliferate, enabling plants to exploit a larger area of the soil profile for water and nutrients. Therefore, in this case, the net effect of improved soil structure, resulting from soil biodiversity, is an increased retention and/or uptake of water and materials by plants.

Material transformations. Perhaps one of the most important roles of soil organisms in soil CTZ is the transformation of inputs to more mobile forms, making them susceptible to leaching and hence to transfer across ecosystems. Many microbial processes in soil CTZ transform nutrients, heavy metals, and organic pollutants to a more mobile state. However, the role of microbial diversity in controlling these processes is not entirely clear. On one hand, we could argue that these processes should

not be strongly influenced by microbial diversity, as they tend to occur only under specialized physico-chemical conditions. For example, nitrification, a microbial process responsible for the conversion of NH_4^+ to the more mobile oxidized states NO_2^- and NO_3^- , requires oxygen and therefore aeration, which in turn is controlled by soil moisture and soil structure. Conversely, the formation of local anaerobic microsites in soils by earthworms can act as a sink for nitrate and create hot spots for denitrification (Elliott and others 1991). Likewise, the reduction and oxidation of iron and manganese, which determines their solubility and mobility and their release into groundwater, is carried out by a wide range of microorganisms, both bacteria and fungi, but it is ultimately controlled by the availability of oxygen and the status of soil water within the soil matrix (Paul and Clark 1996). The mobility of persistent organic pollutants, such as polychlorinated biphenyls (PCB) and polynuclear aromatic hydrocarbons (PAH), may also be influenced by soil organisms that affect both the degradation of the material and its "aging," an important determinant of pollutant mobility in ecosystems (Hatzinger and Alexander 1995). Arguing against this perspective, however, is the fact that many of these processes are physiologically narrow (*sensu* Schimel 1995). That is, they are carried out by a limited number of specific enzymatic pathways and by a phylogenetically limited group of organisms. Thus, differences in the characteristics of the specific organisms involved may have a significant effect on the rate and controls on the processes involved. This follows the arguments we have made above; when a limited suite of organisms is responsible for a process, the specific characteristics of those organisms may be important. The specific role played by the microbial community composition of the soil in ecosystem-scale processes has been discussed elsewhere (for example, Schimel 1995; Brussaard and others 1997; Schimel and Gullledge 1998; Groffman and Bohlen 1999; Wall and Moore 1999).

Plant uptake and evapotranspiration. Although we are not concerned directly with the effect of plants on soil CTZ hydrological pathways, soil biodiversity can be an important determinant of plant productivity and composition, which in turn may have strong effects on the uptake and evapotranspiration of water, as well as the availability of nutrients in soil solution, both within the catchment and the riparian zone. For example, van der Heijden and others (1998) found a positive correlation between the diversity of mycorrhizal fungal species in soil and plant diversity. Presumably, such changes in plant diversity will have profound effects on root

architecture and root biomass, which in turn will influence water relations and movement in the soil. Other organisms also have strong effects on root growth and plant competition, which might translate to altered hydrology. For example, studies by Bardgett and others (1999) showed that low levels of infestation by obligate nematode root-feeders can alter competitive interactions between plants by enhancing the root growth of both their host and neighboring plants. Such effects will feed back to the soil in terms of changed water relations and thus altered water movement. Insect herbivores have also been shown to strongly affect root systems, and attacked areas often respond by a proliferation in the growth of lateral roots (Brown and Gange 1990), which again might strongly influence water relations. There are numerous other feedbacks between plants and soil organisms at many spheres of influence—for example, combined effects of burrowing macrofauna, root exudation, nutrient cycling in the rhizosphere, and aggregate formation, as well as trophic interactions. These feedbacks can have net negative or positive effects on plant growth (Beare and others 1995; Bardgett and others 1998) that will ultimately influence ecosystem processes of water and material movement across landscapes and through soil CTZ.

Effects of Diversity per se

We have highlighted the important roles of specific (often dominant) soil organisms in soil CTZ through their indirect effect on water infiltration, soil aggregate formation and macroporosity, and the transformation of materials to more mobile states. It is not clear, however, how the diversity of soil organisms per se—that is, their richness—influences these processes in soil CTZ. In other words, is there a high degree of redundancy within these different functions? Thus far, all of the evidence presented here suggests that the roles played by soil biodiversity in these hydrological processes and other ecosystem processes, are mainly derived from examples of a few dominant organisms. These dominant organisms may be further divided into either "ecosystem engineers", which influence hydrological pathways by modifying the physical environment in which they live, or "keystone species", which influence material transfer through their trophic relations and dramatic effect on community composition (Jones and others 1994; Anderson 1995; Lavelle and others 1997). Because we still do not understand the roles of individual species—especially microorganisms, microfauna, and mesofauna—it is difficult to identify the unique species functions that might be central to these hydrologi-

Table 1. Attributes of Biodiversity and Biophysical Diversity of Soil Organic Matter (SOM) and Soil Physical Structure (Anderson 2000)

Parameter	Biodiversity	Biophysical Diversity
Component	Functional group, species, genotype	SOM, aggregates, porosity
Richness	Number of species	Number of fractions or void classes
Evenness	Equitability of species	Equitability of mass or voids
Resilience	Size and physiological tolerance	Chemical/physical stability
Disturbance	Dominance by a few species Loss of species	Dominance of resistant fractions Loss of structure
Recovery	Increased diversity Restoration of functional complexity	Increased diversity Restoration of functional complexity

cal processes and other processes in soil CTZ. Indeed, potentially, as many as 99% of soil bacteria and nematode species are still unknown, making species-level assessments on larger-scale processes impossible (Wall and Virginia 1999).

