

Mutualistic biodiversity networks:

the relationship between soil biodiversity and mutualism, and their importance to ecosystem function and structural organisation.

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[A glossary is included, on page 9]

The debate over whether or not biodiversity *per se* directly benefits ecosystem function has not been completely resolved. However, sufficient validating evidence exists to warrant wider consideration of the relationship. If confirmed, we will want to understand its nature and origin. Conclusive evidence, assuming it arrives, should not be born into a vacuum of forethought. This review paper endeavours to reveal some understanding of the relationship, to these ends.

Emphasis is made on the kinship between biodiversity and mutualistic associations, as the framework for a functional ecosystem. As shall be seen, species are inextricably linked, forming networked systems. They benefit from innumerable complementary interactions within networks that encompass the species, trophic, guild, ecosystem, biome and biosphere scales.

The factors that initiate and maintain these networks are examined, as are those that can activate system collapse. Man's influence in destabilising ecological systems is put in context, and it is demonstrated how natural structures can be used as a model for man-made systems.

Soil biodiversity

Current knowledge and understanding of subterranean ecosystems is poor, relative to those above-ground. Yet, the species richness, or biological diversity (biodiversity), of the former is staggering. There may be several thousand bacterial species in a single gram of soil (Torsvik *et al.*, 1994). Among soil fauna, 100 000 protozoan species, 500 000 nematode species (Hawksworth and Mound, 1991) and 3000 earthworm species (Lee, 1985) are estimated to exist.

The importance of individual soil species and functional groups to ecosystem function

Contribution by individual species and functional groups to the soil ecosystem is multi-faceted and all-important. The activities of one group will benefit others as, for example, essential nutrients and substrates are supplied and cycled, ultimately back to the primary producers. The examination of these contributions is essential background to considering how biodiversity relates to ecosystem function.

The soil is the domain of the decomposers. Dead organic matter on the soil surface is digested and decomposed by soil microfauna and micro-organisms, liberating simple nutrients that enable plant growth. Physical soil structure is sculpted by biota. For example, burrowing animals aerate the soil, provide channels for roots to follow and turn over material between different soil layers. Lumbricidae earthworms build gallery networks of up to 8900 km ha⁻¹, with an internal surface of up to 12 ha ha⁻¹ (Kretschmar, 1982 in Lavelle *et al.*, 1995). Blended mineral and organic matter creates soil crumbs and pores that provide aeration, drainage and microhabitats for many animals and feeding grounds for others.

Different soil species, often assigned to separate functional groups, contribute variedly to nutrient cycling. For example, lumbricid worms ingest decaying organic matter and mineral soil, thus playing a major part in the decomposition and mineralisation process, preventing accumulation of organic debris on the soil surface. For example, these earthworms contribute up to one-fifth (150 kg ha⁻¹ yr⁻¹) of annual nitrogen mineralisation in pasture (Slack, 1982). Herbage ingestion and worm cast production increases short-term phosphorous availability two- to three-fold (Slack, 1982).

Field studies have suggested that only 6-7% of ingested food can be utilised by millipedes, and other mandibulate arthropods (Wallwork, 1970). Their main decomposition activity, therefore, is mechanical break-up of detritus and production of excreta that is a suitable substrate for other decomposers to work on.

Fungi are vital decomposers, since they degrade and recycle large, resistant molecules, e.g. cellulose and lignin, that worms, microarthropods and others cannot.

Free-living, nitrogen-fixing bacteria mineralise atmospheric nitrogen, thus replenishing soil stocks lost in biotic de-nitrification processes, leaching and run-off.

Organic matter ultimately decomposes to inorganic molecules. These dissolve in soil water and are drawn up by plant roots, returning to above-ground ecosystems.

Clearly, some degree of biodiversity amongst soil species is necessary to maintain this functional diversity. However, the quantity and structural nature of that diversity is by no means obvious.

Biodiversity in ecological models

There are three basic, hypothetical models that describe the relationship between biodiversity and ecosystem structure:

Redundancy

This model suggests that biodiversity *per se* is unimportant: given sufficient biomass, ecosystem function requires just one representative species from each functional group (Lawton and Brown, 1994). Functional redundancy has been concluded from observation that functional diversity, though large, is greatly exceeded by species diversity (di Castri and Younes, 1990). Thus, rate changes of biotic processes are inferred not to reflect biodiversity loss (Franklin, 1993).

