CHAPTER 1

Soil Macrofauna: An Available but Little-Known Natural Resource

J. J. Jiménez, T. Decaëns**, R. J. Thomas**, and *P. Lavelle****

Amazingly to the casual observer, soils shelter among the most diverse biological communities on the planet. The number of animal species living in a soil has been estimated as being between 5 and 80 million, comprising principally arthropods (Giller et al. 1997). In a European beech forest, 1 g of soil can contain as many as 40,000 bacterial species (Tiedje 1995) and 1 m^2 can hold more than 1000 species of invertebrates (Schaefer and Schauermann 1990).

Despite the extraordinary array of life forms, the taxonomic knowledge of soil organisms is incomplete, with many genera that are neither identified nor classified at the species level (Brussaard et al. 1997; Giller 1996; Giller et al. 1997; Lavelle 1996). So far, about 3700 earthworm species have been described, but they probably represent less than half of the actual number of species (Fragoso et al. 1999; Reynolds 1994). This lack of knowledge is particularly marked for tropical soils, which are at greatest risk from changes resulting from agricultural intensification with its consequent loss of biodiversity (Giller et al. 1997).

Soil Biota as a Diverse Functional Entity

Biodiversity *sensu* Wilson and Peter (1988), or biological diversity, is defined as "the quantity and structure of the biological information contained in hierarchical living ecosystems" (Blondel 1995). Living systems can be considered at different levels of organization, from genes to the biosphere, which, in its turn, ranges from populations of species and communities to landscapes (Solbrig 1991b, 1994). An ecosystem characterized by broad species diversity is defined by the coexistence of its communities and by the relationships between them (Blondel 1995).

Petersen and Luxton (1982), working for the International Biological Programme (IBP, of the International Union of Biological Sciences [IUBS]), compiled most of the data available on microbial communities, macroinvertebrates, and their dynamics. Swift et al. (1979) also contributed to a synthesis of

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* Soil and Plant Nutrition Unit, CIAT, A.A. 6713, Cali, Colombia.

** Laboratoire d'Ecologie, UFR Sciences, Université de Rouen, F-76821 Mt Saint Aignan Cedex, France.

*** Laboratoire d'Ecologie des Sols Tropicaux, Institut de Recherche pour le Développement (IRD), 32 Av. Henri Varagnat, F-93143 Bondy Cedex, France.

knowledge on the processes of decomposition, and developed new thinking on interactions among biological, chemical, and physical components.

During the last decade, biological diversity has been a widespread political issue, resulting from the realization that man is affecting the terrestrial and aquatic ecosystems at scales ranging from the landscape to the biosphere (Blondel 1995; Schulze and Mooney 1994; Solbrig 1991b). These changes include the effects of agricultural intensification, modification of global carbon and nitrogen cycles, pollution, greenhouse effect, urbanization, and desertification (Asner et al. 1997; Pimm and Sugden 1994; Schulze and Mooney 1994; Solbrig 1991b, 1994).

The loss of biodiversity in an ecosystem inevitably leads to changes in its principal functions. A direct relationship exists between species richness; the intensity of some fundamental processes such as respiration, decomposition, nutrient storage, and primary production; and water (Asner et al. 1997; Pimm and Sugden 1994; Schulze and Mooney 1994; Solbrig 1991b, 1994). Soils, for example, shelter complex communities of microinvertebrates that stimulate the decomposition of organic matter (Coleman et al. 1998; Setälä et al. 1991; Vedder et al. 1996).

More recently, various studies have suggested the possible existence of redundant species or ecological equivalents (Lawton and Brown 1994). These species carry out essentially the same ecological functions and should one or another be absent, no detectable changes would occur in the ecosystem's functioning—in much the same way that a factory can continue operating even if it lacks a worker. However, should a functional group, that is, an entire set of equivalent species that perform a specific function (Blondel 1995), be absent, then the ecosystem's functioning would be clearly affected. The existence of redundancy confers a functional stability to the ecosystem against accidental decrease in a community's specific diversity (Blondel 1995; Lawton and Brown 1994). Experimental results from numerous recent studies support this theory (Grime 1997; Hooper and Vitousek 1997; Tilman et al. 1996, 1997).

