



Hypersea and the land ecosystem

Mark A.S. McMenamin*, Dianna L.S. McMenamin

Department of Geography and Geology, Mount Holyoke College, South Hadley, MA 01075-1484 USA

Abstract

The land ecosystem, in spite of its relative youth, outstrips the marine ecosystem in terms of greater primary productivity and species diversity per unit area. This occurs because land eukaryotes actively direct the flow of nutrient-rich fluids. The body fluids of land eukaryotes have had a significant evolutionary and geochemical impact, and we here refer to these fluids, and the organisms through which they flow, as 'Hypersea'. Hypersea is a previously unrecognized biogeophysical entity formed by eukaryotic life and its symbionts, parasites and hyperparasites on land. The oldest convincing evidence for Hypersea consists of fossil tracheophytes, mycorrhizal fungi, and protoctists displaying intimate ecological interactions in the Lower Devonian Rhynie Chert (approx. 400 million years old), just older than the first major coal deposits. We use the concept of hypermarine upwelling to help explain both (a) the genesis of coal and (b) why the average species diversity per unit area and biomass production of the land biota has exceeded that of the marine biota for hundreds of millions of years.

Key words: Hyperparasitism, Rhynie Chert; Mycorrhizae, Biodiversity, Coal, Marine and terrestrial ecosystems

1. Introduction

The body fluids of land vertebrates are quite salty. Struck by the chemical similarity of blood and sea-water, A.B. Macallum (1926) proposed that one could determine the solute composition of the Paleozoic seas by analyzing the body fluids of non-marine vertebrates.

Conway (1943) refuted this 'blood as sea-water' idea when he showed that there has been very little change in the concentration of the major ions of sea-water during the Phanerozoic (i.e. the past 600

million years). Recent direct measurements of the composition of Permian sea-water (Horita et al., 1991) bear out Conway's conclusions. Thus, the blood of non-marine vertebrates cannot be considered to be a 'sample' of the Paleozoic sea, as Macallum thought.

Nevertheless, the ionic composition of blood almost certainly reflects the environmental conditions (such as ionic content) of the sea in which primordial life appeared. The chemistry of body fluid carries a historical signature of its marine origin, albeit one that has been greatly modified by the demands of physiology.

Macallum's (1926) falsified hypothesis is an

* Corresponding author

antecedent of the new scientific generalization proposed in this paper. We see the aggregate body fluids of land organisms not as relict sea-water but rather as a new type of sea-like environment, termed 'Hypersea'. Hypersea consists of the body fluids of land-dwelling (i.e. air and soil-dwelling) eukaryotes that live in intimate symbioses, ranging from mutualism to parasitism, with other organisms. Hypersea includes all these organisms (eukaryotes, prokaryotes, viruses, viroids, or prions) and any direct interconnections between them. The first abundant eukaryotic land organisms, with their large internal water content, created this 'new ocean' in the Paleozoic. Hypersea organisms caused important biological and geochemical repercussions, including a 100-fold increase in Earth's biomass and the first major coal deposits.

The concept of Hypersea is necessary to explain the qualitative and quantitative differences between marine and land biotas. These differences raise three main questions, as follows:

Direct physical linkages between unrelated organisms are common on land. Thus the first question is, why are there so many more direct physical linkages between organisms on land than in the sea? Secondly, why do there appear to be more hyperparasites of higher degree (i.e. hyper-hyperparasites) on land than in the sea? Thirdly, why, per unit area of planetary surface, are there more species on land than in the sea, and how long has this been true?

The conventional way of describing the differences between the land biota and the marine biota is to attribute them to 'basic differences in the adaptations of organisms to each of these realms [i.e. land and sea]' (Ricklefs, 1976, p. 155). This approach is scientifically limited, however, because it raises the questions regarding (i) how terrestrial biotas arose in the first place (McMenamin and McMenamin, 1993, in prep.), (ii) why terrestrial ecosystems have such high primary productivity and species diversity, despite their relatively recent lower Paleozoic appearance and low ecological efficiency (high energy loss between links in the conventional trophic chain, Ricklefs, 1990) in comparison with marine ecosystems and (iii) why in fact the terrestrial biota

appears to have such a low ecological efficiency. The Hypersea concept is a potent new tool for addressing these questions.

The next four sections of this paper will present observations and descriptions of a number of phenomena specific to the land biota. The phenomena, ranging in age from the Paleozoic to the present, include hyperparasitism, symbionts of embryophytes (plants) and mammalian parasites. These examples are followed by their placement within the framework of the Hypersea model.