Keystone

From each functional group, certain ("keystone") species are considered essential to ecosystem function, others being redundant (Bond, 1994). Evidence includes observation of community change and local extinction driven by environmental changes, or changes of particular species' abundance, with cascading effects on other ecosystem members (Shaffer, 1981).

Rivet

This suggests that all species are interdependent "rivets" in ecosystem structure and each contributes to function (Ehrlich and Ehrlich, 1981). Greater diversity equates to increased linkage and stability.

The backup system: a temporally linked structure

"Nature does nothing uselessly." - Aristotle

All species potentially maintain ecosystem function synergistically, though not synchronously, throughout environmental variation. In other words, temporal ecosystem stability arises from biodiverse, duplicative function.

Keystone species, whose value stems from functional dominance in environmentally (or experimentally) favourable conditions, cannot boast enduring indispensability. Since functionally similar species have various and often narrow (Postgate, 1982) environmental tolerances, physiological requirements and microhabitat preferences (Perry *et al.*, 1987; Pirozynski, 1981), i.e. niches, environmental change will depose dominant species. For example, earthworms' intolerance of pH change implements functional replacement (Bardgett, personal communication).

When keystone species become redundant, former "redundants" secure ecosystem function. Environmental deviation would be catastrophic without this backup system, one broken link provoking system collapse (Perry *et al.*, 1989). This is analogous to a car's spare tyre: it is only redundant until a tyre bursts; on a particularly remote road it could become a lifesaver.

Biotic interactions

Biodiversity as a backup system will help sustain ecosystems in the face of change. However, if biodiversity only functioned as a backup, it could surely not be profitable and preserved under constant environmental conditions, awaiting service when changes occur. Studies suggest that biodiversity does indeed improve short-term ecosystem properties, e.g. primary productivity and nitrogen acquisition (Tilman *et al.*, 1996) and is maintained by an integrated system of positive feedback interactions between biotic “rivets” (Perry *et al.*, 1989). Greater complexity of biotic interaction increases probability that indirect effects will be important to regulating ecosystem function (Price, 1988), denying the redundancy and keystone (Mills *et al.*, 1993) hypotheses and implicating the rivet hypothesis.

Negative, e.g. competitive and predatory, interactions have been extensively investigated, largely for their role in nutrient cycling (Coleman *et al.*, 1983; De Ruiter, 1993; Santos *et al.*, 1981). Some studies (Hall *et al.*, 1970; Janzen, 1970; Paine, 1966) have found that competitive exclusion reduces biodiversity when a population from the next higher trophic level is removed.

Positive, e.g. mutualistic and associative, interactions have had a shorter investigative history, though they encourage greater ecosystem stability and resilience (Perry *et al.*, 1989; Lavelle *et al.* 1995) and have potentially wider implications, as will be discussed.

Biotic interactions are commonplace, yet individually unique and potentially, functionally advantageous. So redundancy, while possible in a single function, is unlikely for a species’ entire functional range (Beare, *et al.*, 1995). Hence, reductionist studies that extrapolate redundancy in one or two functions to judge the whole range are quite misleading. Moreover, to suggest functional redundancy is to assume knowledge of all functional species-ecosystem interactions, which is a groundless assumption. The number of subtle interactions required to maintain a healthy ecosystem could be truly vast. Hence, perhaps the assertion that only one species is required from each functional group is only misleading, not wrong.

A group effort: positive biotic interactions contribute to ecosystem function

Though individual species and functional groups contribute greatly to ecosystem function, contribution is often a combined effort, with direct inter-specific interactions. Understanding of these will elucidate the vital relationship between mutualism, biodiversity and ecosystem function.

Increasingly complex interaction is well illustrated in anisymbiotic (mutualism between organisms of contrasted sizes) digestive systems:

Microbial growth is enhanced on partially digested (comminuted, fractionated and humidified) organic matter in invertebrate excreta. Most epigeic arthropods and some annelids periodically reingest faeces, taking advantage of assimilable compounds derived from microbial action (Swift *et al.*, 1979). Such invertebrates are said to have an external rumen (Lavelle, 1996).