Hierarchical Regulation of Soil Processes

A hierarchical model (Figure 1) explains the functioning of soil processes via a series of factors determined by spatial and temporal scales throughout the hierarchy (Lavelle et al. 1993).

The proposed hierarchy is a control hierarchy (*sensu* Solbrig 1991a) in that those factors operating at higher spatial and temporal scales control those factors operating at lower scales. But the model is not rigidly hierarchical, because factors

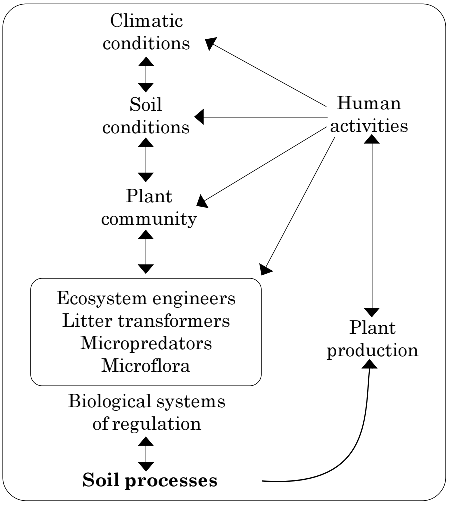

Figure 1. Hierarchical model of the principal determinants of soil processes (adapted from Lavelle et al. 1993).

that influence a large variety of processes may operate at different scales at which the relative importance of the determining factors may vary (Lavelle 1996).

Functional Classification of Soil Fauna

The functions that soil invertebrates carry out depend largely on the efficiency of their digestive systems (which themselves depend on their interactions with soil microflora) and on the occurrence and abundance of the biological structures that they produce in the soil (Lavelle 1996, 1997). Using these two criteria, we can distinguish three large functional groups of invertebrates (Figure 2).

Micropredators

This group contains the smallest invertebrates, protozoa, and nematodes. They do not produce organo-mineral structures (Lavelle 1996, 1997), and their principal effect is to stimulate the mineralization of soil organic matter (Coûteaux et al. 1991; Ingham et al. 1985).

Litter transformers

Mesofauna and some macrofauna are involved in litter decomposition (Lavelle 1996). When these invertebrates re-ingest their excretions, which serve as incubators for microflora, they assimilate metabolites liberated by microbial actions.

Ecosystem engineers

The “ecological engineers” or “ecosystem engineers” (*sensu* Jones et al. 1994) are those organisms that produce physical structures through which they can modify the availability or accessibility of a resource for other organisms. Their activities and production of biogenic structures can

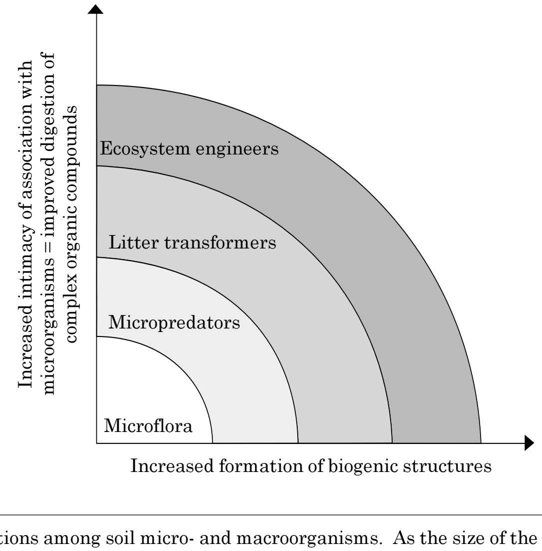

Figure 2. Interactions among soil micro- and macroorganisms. As the size of the organism group increases, its relationships with microflora gradually shift from predation to external and internal mutualism, and they produce biogenic structures of increasing strengths (Lavelle 1997).

modify the abundance or structure of their communities (Jones et al. 1994, 1997).

Of the innumerable life forms that inhabit soils, only a small number of macroinvertebrates (earthworms, termites, and ants) are distinguished by their capacity to excavate soil and produce a wide variety of organo-mineral structures, such as excretions, nests, mounds, macropores, galleries, and caverns. These organisms have been described as "ecological engineers" of the soil and their structures as "biogenic structures" (Anderson 1995; Lavelle 1996, 1997). The functional role of these structures is thought to be important and to represent sites where certain pedological processes occur such as the stimulation of microbial activity, the formation of soil structure, the dynamics of soil organic matter, and the exchange of water and gases (Anderson 1995; Beare and Lavelle 1998; Lavelle 1996).