2. Paleozoic land symbionts

Vesicular-arbuscular mycorrhizal (VAM) fungi of the family Glomaceae are known as fossils back to the Devonian (Pirozynski and Dalpé, 1989). These mycorrhizal fungi are characterized by traits such as vesicles (resting cysts), formation of inner spores by internal proliferation (Koske, 1984), arbuscles (bush-shaped haustoria formed inside plant root cells), and habitat (obligate symbiosis within the root cortex and occasionally stems of embryophytes). VAM fungi are not only the most common type of mycorrhizal fungus but are also among the most abundant fungi of any kind. Some land plants are obligately mycorrhizal and VAM fungi in a number of cases provide nutritive linkages between unrelated vascular plants.

Pirozynski and Dalpé (1989) identified fossil VAM fungi within silicified stems of embryophytes from the Lower Devonian Rhynie Chert of Scotland. The inference of a symbiotic relationship between the fungi and the plants has been questioned, because no arbuscles have been demonstrated within Devonian plant cells (Stubblefield et al., 1987a). Nevertheless, the circumstantial evidence of the VAM fungal morphology shown by Pirozynski and Dalpé (1989) is sufficient to permit the interpretation of the fungus-plant relationship in the Rhynie Chert as one of symbiosis, or at least incipient symbiosis.

Well-preserved specimens are known from Rhynie Chert thin sections of radiating, stalked chlamydospores (sporocarps) of a fungus morphologically identical to modern *Sclerocystis* (Kidston and Lang, 1921, Plate 4, Figs 46–47). *Sclerocystis* is a glomacean (Almeida and Schenck,

1990), which is also known to occur as a Triassic fossil (Stubblefield et al., 1987b, Taylor, 1990)

In addition to glomacean fungi, the Rhynie Chert contains fossil chytrids, which are fungus-like protocists. Most chytrids are saprotrophic, but many are parasites on other eukaryotes. Chytrids were first described as fossils by Renault (1895), who found Carboniferous chytrids preserved in the tracheids of *Lepidodendron*. Taylor et al. (1992) recently described well-preserved fossil chytrids from the Rhynie Chert.

The fossil chytrids from the Rhynie Chert (Taylor et al., 1992) are associated with the embryophytes *Aglaophyton*, *Lyonophyton* and *Horneophyton*. The chytrids in *Horneophyton* occur within the plant's rhizome cortex and aerial axis, within the cells of chlorococcalean chlorophyte cells resembling *Pediastrum*. The *Pediastrum*-like cells are attached to a cortical cell wall of *Horneophyton*.

Chytrid thalli are also found in the Rhynie Chert attached to the germinating gametophyte of an *Aglaophyton* spore (Taylor et al., 1992), as well as in the sporangia of *Aglaophyton*. In other examples, a fungal spore within the gametangio-phore and one within the tissues of the gametophyte of *Lyonophyton rhyniensis* are covered by epibiotic chytrid zoosporangia.

3. Hyperparasitism

The incidence of hyperparasitism in animals appears to be higher on land than in the sea. Three orders of hyperparasitism are found among the parasitoid hymenopterans. In ichneumon wasps, for example, hyperparasitoids (3°) infect other hyperparasitoids (2°), which themselves infect other hyperparasitoids (1°), which infect parasitoids of a (non-ichneumon) free-living host (Silvestri, 1906).

In such cases the body of the host is essentially a self-contained habitat, complete with territorial interactions between parasites. The larva of ichneumon *Venturia canescens* attacks other intrahost parasites with its prominent sickle-shaped mandibles (Speirs et al., 1991). Chalcid wasps of the family Encyrtidae form polyembryonic clusters (polygerms) within the body of the host. These

polygerms generate both normally developing larvae and precocious larvae whose sole function is to seek out and destroy competing parasites (both conspecifics and members of unrelated species) within the host's body (Grbić et al., 1992).

Unrelated parasitoids can successfully come to maturity within the body of the same host (Dogiel, 1966). Parasitoids can also come to maturity in the presence of non-parasitoid parasites of the host. The hymenopteran parasitoid *Apanteles militaris* is able to successfully complete its development and pupate within its host (the army worm *Pseudaletia unipuncta*) even if the army worm becomes infected with the nematode parasite *Neoaplectana feltiae* (Bedding, 1984).