Favourable conditions in invertebrate guts are provided for non-specific microflora ingested with soil or litter material. The invertebrate may then exploit assimilable metabolites released by enhanced microbial activity. Ingested soil is homogenised by mixing with water and intestinal mucus in *Pontoscolex corethrurus*, a pantropical, endogeic, geophagous earthworm (Barois and Lavelle, 1986). Mucus increases bacterial activity and primes digestion of organic matter. Mixing is critical in this priming effect, since it fragments soil aggregates and exposes organic substrate from its clay skin (Lee, 1978). Digestive products released into the gut are partly reabsorbed by the worm. Such facultative mutualism has also been observed in wood and leaf-litter feeding Diptera and Coleoptera larvae (Campbell, 1929) and termites (Breznak, 1984).

Some invertebrates carry specific gut microflora to digest lignocellulose, e.g. certain flagellated protozoa and bacteria are only found inside phylogenetically “lower” termites. Protozoa degrade lignin anaerobically and release products used by the host (Kirk and Farrell, 1987). Bacteria provide growth factors for protozoa, but termites can survive without the former (Yamin, 1981). Neither termite nor protozoa can independently exist. Such association is obligate mutualism or symbiosis and is considered the most efficient, although facultative mutualism is more flexible (Margulis, 1981).

Lynch and Harper (1985) described a tripartite microbial association on straw: fungal cellulase activity provided simple sugars to nitrogen-fixing bacteria, and polysaccharide-producing bacteria maintained the anaerobic environment necessary for nitrogenase activity.

Plant roots are considered functionally analogous to macroinvertebrates due to their capable locomotion (by growing new tips) and limited ability to independently use non-mineralised nutrients (Lavelle *et al.*, 1995). They embody the most direct link between above- and below-ground ecosystems. Root exudates, containing carbohydrates and proteins, stimulate micro-organisms and thus support microbivorous nematodes. Plants contain more nitrogen when grown in the presence of the latter (Ingham *et al.*, 1985), as nematodes excrete up to 90% of ingested nitrogen.

Tripartite associations of the nitrogen-fixer *Frankia*, the vesicular-arbuscular mycorrhizal (VAM) fungus *Glomus* and *Alnus* trees stimulate nitrogen-fixation and enhance productivity and phosphorus content of host plants in soils of low fertility (Jha *et al.*, 1993). Other plant, symbiotic VAM and rhizobia interactions (Allen, 1992) are more widespread. In many cases, one or more of the mutualists have a restricted or obligate relationship with the plant, making these relationships especially sensitive to species loss (Janos, 1980) and emphasising the importance of biodiversity to ecosystem function (Molina *et al.*, 1992).

Mycorrhizae are symbiotic with roughly 90% of plant species (Perry *et al.*, 1989). Large amounts of photosynthate are either diverted to mycorrhizae or exuded into the surrounding rhizosphere or mycorrhizosphere. Roots and mycorrhizal fungi may account for over 80% of net primary production in Pacific silver fir (Vogt *et al.*, 1982) and Douglas-fir (Fogel and Hunt, 1983) ecosystems. Up to 40% of photosynthate fixed by cereals passes from roots into the rhizosphere (Whipps and Lynch, 1986). Such photosynthate input supports a diverse soil community. Rhizospheric community structure is shaped by mycorrhizal fungi, through influences on the character of root exudates (Meyer and Linderman, 1986). In turn, numerous rhizosphere processes contribute significantly to the health of both individual plants and the ecosystem as a whole (Bowen, 1980; Coleman, 1985; Janos, 1980; Linderman, 1986; St John and Coleman, 1982).

As can be seen, species that perform essential soil processes often depend upon others. This aspect is often disregarded when assigning “keystone” species. One begins to realise a picture of the system where abundant biotic activity, far from functional irrelevancy, has very real significance. This variety of co-operative interaction requires considerable biodiversity. However, such biodiversity transcends simple maintenance of the independent functional groups that limit the redundancy and keystone hypotheses.

Mutualism: the bolt between the rivets

Biodiversity provides scattered species that mutualism binds together. One nourishes the other and neither can independently exist. Combined, they create the basis for an efficient ecosystem.