The classical study of the biology of each species of a community has given way to the study of biogenic structures produced by the ecosystem engineers. In effect, this latest concept, and the functional domains associated with the engineers' activities, has been useful for explaining the functional role of biodiversity and its effects on the soil (Jones et al. 1994; Lavelle 2000; Lavelle et al. 1997). It has also facilitated an understanding of the indirect effects linked to the biogenic structures that can exist between soil macroinvertebrates and other smaller organisms.

Functional domains are specific sites in the soil, and are influenced by either a biotic (e.g., an ecosystem engineer or plant root) or abiotic (e.g., alternative periods of dryness or wetness, hot or cold temperatures) regulator. These sites are characterized by an organic resource (litter or other organic matter) and the biotic regulator creates a series of structures, such as fecal pellets, galleries, and fissures, which are then occupied by small invertebrates and microorganisms. A biological community is ultimately dependent on such small organisms (Lavelle 2000).

A domain can be physically identified in the soil and each structure present in the soil forms part of that functional domain. Sometimes, the limits of a domain are sufficiently diffuse to make its identification from adjacent or surrounding functional domains difficult.

In invertebrate communities, species exist that, owing to their intense mechanical actions and effective relationships with microflora, determine the abundance and activities of organisms that do not possess these abilities. For example, macro- and microarthropods, enchytraeids, and litter transformers depend on the activities of a principal regulator. Such organisms, essentially earthworms, termites, and ants, create the functional domains in the soil, that is, the drilosphere, termitosphere, and mirmecosphere. Other functional domains exist such as the rhizosphere (roots' area of influence) (Hiltner 1904) and the detritusphere (area of influence of arthropod litter transformers) (Beare et al. 1994).

Although not all soil groups have been studied in detail, whatever change produced in the populations of ecosystem engineers will obviously have direct consequences on the diversity and activities of subordinate groups. For example, the activities of earthworms determine the abundance and activities of macroarthropods (Loranger et al. 1998) and nematodes (Boyer 1998).

The Example of Earthworms and their Biogenic Structures

Earthworms are the most abundant group of soil macrofauna in terms of biomass (Lee 1985). They intervene directly or indirectly in the diverse physical, chemical, and biological processes of the soil (Anderson 1988; Lavelle 1988). Through their functional domains, earthworms and macroinvertebrates generally intervene in the regulation of important soil functions.

Soil physical properties

Earthworms selectively ingest organic and mineral material, producing structures that directly influence the soil's physical properties (Figure 3), such as increasing porosity and aeration; improving hydraulic conductivity; and improving structural stability, including the formation of macro- and microaggregates (Aina 1984; Casenave and Valentin 1988; Lavelle 1997; Lee 1985; Urbanek and Dolezal 1992).

Earthworms also influence soil structure to produce large quantities of organo-mineral aggregates in their casts and in the walls of their galleries. These are unstable when fresh but, as they dry out, become more stable than similarly sized aggregates in bulk soil (Blanchart et al. 1993; Marinissen 1990, 1994; Shipitalo and Protz 1989). Moreover, the casts' size largely determines the effects on soil structure. In the savannas of Côte d'Ivoire (West Africa), two types of casts, produced by different groups of earthworms, are identified as either "compacting" (large compact casts) or "decompacting" (small casts) species (Blanchart et al. 1997), and are thus responsible for forming and maintaining the soil structure (Blanchart 1998; Blanchart et al. 1999; Rossi 1998).

Dynamics of soil organic matter

Earthworms digest organic matter through enzymes that they themselves produce and through the mutualistic microflora found in their digestive