For clarity's sake, we propose that in symbiotic relations among heterotrophic organisms the degrees of hyperparasitism be described in the following fashion. On the land, the non-parasitic (largest) host organism will be designated H_1 . Its primary parasite, the next-largest, will be designated H_2 , the first-order hyperparasite — parasitic on the primary parasite, becomes H_3 ; the next hyperparasite on that hyperparasite would be H_4 , and so on.

This numbering system will avoid the confusion caused by the fact that, for instance, the third level of parasitism is the same as second-degree hyperparasitism. Also, this scheme provides an easy reference to the number of links in the host-parasite-hyperparasite trophic chain.

Miscounting is easy under the older systems. Rhode (1982, p. 50) apparently miscounted the data in Dogiel (1966) when he stated that fourth-degree hyperparasites (or five levels of parasites, equivalent to our H_6) occur among the ichneumons. Although we would not be surprised if examples of H_6 existed among hymenopterans (we suspect that they do), to our knowledge H_5 in ichneumons is the highest level yet confirmed (Silvestri, 1906). H_4 has been reported in frogs (frog \Rightarrow opalinid \Rightarrow *Entamoeba* \Rightarrow chytrid) by Chen and Stabler (1936).

For marine organisms we introduce here the equivalent numbering system M_1 , M_2 , etc. The highest level yet reported from marine ecosystems is M_3 (e.g. Pohle, 1992), although the existence of M_4 is not unlikely. Higher levels of both H_n and

M_x will probably be found as more knowledge is gained about microbial hyperparasites

4. Tree symbionts

The interaction between a scale insect, a tree and the gelatinous fungus *Septobasidium* (Evans, 1988) provides an example of biotic fluid transfer. The sap-sucking insects are penetrated by *Septobasidium* hyphae, which branch within the body of the insect into complex, coiled haustoria (analogous to arbuscles of VAM fungi). Since *Septobasidium* haustoria are similar to the fungal haustoria that penetrate the cells of a lichen phycobiont (usually a chlorophyte or cyanobacterium), the *Septobasidium*-associated insects can be thought of as having been 'lichenized'. The lichenized insects are paralyzed but not killed, and the dense mycelial growth of the fungus shelters the free-living remainder of the insect colony. The scale insect's suctorial tube extends for nearly twice its body length into the medullary ray cells of the host plant. At least 28 species, representing 9 genera of insects, are lichenized by *Septobasidium* (Couch, 1938).

Chalcid wasps parasitize the scale insect *Aspidiotus* as it grows in intimate association with *Septobasidium burtu* (Couch, 1938). The wasp preferentially lays eggs on the sessile, lichenized insect hosts. The hymenopteran and fungus temporarily coexist within the body of *Aspidiotus*. In this case body fluid passes from mycorrhiza into tree, through insect, to fungus and/or insect parasitoid. Members of at least three kingdoms participate in this flow. All five kingdoms as well as viruses and/or viroids are represented if one includes bacteria and the bacteria-like objects (BLOs) in endomycorrhizal fungi (Scannerini and Bonfante-Fasolo, 1991), methylotrophic bacteria on the leaf cuticle (Corpe and Rheem, 1989), protoctists associated with *Aspidiotus* or *Septobasidium*, and viruses employed by the wasp to weaken the host insect's immune system (Webb and Summers, 1992, Price, 1991). Fluid flow is not unidirectional: fungal metabolites are injected by the insect into the plant (Pirozynski and Hawksworth, 1988). Methylotrophic bacteria reside in cracks in the leaf cuticle, they apparently

receive fixed carbon from the plant (P. Mankiewicz, pers. commun.) and in turn provide the plant with the essential metabolic cofactor B_{12} , which only bacteria can produce (Corpe et al., 1986; Corpe and Rheem, 1989).

Endomycorrhizal fungi are also hyperparasitized by other fungi (Daniels and Menge, 1992), and it may be possible for bacteria-like objects to infect the hyperparasitic fungi. Thus a tree can have H_4 to H_5 continua both below ground (tree \Rightarrow mycorrhizae \Rightarrow hyperparasitic fungi \Rightarrow bacteria-like objects) and above ground (tree \Rightarrow scale insect \Rightarrow fungus \Rightarrow hymenopteran \Rightarrow virus). As in a traditional food chain, the steps in these continua are not always discrete. For example, the BLOs may occur in both the mycorrhizae and the hyperparasitic fungi, and viruses infect both the hymenopteran and its insect host, the extent of such overlap is not always clear.