Efficiency stems from the resource base shared between mutualists. There is closer integration, hence efficiency, of metabolic systems (e.g. Margulis, 1981), i.e. proximity to and provision of otherwise elusive essential nutrients or factors, and supply of otherwise unexploitable or unobtainable resources. This encourages efficiency of ecosystem nutrient cycling. Partners become better nourished and need not expend so much energy, e.g. foraging, sustaining high root density, or maintaining immune systems, i.e. they become individually more efficient. They will, therefore, be naturally selected in the ecosystem (along with the mutualistic trait), and may potentially exploit lower quality resources, though preserve vitality. Functional diversity will develop to realise this potential (Lavelle *et al.*, 1995), again enhancing efficiency of ecosystem nutrient cycling. The most successful (dominant) functional analogue will stimulate niche separation (due to competitive exclusion) and consequently biodiversity. Further mutualism occurs because greater biodiversity increases the likelihood of compatible associations, which are fostered due to improved efficiency. In this way, biodiversity and mutualism are bred hand in hand over time until limited by environmental conditions, when an equilibrium state is reached.

Increased efficiency of a mutualistic association, stimulating

resource extension and functional diversity, has been empirically observed in field studies. Lavelle (1983) found increased ability amongst earthworms to exploit lower quality resources (from litter, through soil-litter mixtures, to soil organic matter at increasingly lower concentrations) along a thermo-lattitudinal gradient from cooler to hotter climates. Greater metabolic efficiency was achieved by higher activity of intestinal micro-organisms at tropical temperatures (Barois, 1987), reducing production of activity-inducing mucus and ingestion of high quality resources (Trigo *et al.*, 1992). Along the gradient, functional diversity was observed to increase with the expanding resource base (Lavelle, 1983). Biodiversity reflects this trend: the British Isles have 28 earthworm species, most of which are found throughout northern Europe, while India has 365 species and 38 of the 58 genera are endemic.

Mutualistic associations are exchanged benefits and fortified weaknesses of species' adaptive strategies. When soil micro-organisms and invertebrates co-operate, their distinct strategies complement one another: Micro-organisms have very limited locomotion, affecting proximity to resources and required microhabitat conditions, but capably digest most organic substrates. White-rot fungi, for example, quickly degrade complex molecules. Others operate less rapidly, unless enhanced by passage through an earthworm or termite gut (Toutain, 1987). Invertebrates have competent locomotion, favourably alter physical environments, e.g. through burrowing and cast-production, and render organic matter more favourable to subsequent feeders, e.g. through mechanical activity or partial digestion. However, the vast majority cannot produce enzymes to directly digest the cellulose, lignin, tannin and humic complexes that comprise most soil resources. Similarly, roots are rarely able to assimilate more than dissolved mineral nutrients. Indeed, the average nutritive value of available soil resources is relatively poor (Lavelle, 1996): they have high carbon: nutrient ratios, largely comprise high molecular weight carbohydrates, e.g. lignocellulose (Swift *et al.*, 1979) and tannin-protein complexes sequester nitrogen (Toutain, 1987). Strategic co-operation subsidises partners' limitations through shared talents, e.g. invertebrates physically process organic matter, which is assimilated, following microbial chemical degradation.

Lavelle (1986) hypothesised that, like earthworms in the drilosphere, increased efficiency of mutualistic associations with rhizospheric microflora would provide roots access to an enlarged resource base, promoting functional- and bio-diversity. Indeed, drilosphere and rhizosphere systems are functional analogues (Lavelle, 1986). Root exudates promote microbial activity (Bowen and Rovira, 1991) and consequent mineralisation of local nutrients and are, therefore, functional equivalents of earthworm intestinal mucus (Barois and Lavelle, 1986). As Janzen (1985) put it, "plants wear their guts on the outside."

Beyond the soil

Mutualism disseminates into increasingly complex structures. For example, inter-trophic collaboration between species enhances biodiversity, mutualism and ecosystem function in each trophic level. As previously cited, increased biodiversity of rhizospheric microflora (decomposers) will stimulate mutualistic association with plants (producers), and consequent plant diversity. Likewise, plant diversity will stimulate mutualism with, and biodiversity of, consumers. Transmission of biodiversity via mutualism will eventually come full-circle, returning to decomposers. To some degree, the implicated consumers are co-operatively associated with the original soil micro-organisms. Overall system efficiency and coherence will mature, raising the equilibrium state. This is the basis for natural succession from a vulnerable assortment of loosely associated species to a stable and united climax community (Read, 1994).

Stability (maintenance of efficiency) in climax communities results from highly developed, co-ordinated networks of positive feedback connections. Clearly, these surpass the mere nutrient exchanges largely supposed by the redundancy and keystone hypotheses. As May (1973) suggested, "Complex communities contain much more information than can be estimated by counting links in the trophic web." Indeed, though numerous studies (e.g. Tilman *et al.*, 1996) suggest that increased diversity of live plants improves ecosystem properties (i.e. the rivet hypothesis), Wardle *et al.* (1997) found that diversity of dead plant material did not.