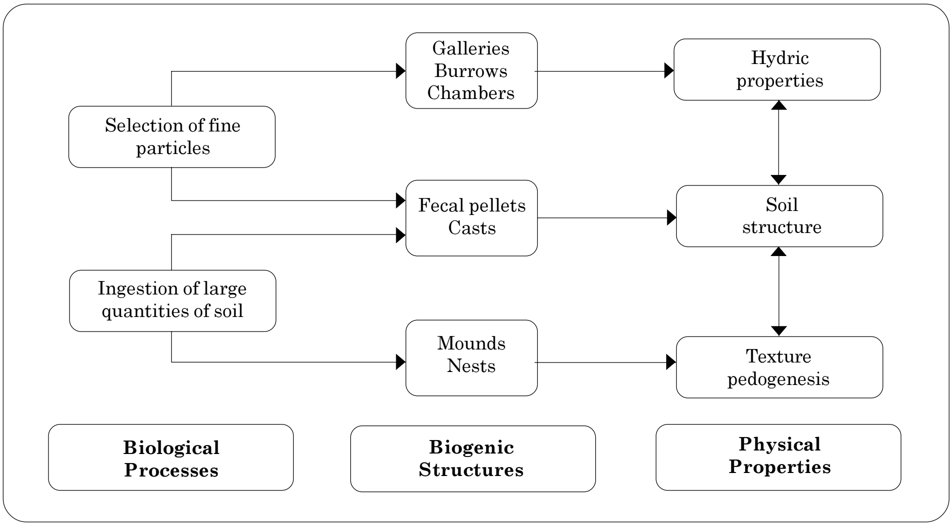

Figure 3. Effects of ecosystem engineers on soil physical properties (Lavelle 1997).

tracts. The effects of earthworms on the dynamics of organic matter depend on the spatial and temporal scales considered (Figure 4).

For the short term (i.e., in hours), digestion breaks down organic residues and frees certain nutrients such as nitrogen and phosphorus that plants can assimilate (Barois et al. 1987; Lavelle et al. 1992; Sharpley and Syers 1976). The dynamics of organic matter are altered in biogenic structures over the medium term (days to months). Over a longer term, the rates of mineralization decrease until immobilization occurs (Martin 1991). What the global effects are over years or decades is not known, because of a lack of long-term experiments (Lavelle 1997).

Plant growth

The combined effect of earthworms on (1) soil structure, (2) organic matter dynamics, and (3) nutrient release is, usually, to stimulate plant growth. Most studies have shown that this effect is positive (Curry and Boyle 1987; Derouard et al. 1997; Gilot-Villenave et al. 1996; Hoogerkamp 1987; Hoogerkamp et al. 1983; Pashanasi et al. 1992; Rose and Wood 1980; Stephens et al. 1994; Stockdill 1982), even though not all plants respond equally and the response is proportional to the earthworms' biomass. Response is termed "significant" when the fresh earthworm biomass per square meter is more than 30 g (Brown et al. 1999).

Key role of biogenic structures

Jones et al. (1994, 1997) have demonstrated that the quantity, nature, and function of the biogenic structures produced by earthworms and other ecosystem engineers are highly important.

The structures' abundance and diversity are, without doubt, important for maintaining the ecosystem's soil functions (Lavelle 1996). A clear example is the complementary effects of the previously described "compacting" and "decompacting" earthworms (Blanchart et al. 1997). In soils that have been drastically altered, where only one "compacting" species exist, the casts result in soil compaction, reduced rates of water infiltration, and reduced plant growth (Barros et al. 1998; Blanchart et al. 1999; Chauvel et al. 1999; Rose and Wood 1980).

The production of certain structures also affects the diversity and abundance of communities of less mobile organisms (hypothesis of nested biodiversities, Lavelle 1996). Earthworm activities have been amply shown to regulate microbial activity (Barois and Lavelle 1986; Daniel and Anderson 1992; Scheu 1987; Trigo and

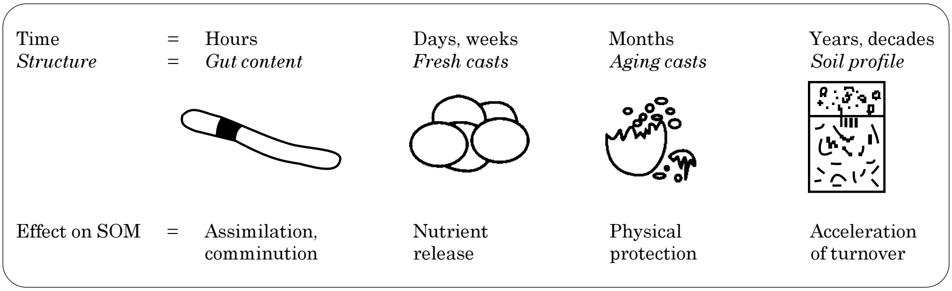

Figure 4. Effects of earthworms on soil organic matter (SOM) at different spatial and temporal scales (Lavelle 1997).