A possible subterranean analog of the case of *Septobasidium* and scale insects is seen in the sugar-beet nematode, *Heterodera schachtii*. A culture of *H. schachtii* hyperparasitized by the glomacean mycorrhizal fungus *Glomus* sp. has been maintained for several years on tomato roots by Steele (1984).

Trees also harbor H_3 continua such as hyperparasitized root nematodes (tree \Rightarrow nematode \Rightarrow *Pasteuria penetrans*; Oostendorp et al., 1991) as well as H_2 -level associations such as angiosperm root hemiparasites (some of which are connected through these mycorrhizae and thus are more properly H_3), epiphytes, leaf-spotting fungi, gall-forming insects and bacteria, tree viruses, tree viroids, and other symbionts.

5. Mammalian parasites

In spite of advances in health care during the last century, access to our own tissues by other organisms is not as restricted as we might like to think. The protoctist *Toxoplasma gondii* is present in 15–85% of adult human populations (Sibley and Boothroyd, 1992), and as much as half of the world's population harbors the follicle mite *Demodex* (Bonnar et al., 1991). Both parasites are typically asymptomatic.

All human metazoan internal parasites may be subject to hyperparasitism by *Toxoplasma* (D Bermudes, pers commun, 1992). Furthermore, recent evidence suggests that the mycoplasma *Mycoplasma penetrans* is a co-factor, along with HIV-1, in AIDS (Lo et al, 1992; Wang et al, 1992)

Hard ticks, members of the family Ixodidae, are capable of transmitting to their mammalian hosts a wide variety of microbes, including viruses, bacteria, and sporozoan protoctists. The best-known bacterial pathogen transmitted by a hard tick (*Ixodes dammini*) is the spirochete *Borrelia burgdorferi*, which causes Lyme disease (Oliwstein, 1993). The hard tick *Ixodes ricinus* is parasitized by the ichneumon *Ixodiphagus caucurtei* (Dogiel, 1966). Cases of hyperparasitism at the H₄ level, although not yet demonstrated, are likely to be present in the interactions of mammals, hard ticks, hymenopterans, and microbes

6. The diversity paradox

Hypersea was established, probably 450 million years ago, by the development of subaerial symbiosis (McMenamin and McMenamin, 1992). Hypersea first flourished during the Devonian-Carboniferous (approx 400–300 million years ago), and direct evidence for its existence at that time is present in the form of convincing examples of land H₂ interactions (*Lepidodendron* ⇒ chytrid, Rhynie Chert embryophyte ⇒ glomacean VAM fungi, *Aglaophyton* gametophyte ⇒ chytrid) and possible examples of H₃ interactions (*Horneophyton* ⇒ chlorophyte ⇒ chytrid, *Lyonophyton* gametangiophore ⇒ fungal spore ⇒ chytrid zoosporangium, embryophyte sporangium and stem ⇒ arthropod ⇒ fungal resting spore) (Rolfe, 1980). Hypersea is a dominant feature of the modern world, even mammalian tissues are very much a part of Hypersea.

Hypersea can help resolve what we call the diversity paradox. Simply put, the paradox is: why does the land biota appear to be so diverse in comparison with the marine biota? In an early attempt to answer the question, Hutchinson (1959) argued that the high diversity of terrestrial plants was responsible for much of land arthropod diversity.

More recently, Briggs (1991) felt that there were more species on land because the primary producers on land are quite large and can support more species.

Grassle and Maciolek (1992) presented data and statistical arguments suggesting that the diversity of marine animals is much greater than previously thought. Chaloner (1992, p 265) noted that, if Grassle and Maciolek were correct in their revision of marine diversity, then 'the discrepancy between the marine and terrestrial realms is not so vast as to need some special explanation'. Both Briggs (1991, 1992) and May (1992), however, questioned the validity of Grassle and Maciolek's statistical inferences concerning the diversity of marine organisms.

Regardless of the ultimate outcome of this global species count, it is likely that the average species diversity per unit area of planetary surface is substantially greater on land than it is in the sea. Such a discrepancy is still paradoxical, and in our view the Hypersea concept can help resolve the diversity paradox.

Table 1 shows the proportions of extant species falling into each of five categories. Note that according to our estimates, Hypersea elements

Table 1
Estimated species composition of the global biota

Category	Percentage of total species
1 Land plants and mycorrhizal fungi in symbiosis	18
2 Herbivorous insects and their symbionts	28
3 Endoparasitic wasps and associated viruses and parasitic nematodes	8
4 Other land and freshwater organisms (some of which are Hypersea species)	13
5 All marine organisms	33
Total	100

Categories 1–3 and part of 4 constitute Hypersea. Modified from Price (1991)

account for at least 50% of global species diversity, even though not all land organisms belong to Hypersea.