Stability: maintaining mutualism and dealing with stress

Positive feedback links between species are the system's strength, but also permit rapid amplification and spread of stress from one part to the whole (Perry *et al.*, 1989) which, if unchecked, could destabilise the framework. It has been hypothesised (McNaughton, 1988; Pimm, 1984) that more diverse systems are more resistant, i.e. more easily tolerate environmental change, and more resilient, i.e. more easily return to their equilibrium position once displaced (McNaughton, 1994). This has been empirically observed in plant communities (Frank and McNaughton, 1991; McNaughton, 1977, 1985; Naeem *et al.* 1995; Tilman, 1996) and applies equally to soils (Wardle and Giller, 1997). Appreciation of the biodiversity-mutualism marriage may elucidate the stabilising mechanisms.

Diverse environmental tolerances allow suited species to support stressed partners, extending their vital environmental range and conferring community stability. Duplicative function (the "backup system") maintains ecosystem integrity by functional replacement of stressed with suited species. This could provide temporary relief from environmental fluctuation or more long-term restructuring.

Despite frequent replacement following environmental alteration, plants retain mycorrhizal partners throughout their lives. Thus, mycorrhizae with various environmental tolerances buffer the plant-soil system by extending the environmental range in which positive net photosynthesis is maintained (Perry *et al.*, 1987). Conversely, several plant species (forming a "guild") may share the same microflora. The most environmentally favoured plants will maintain soil organisms required by others (Borchers and Perry, 1987). This mechanism allows gradual succession in a maturing environment and lessens detrimental consequences of environment change.

A climax community is highly integrated at every resolution and thus exhibits exceptional coherence and stability. Potentially invasive pest and disease organisms have limited success, as they are not themselves backed by the system and confront not only hosts, but all those that support them. Such internal "integrated pest management" will endure as long as the fundamental conditions for the system do not alter too rapidly and drastically for adjustment.

Beyond the biome

Several hierarchies of function, with progressively complex co-operation, have been discussed so far: individual function, species partnerships, guilds, trophic levels and ecosystems. Mutualistic association in each level is a consequence of mutualism throughout all previous ranks. As has been demonstrated, biodiversity and mutualism are potentially self-perpetuating, and spread to encompass and unite successive levels of complexity. They appear to be fundamental characteristics of efficient, biotic organisational structures, independent of observational scale. In this sense, they have fractal quality. It is not unreasonable to assume that these attributes transcend the ecosystem level of resolution, to deeper layers of ecological interconnectivity. Indeed, ecosystems are by no means closed systems. Thus, biomes will functionally depend on the diversity and integration of their ecosystems, and the biosphere on biome diversity and coherence. From this perspective, functional contribution from a single species, or even organism, will ultimately benefit the biosphere.

Lovelock's (1972, 1979) Gaia hypothesis provides a useful model for conceptualising biodiversity and mutualism in their most advanced marriage. It describes the earth as a superorganism comprising biotic feedback processes that homeostatically keep atmosphere, oceans, climate and crust comfortable for existence. Biodiversity at its greatest, and co-operation at its most subtle and pervasive intertwine, nourishing one and all.

Life processes have long maintained a chemically non-equilibrium atmosphere (Margulis and Lovelock, 1974). For example, CO₂ is concentrated up to 40-fold in soil spaces, e.g. by decomposition of dead plants that extract atmospheric CO₂, and buried in oceanic calcium carbonate rock (Lovelock, 1991). This dramatic reduction of atmospheric CO₂, a "greenhouse gas," lowers temperatures and permits the persistence of liquid water and hence oceans. By-products of calcium carbonate production runoff into oceans, where they are utilised in coccolithophore and diatom skeletons and later buried as sediments. Furthermore, biotically concentrated CO₂ chelating agents, inorganic and organic acids weather basalt rock to release nutrients and form soil one

thousand times faster than under abiotic conditions (Schwartzman and Volk, 1989). There is growing evidence that soil formation from bedrock, and ordered distribution of major inorganic soil components, is partly determined by biologically mutualistic systems (Lavelle, 1996). In an impressive review of soil biota and biospheric regulation, van Breemen (1993) concludes that the long-term geochemical cycle and the short-term hydrological cycle, both global suppliers of nutrients to ecosystems, can be seen as consequences of life.