Despite our lack of knowledge about the role of individual species, it is evident that the total soil biota, together with the diverse forms and functions of plant roots, play critical roles in the development of soil structure and the soil's functional properties. These biophysical properties, in turn, exhibit a complex spectrum of types and abundances of components, such as pore sizes, aggregate sizes, and soil organic matter fractions, which reflect the cumulative activities of the total soil biota over time. The consequence of severe stress and disturbance to biotic communities is generally a reduction in species richness and an increase in the dominance of physiologically robust or fast-growing species (Bardgett and Cook 1998). These relationships are widely used in ecology as diagnostics of ecosystem responses (resistance) and recovery (resilience) from natural and anthropogenic perturbations (McNaughton 1994). Analogous components and responses can be identified in the components of biophysical diversity and could be used to relate soil biotic community structure to ecosystem functioning (Table 1).

The resistance and resilience of soils, and hence soil CTZ, to anthropogenic disturbances (for example, pollutants, tillage) and natural perturbations (for example, wind damage to forests) is determined mainly by biophysical properties, such as the mass of organic matter, cation exchange capacity, and soil structure, which have developed with the help of soil organism activities over a long period of time. Operationally, these constituents are often considered as single pools or large aggregated groups (for instance, fast and slow soil organic matter pools; sand, silt and clay fractions; micropores

and macropores), but they actually contain a very large diversity of components with different functional properties and turnover times. Soil structure, for example, may exhibit more or less steady-state biophysical characteristics (for example, pore and aggregate size distributions) in undisturbed ecosystems, but these are highly dynamic entities with turnover rates determined by long-term soil animal and microbial activities, plant root dynamics, and the slaking of soil pores (Anderson 2000). Therefore, when soils are disturbed or degraded, the diversity of these biophysical properties is reduced and process rates are determined by the characteristics of the subsequent dominant components. For example, when compaction eliminates macropores, rates of infiltration and hydraulic conductivity are determined by the properties of meso- and micropores until biotic activity (or tillage) restores soil structure (Deuchars and others 1999). Likewise, the recovery of soil biophysical properties through conservation management following degradation by intensive cultivation involves the long-term reestablishment of soil biological and root activities that help to restore soil structure (Juma 1994). Consequently, the effects of soil biodiversity on landscape-scale hydrological pathways and soil CTZ processes may take a long time to become apparent (Anderson 2000); delayed responses to changes in soil biodiversity, which occur when the soil's biophysical properties have been restored after disturbance, may be more important.

The above argument also extends to the loss of soil biodiversity—for example, through soil pollution—and the ways in which its loss might influence the stability of landscape-scale hydrological pathways and transfers—that is, their ability to resist and recover from environmental perturbations. It has been suggested that more diverse or complex systems are: (a) more resistant (that is, better able to maintain a state in a fluctuating environment) and (b) more resilient.

(that is, better able to return to a ground state when displaced) (McNaughton 1988). In soils, however, it is difficult to identify the role of soil biodiversity in stabilizing hydrological pathways or other ecosystem processes because they tend to be strongly buffered by the biophysical properties. Consequently, short-term changes in soil biodiversity resulting from environmental stress/disturbance may not manifest their effects on hydrological pathways and soil CTZ processes until long after key organisms are lost. Thus, delayed responses may be a significant legacy of changes in soil biodiversity.

CONCLUSIONS

In this review, we set out to show how processes regulating hydrologic fluxes across and through the soil CTZ are influenced by the soil biota. Our message is fourfold. First, there are a variety of ways in which soil biodiversity, in terms of richness and dominance, can influence hydrological pathways in soil and thus the transfer of materials through and across riparian soils, as well as the flow of water into the riparian zone from the surrounding uplands. Second, the influence of soil organisms on these hydrological pathways within the catchment and riparian zone is very much interlinked with other environmental, soil biophysical, and vegetation factors that operate at different spatial and temporal scales. Third, we propose that the influence of soil biodiversity on hydrological pathways is most apparent (or identifiable) relative to other factors in situations that lead to the dominance of certain organisms, such as larger fauna. Fourth, soils are buffered against environmental change by biophysical properties that have developed over long periods of time. Therefore, the effects of changes in soil biodiversity on hydrological processes in soil CTZ might be delayed and only become apparent in the long term.

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