Lavelle 1993). That earthworm biogenic structures also affect the activities of micro- and mesofauna has been demonstrated in various studies (synthesized by Brown 1995).

Neotropical Savannas

The neotropical savannas cover about 275 million hectares, and include those in Brazil (250 million), Colombia (17 million), Venezuela (10 million), Guyana, Suriname, French Guyana, and Paraguay, representing about 45% of the total surface of the South American continent (Cole 1986). They are located wherever the climate is characterized by high temperatures and marked dry periods, that is, mostly between equatorial forests and mid-latitude deserts. Savanna vegetation consists of a herbaceous stratum, with or without trees, or with shrubs of variable density and height. That savannas should occur in this climatic zone, where the dominant vegetation should be tropical forest, is a result of marked dry seasons, differences in soils, and frequent occurrence of fires (Blydenstein 1967; Cochrane 1978).

The length and severity of a dry period are variable according to savanna type, but all savannas have in common the presence of plant species with some structural and functional adaptive strategies that confer tolerance of dry periods that can be between 3 and 8 months long. These plants can usually extract water from deep in the soil profile and also avoid water stress by dropping leaves (estivation), thus surviving the dry periods (Cole 1986). Savannas therefore comprise a dynamic ecosystem, showing periodic rhythms with periods of growth and productivity.

The Colombian Savannas

The Colombian “Llanos” (Colombian Eastern Plains) occupy about 19% of the national territory (16.9 million hectares). About 80% of the Plains are covered by herbaceous vegetation (grasses), which supports an extensive cattle-grazing industry (Vera and Seré 1985), even though the native vegetation is of poor nutritional value (Alvarez and Lascano 1987).

Although fire is thought to be a major determinant in the savannas’ physiogeography by maintaining them as open structures, the savannas’ distribution suggests that they do not derive from forests as a result of burning.

The Colombian savannas can be distinguished into five physiogeographic units: the Andean piedmont, alluvial terraces, high plains, dissected plains (or “serranía”), and inundated (or flooded) savannas (Botero 1989; Kleinheisterkamp and Häbich 1985). Differences of relief and degree of flooding determine vegetation composition (Cole 1986).

Soils

Soils in the Colombian Eastern Plains can be divided into two large groups: Oxisols and Ultisols (USDA classification, 1975). The Oxisols occupy about 75% of the area (Rippstein et al. 1996). The presence of a lateritic crust in the subsoil, which is sometimes exposed at the surface through erosion, is a significant characteristic of the Plains. This crust is formed from iron and aluminum oxides, and largely determines the savannas’ physiognomy. Few trees are able to penetrate the lateritic layer, and the vegetation becomes dominated by herbaceous plants (Cole 1986).

Those trees that do succeed in growing in the savannas develop extensive but superficial root systems as, for example, *Curatella americana* (Dilleniaceae), *Byrsonima crassifolia* (Malpighiaceae), and *Bowdichia virgiloides* (Leguminosae).

The "morichal" palms of the genus *Mauritia* (*M. minor* and *M. flexuosa*) are also found in the savannas, around swamp edges and other low-lying areas.

Management

The Colombian Eastern Plains are used for extensive grazing, but rates of animal productivity and reproduction are low, with productivity rates ranging between 15 and 30 kg animal liveweight gain per hectare per year (Kleinheisterkamp and Häbich 1985; Lascano 1991; Paladines 1975; Rippstein et al. 1996; Vera and Seré 1985; Vera et al. 1989). These rates are associated with low stocking rates of 0.2 to 0.3 animals/ha (Guzmán and Vera 1991).

Animal production is limited principally by the low nutritional quality of native savanna grasses, which, moreover, are productive only during the initial part of the rainy season (Rippstein et al. 1996). Farmers rarely use supplementary minerals. As the native pasture grows, the nutritional value decreases and animals begin showing symptoms of deficiency. Burning is a common practice for getting rid of excess vegetation and stimulating the re-growth of new and more nutritious plant material (Rippstein et al. 1996). Such management helps determine the structure of savanna vegetation communities.