Organisms are observed to function in such a way that they contribute to biospheric function, i.e. co-operate with other biota to render the abiotic Earth more suitable for life. However, conventional neo-Darwinian hypotheses for natural selection may be difficult to apply to the biospheric "ecosystem." Van Breemen (1993) discusses various ideas that suggest how the immediate selective advantage of a species' behaviour could concord with overall functional benefit to the biosphere. Wynne-Edwards (1986; reviewed in Wynne-Edwards, 1991) provides evidence that group selection is slower acting and more powerful than individual natural selection, and more decisive when individual selection threatens group survival. Lovelock (1993) argues that an organism's evolutionary strategy includes capacity for environmental modification, i.e. there is genetic expression beyond phenotype. Lavelle (1996) suggests that the development of mutualism in soils has increased the importance of life as a major regulator of planetary processes.

System collapse

Just as functionally beneficial species are necessary to maintain a healthy ecosystem, functionally beneficial ecosystems and biomes will be necessary to maintain a healthy biosphere. A biodiverse ecosystem comprising positive feedback, mutualistic links will be stable against disturbances that characterise its environment, but perhaps quite vulnerable to foreign disturbances or disturbance patterns. There are countless documented cases of ecosystem collapse and transformation, often initiated by man's activities. The implications of these for the biosphere are concerning, to say the least.

There is a threshold of environmental change that can overcome the damping effect of biodiversity-mutualism, with an associated breakpoint of ecosystem function to a new equilibrium level (May, 1977). Change may come in a variety of forms, e.g. flooding, drought, temperature extreme, but damage limitation mechanisms may operate. For example, after extensive, stand-destroying wildfires in Oregon, partially decayed logs averaged 150% moisture content ([wet weight - dry weight]/ dry weight) and contained living mycorrhizae and fungal hyphae, which could seed ecosystem re-establishment (Amaranthus, Parrish and Perry; in Perry et al, 1987). Such logs are sometimes water reservoirs for roots and hyphae, during drought periods (Harvey *et al.*, 1983). For these ecosystems, re-establishment of climax conditions would take considerable time. Meanwhile, their significantly lower equilibrium state would yield very low efficiency and stability.

An example of human disturbance is industrial pollution, which reduces mycorrhiza formation (Kowalski, 1987). Positive feedback occurs in polluted forests, where weakened trees support fewer mycorrhizal mutualists, leading to increased susceptibility of trees to pests and pathogens (Meyer, 1985; in Perry *et al.*, 1989). In a destabilised ecosystem such as this, many plant-soil links will be broken or weakened and opportunistic invaders may be competitively advantaged, e.g. due to independence from mycorrhizae. In the absence of coherent strength (efficiency) or defence (stability), the ecosystem may become dominated by the invader, breaking weakened links and shifting vegetation. Probably unlike the ecosystem it replaced, the new vegetation would not have an established history of biodiverse, interconnected and efficient mutualism that benefits the biosphere. In some small way, its diminished equilibrium will undermine the whole.

Plundering the biosphere: agriculture and deforestation

"...by far the greatest damage we do to the Earth, and thus by far the greatest threat to our own survival, comes from agriculture...As polluters, we alter the atmosphere, waters, and soils...and so increase the stress to which the natural ecosystems are subject. But as farmers we do still greater harm, by clearing the land and so reducing the capacity of the whole system to deal with stress." James Lovelock, 1991

By the year 2000, approximately 65% of the world's forests will have been stripped and replaced by agricultural systems (Lovelock, 1991). When biodiverse, integrated forestry ecosystems are replaced by food crops and cattle farms, the land's ability to regulate its own climate and chemistry is greatly diminished. The Earth's rainforest biomes evapotranspire immense volumes of water vapour and thus may be viewed as the planet's air-conditioning system. Analogous to the seeming redundancy observed in ecosystems, a proportion of this system may be lost without noticeable damage, but extra provision is made for a time of need. Changing global weather patterns in recent years may be testament to the notion that that time could be soon. Again analogous to the ecosystem, positive feedback connections ensure that structural collapse will occur before total loss of diverse resources. 35% is quite a small proportion to be dependent on, and that figure assumes no further destruction. It cannot be known what would survive such a crash.