Changes in marine species diversity and Hypersea species diversity through time are compared in Fig 1. The absolute numbers in this figure are conservative. Ehrlich and Wilson (1991, p. 759) conjecture that 'it is easily possible that the true number [worldwide total] of species is closer to 10^8 than 10^7 '.

The diversity of Hypersea has exceeded that of the ocean for more than 300 million years. Hypersea diversity and marine diversity have converged somewhat during the past 150 million years, during which time the continents have been in latitudinal positions that are unusually

favorable to the speciation of marine invertebrates (Valentine, 1985, Signor, 1990). During the Cenozoic most continents were separated by north-south oceans, and numerous new species of coastal marine organisms have evolved to adapt to the latitudinal temperature gradients along each coastline.

The crossover point (Fig. 1) at which hypermarine diversity overtakes marine diversity occurs during the Mississippian or earliest Carboniferous, approx. 350 million years ago. Interestingly, uppermost Devonian and Lower Mississippian marine strata in many localities record a widespread episode of deposition of low-oxygen, organic-rich strata in middle Paleozoic shelf seas (Savoy, 1992). Savoy's model for the deposition of these organic-rich sediments entails the shoreward influx of an expanded and intensified marine oxygen-minimum zone during a latest Devonian to earliest Mississippian transgression (rise in sea level).

River-carried organic detritus can also cause an expansion of the oxygen-minimum zone, because microbial decay of the organic material consumes oceanic oxygen. The major Devonian-Mississippian low oxygen event in the ocean was enhanced, if not caused outright, by land-derived organic material shed from a rapidly expanding Hypersea during the time when Hypersea was about to overtake the marine realm in terms of total species diversity and was beginning to lay down the economically important coal deposits that lent their name to the Carboniferous (Algea and Maynard, 1993).

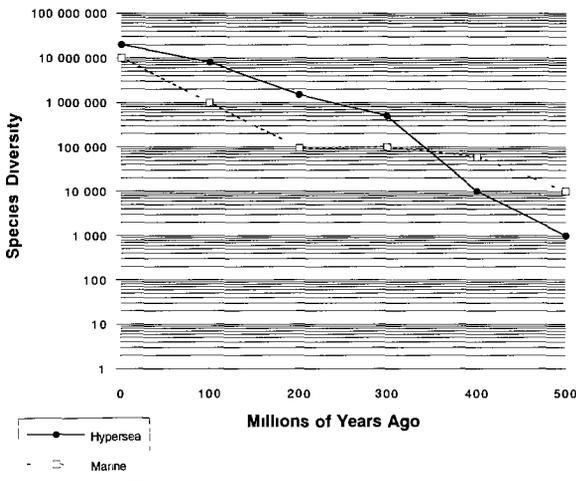


Fig 1 Semilog plot comparing Hypersea and marine diversity through time. Estimated values are based on Valentine (1985), Signor (1990) and Wilson (1992), assuming a total pre-industrial global species diversity (including viruses and viroids) of 30 million (May, 1992, Margulis, 1992). These estimates are conservative in absolute terms (Ehrlich and Wilson, 1991, Grassle and Maciolek, 1992, Poore and Wilson, 1993) and are intended only to give a general impression of biodiversity at set points in geological time. The estimates do, in our opinion, accurately portray the relative proportions of marine and hypermarine species diversity. Hypersea diversity is denoted by filled circles, marine diversity by open squares. Note that the plots cross approximately 350 million years ago (in the Lower Carboniferous or Mississippian). Non-Hypersea terrestrial organisms (such as rock varnish bacteria) and exclusively fresh-water species are not included here.

7. Conclusions

We now turn to the Hypersea concept to resolve the three main questions posed in the Introduction. Firstly, Hypersea formed as the result of direct physical connections between land organisms striving to conserve water in the desiccating subaerial environment. Nutrients on land also came to be distributed between unrelated organisms via direct physical connections.

Secondly, land hyperparasitism may exceed that of the sea because it represents the opportunistic exploitation of Hypersea. We predict that, for at least the past 200 million years, the land biota has

had several more higher orders of hyperparasitism than has the marine biota. In other words, $x(\max) - y(\max) \geq 2$ (where x and y are the subscripts of $H_{x(\max)}$ and $M_{y(\max)}$, respectively) Evaluation of this prediction will serve as a major test of the Hypersea model.