During the last 20 years, the amount of land used for the more intensive production of food has significantly increased. These include systems of improved pastures based on introduced grasses from Africa, principally *Brachiaria* and *Panicum* species, with or without the forage legumes of the *Stylosanthes*, *Arachis*, and *Pueraria* genera. Other systems include annual cropping, mainly of upland rice and soybean, with inputs of fertilizers and lime. These systems have resulted in a rapid increase in agricultural production but the long-term sustainability of these systems is limited.

A major limitation of these production systems is the small number of cultivars adapted to acid-soil conditions. For monocropping, the agricultural practices used can result in deteriorated soil physical properties and increased incidence of pests, diseases, and weeds. Pastures based on introduced grasses and legumes can improve soil properties but require relatively small amounts of fertilizers that can be costly for most farmers. The lack of legume persistence over the long term is another limitation (Friesen et al. 1996; Thomas et al. 1995).

Before the research reported here was conducted, no studies had been carried out on the effects of land use changes in the Eastern Plains on populations of soil macrofauna or other soil biota.

The Meaning of "Intervention"

Studies done in the savannas arose partly from the excessive pressure exerted on tropical forests, which comprise not only significant reserves of biodiversity but also play a key role in the carbon cycle and control of greenhouse gases. Interventions in the savannas are thought to help halt or decrease the rate of exploitation of tropical forests. The substitution of native savanna with introduced grasses from Africa is widely accepted in the Colombian Eastern Plains and Brazilian savannas ("Cerrados"). However, we know little about the biological processes involved, nor do we know how these changes can alter fundamental ecosystem processes and services such as water quality and quantity. Moreover, studies of the Brazilian "Cerrados" have shown that the biodiversity of the neotropical savannas is, in fact, more threatened than is that of the Amazon forests (Smith et al. 1998).

The study of diversity, and of ecological processes associated with diversity patterns and ecosystem functioning, constitutes the basis for understanding and managing natural and intervened ecosystems (Giller 1996). In general, soil fauna communities are sensitive to those climatic and edaphic factors that determine food resource availability and microclimatic conditions. Thus, disturbance of natural ecosystems will alter macroinvertebrate communities found in the soil.

Soil fauna can be considered as a natural resource with potential for the sustainable management of agricultural systems. To achieve this objective, we need to (1) gain a better and more precise knowledge of the life cycles of different species that make up a soil biotic community, and (2) evaluate the effects produced by "engineer" species on a soil's physical, chemical, and biological properties at different spatial and temporal scales. With this knowledge, we can develop guidelines for managing macrofauna activities in soils of different agroecosystems.

We chose to evaluate the role of earthworms, because the communities of these representatives of savanna soil macrofauna are well known to suffer drastic modifications, or even destruction, from agricultural practices. Lavelle et al. (1989), Stork and Eggleton (1992), and Swift (1984) have documented the beneficial aspects of earthworm biological activities in different agroecosystems, showing that their effects depend on the functional structure or ecological composition of their communities (Lavelle 1988). While an individual earthworm or population of earthworms can show some degree of resistance or resilience to disturbance, at the community level (different populations of different species), the diversity of species and functional structure can change with different effects on the ecosystem. This ability to respond could comprise a means by which to manipulate these communities to the farmer's benefit (Lavelle et al. 1994), although it should be remembered that, in some cases, earthworms, together with land use mismanagement, can provoke soil degradation (Chauvel et al. 1999).

The Book's Organization

The work reported in this volume is organized into three parts, finishing with a synthesis:

Part I. The impact of agroecosystems on soil macroinvertebrate communities

Before we can develop guidelines for managing macrofauna, we need to develop detailed knowledge of that fauna's composition. Thus, this section is an inventory of soil faunal communities under different land management practices.

Part II. Life history and biology of earthworms

Chapters in this section focus on the ecology and biology of earthworms, the major representatives of soil macroinvertebrates. Details of the ecology of these important organisms represent a unique and rare source of information for tropical agroecosystems.

Parts III-VI. Effects of ecological engineers on soil processes at different scales of observation

The effects of major ecological engineers (earthworms) on the physical, chemical, and biological processes, from the scale of the biogenic structures produced to the scale of the plot, are presented in this section.

Synthesis and perspectives

Finally, in a concluding chapter, we synthesize the main findings and relate them to possibilities for managing soil macrofauna for higher plant production and improved ecosystem health.

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