With respect to function of ecosystems and greater hierarchies, forest seems to be the most "profitable" land use. Forest ecosystems generally possess greater efficiency, mutualism and biodiversity (Slack, 1982) than other terrestrial systems. When cleared and replaced by sown pasture, the nature of plant litter reaching the soil changes significantly. For example, forest floor litter accumulates, and effectively shelters fauna from extremes of temperature and moisture. However, most surface litter is removed from grasslands by grazing. Hence, returned organic matter comes largely from dead roots and cannot support as diverse a community, though overall numbers and activity may be greater (Slack, 1982). Intensively managed grasslands follow fast cycles dominated by bacteria and labile substrates, while organically fertilised grasslands follow a slow cycle dominated by fungi and more resistant substrates (Coleman *et al.*, 1983). Bardgett and Cook (1997) found the latter to be more likely related to increased complexity during succession, implicating soil resource accumulation, and hence increased ecosystem efficiency and stability. They consequently suggested that low input (or indeed, organic) grassland farming systems are optimal for raising soil biodiversity and hence self-regulation of ecosystem function. If it is necessary for man to convert forest ecosystems for his own purposes, then actively seeking ways to increase ecosystem biodiversity and self-sustenance is essential.

Biodiversity and self-sustenance are two qualities that could never be applied to intensive, monoculture crop systems. The philosophy behind them is often to draw as much yield, as quickly as possible from an inert soil, while providing all the artificial, inorganic "requirements" (Wild, 1993). However, the assumptions are wrong and the intentions are misguided at best. As previously outlined, though inorganic nutrients are clearly ecosystem features, they are by no means solitary. A fundamental characteristic of healthy life systems has been identified as an interactive framework of co-operative associations, that plainly cannot be substituted by mere chemicals. The problems of practicing such agriculture are manifold (Greaves, 1996). With respect to biodiversity, mutualism and ecosystem function, the methods used (and the chemicals they implicate) will eliminate most non-crop species, virtually destroying all positive feedback interactions that would benefit parallel and wider ecological structures. However, the non-sustainable nature of the system ensures that resources will be detrimentally removed from those structures, hastening further decline. The same problems apply to monoculture tree plantations (Rosoman, 1994) and especially to exotic crops, which are unlikely to connect as many local, positive feedback links (Hammond, 1991), and so will instigate a lower equilibrium system.

Towards integrated agriculture

*“Stretch a bow to the very full,
And you will wish that you had stopped in time.”*

Tao Te Ching.

If agriculture is to remain a long-term feature of systems within the biosphere, it must be made to co-operate with and mimic the structure of the remaining systems. It must therefore be sustainable and maintain a high degree of biodiversity, efficiency and mutualistic associations. It must aim for the coherence of climax successional communities. Though these goals have not been fully realised, an agricultural concept that strives for them has been gaining popularity in recent years. “Permaculture” (permanent agriculture) is a complementary fusion between ancient cultural practices and modern, alternative techniques, broadly aimed at total, integrative production (e.g. Mollison, 1988; Fern, 1997). Rather than “managing” the system, the farmer seeks to initiate a structure that matures and self-regulates. Species (including animals) are not separated, as with traditional systems, but mixed for optimum complementation. Maximal energy output for minimal input is sought. The methodology of system design is to constantly consider wastage in the system, e.g. surplus water, plant fibre, human or animal waste, and then locate points at which they can be integrated and woven back into the structure. Hence, resources and energy are tightly cycled, minimising structural leakage. As design skills, experience, knowledge and understanding in this area grow, efficiency should improve. However, it could never be a high-profit scheme for capital gain, as with intensive agriculture. Therefore, perceived lack of importance seems likely to prevent its widespread implementation at present.

Conclusions

The fusion of biodiversity and mutualism seems to produce an organising factor that is stable, yet dynamic and self-perpetuating. Starting from a single inter-specific partnership, it may confer beneficial properties such as efficiency, stability and niche extension, moving up through the very structures it impels, to higher organisational complexity. This essential nature seems only capable of implicating the rivet hypothesis for ecosystem structure.

It may not be so appropriate to say that biodiversity and mutualism provide ecosystem function. Rather, they *are* ecosystem function. Diverse species differ in aptitude and incapability. When networked, the benefits of each are distributed throughout the ecosystem. Diversity of “aptitude” refers to either diversity of beneficial function amongst environmentally favoured species, or diversity of environmental tolerance amongst functionally similar species.