Thirdly, Hypersea can help explain why land biomes are richer in species on a per-unit-area basis than are comparable marine provinces. The comparison is striking considering the relative youth (~400 million years versus ~4 billion years) and low ecological efficiency of the land biota in comparison with the marine biota.

The predicted hyperparasite contrast between land and sea noted above would certainly contribute to higher average diversity of land organisms per unit area. More important, however, is the fact that on land so many species of organisms are capable of thriving in the body fluids of other organisms. Additional species are virtually packed inside or on top of one another. Note, for example, the one-to-one correspondence between eleven Panamanian fig species, their associated fig wasp species, and in turn the eleven different nematode species (endoparasitic in the wasps) that have trivial (or species) names derived from those of the corresponding fig tree species in which their host wasp lives (Herre, 1993). Also, some insects harbor multiple genera of nematodes, such as for instance the bark beetle *Ips*, which is parasitized simultaneously by the nematodes *Contortylenchus* and *Parasitorhabditis* (Kaya, 1984). In the tropics, each herbivorous insect is attacked by up to ten species of parasitoids (Briggs, 1991).

In other words, the colonization of the land by eukaryotes developed as the colonization of two environments. (i) the barren, or prokaryote-inhabited, land surface itself and (ii) the Hypersea environment formed by eukaryote tissues and body fluids.

Furthermore, the concept of Hypersea explains why there are approximately two orders of magnitude difference between the modern land biomass and the modern marine biomass. The usual explanation for this disparity is that land plants store much of this biomass as 'dead' wood. Much of this wood, however, is actively involved either in transport of fluid to adjoining live tissue

or in the nourishment of fungal mycelia. Hypersea host species actively create, rather than passively inhabit, a fluid medium.

The Hypersea model also explains why, as usually tallied, marine food chains are long and land food chains are short. Land food chains are internalized to a large extent. Such internalization may in part explain the high energy losses (low ecological efficiency) between levels of the conventionally portrayed land trophic pyramid. Much of the energy in land ecosystems goes to decomposers such as fungi, but a significant fraction of the 'lost' energy is consumed by xenobionts within their Hypersea hosts.

Hypersea is manifest as a *directed* transfer of fluids. Following the work of the Russian geochemist V.I. Vernadsky, Andrey Lapo (1987, Table 4) tabulated the main 'functions' of living matter in the biosphere as: energetic, concentrating, destructive, medium-forming, and transporting. The most important function for Hypersea is the transporting function. This function involves the transfer of matter against the force of gravity. In what we will call hypermarine oceanography, the fluid-lifting abilities of land organisms allow 'upwelling on demand'. Physiologically important solutes from Earth's crust (or, in the case of nitrogen, from soil air) are continually carried upward by plants.

Ocean surface nutrients can only be replenished by non-biological forces such as wind mixing or by seasonally and/or geographically restricted upwelling. Hypersea organisms effectively bypass this marine nutrient starvation. Hypermarine upwelling is a biotic affair, involving the mycorrhizal fungi and their interconnected vascular plants, and thus explains why the primary productivity of the land so outstrips that of the sea. Nutrient limitation, which so drastically curtails productivity in surface marine waters (Williams, 1992), is less a problem on land. During the active growing season the land biota creates for itself a zone of constant upwelling.

This is not to say that Hypersea has unlimited access to needed nutrients. In spite of the fact that nitrogen-fixing bacteria occur in root nodules, substantial evidence exists that nitrogen availability limits net primary production much of the time in

terrestrial biomes (Vitousek and Howarth, 1991). Early successional moss ecosystems on land are forced to be extremely efficient at retaining nitrogen, whether locally fixed or from bulk precipitation (Bowden, 1991). Thanks to intracellular motility systems and cell junctions, land ecosystems, in contrast to marine ecosystems, modulate nutrient availability through directed fluid flow.

The Hypersea concept thus confirms the sense among ecologists that fundamental differences exist between terrestrial and marine ecosystems (Holling, 1992). Considering the amount of carbon dioxide that can be fixed by Hypersea, hypermarine upwelling is second only to (a) oxygenic photosynthesis and (b) secretion of calcium carbonate sediment by marine organisms as a geochemically significant result of life processes. Coal, a type of rock virtually unknown before 400 million years ago, is a direct result of Hypersea's geochemical impact

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