Recognition of mutualistic biodiversity networks at their simplest, through to the most complex observable scale, i.e. the biosphere, sheds light on humanity's influence in global ecological affairs. For example, the release of industrial pollutants can be seen to destabilise ecological structures, rendering them feeble in the face of otherwise tolerable stresses. Moreover, large-scale downgrading of these biodiverse structures, e.g. deforestation, dislocates them from the remaining biosphere and places huge burden on other structures to carry over their previous function.

However, we are not just informed of our antagonism with Nature, but suggested a framework for closer union. The practice of permaculture exemplifies this framework perfectly. Adoption and development of such systems should be encouraged with all urgency, lest we later regret our neglected responsibility.

Focussed research may be able to clarify and confirm certain aspects of the issue. Indeed, detailed empirical evidence is necessary to ascertain the complex interplay between biodiversity *per se*, positive and negative biotic interactions and the functioning of ecological structures, from organism to biosphere. However, there are no reasonable grounds to deny the importance of biodiversity *per se* for ecosystem function. Action must not be delayed. We are in a time out of balance and soon our efforts could be too late.

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Glossary

Biodiversity Biological diversity; species richness; the degree of species variety. Total (gamma) biodiversity of an ecosystem is a function of (alpha) diversity within habitats and (beta) diversity between habitats, though beta biodiversity is often cited.

Biome Major regional community of organisms, extending over large areas, e.g. tropical rainforest.

Biosphere That part of the earth and its atmosphere that is inhabited by living things; all collective organisms of the earth and their environment.

Climax Community of organisms, the composition of which is relatively stable and equilibrated with existing natural environmental conditions.

Community Naturally occurring group of different organisms inhabiting a common environment, interacting with each other, especially through food relationships and relatively independent of other groups.

Competitive exclusion Principle stating that no two species can occupy the same niche, since one would be more successful at resource exploitation and out-compete the other.

Consumers The trophic level comprised of biota whose predominant activities involve consumption of plants (primary consumers) or animals (secondary consumers), thus converting organic matter from one type to another.

Decomposers The trophic level comprised of biota whose predominant activities involve conversion of organic matter to simple, inorganic molecules, and usually associated with soil flora and fauna.

Decomposition The process by which organic matter is broken down into successively simpler constituents, ultimately producing simple, inorganic molecules.

Detritus Organic debris from decomposing plants or animals.

Drilosphere The part of the soil that is influenced by earthworm activities.

Ecosystem A system involving interactions within a community and with its environment.

Ecosystem function The degree of ecosystem efficiency, and coherence, e.g. may be measured by the rate at which litter decays.

Endogeic Living and feeding below the soil surface.

Environment Physical surroundings and collective conditions (e.g. light, temperature, other organisms) that influence organismal growth and development.

Epigeic Living and feeding on, or very close to, the soil surface, e.g. in surface litter.

Fractal Structural pattern, ratio or algorithm that repeats across (theoretically) all ranges of scale; something that displays this property. E.g. the branching pattern of a tree: trunk, branches, sub-branches, twigs, leaves.

Functional group Classification category, comprising species that perform similar ecosystem processes.

Geophagous Soil eating.

Habitat Region of an ecosystem where an organism lives.

Litter Debris from dead vegetation, forming a surface layer on soils.

Mandibulate Possessing mandibles, mouthparts used for biting and crushing food.

Microhabitat The smallest part of the environment that supports a distinct flora and fauna.

Mineralisation The process by which decomposed organic matter is incorporated into the soil as inorganic nutrients.

Monoculture An ecosystem, usually artificial, comprised (theoretically) entirely of organisms of the same species.

Mutualism Association between organisms of different species that is essential for, or significantly improves, their survival and vitality.

Niche The functional position within an ecosystem to which a species is most compatible, and determined by its microhabitat preferences, physiological requirements and environmental tolerances.

Primary producers The trophic level comprised of biota whose predominant activities involve production of organic matter from simple, inorganic molecules, by the process of photosynthesis, and usually associated with green plants and algae.

Primary productivity Photosynthetic rate, as measured by the amount of organic matter produced in excess of that used in respiration.

Rhizosphere The part of the soil that is influenced by plant root activities.

Succession Progressive change in composition of a community of organisms, from initial colonisation towards a largely stable climax.

Trophic level Classification category comprising species that perform similar transformations of organic and inorganic matter. (See *consumers*, *decomposers* and *primary producers*.)