

Does natural selection organize ecosystems for the maintenance of high productivity and diversity?

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Three types of evidence suggest that natural ecosystems are organized for high productivity and diversity: (i) changes not previously experienced by a natural ecosystem, such as novel human disturbances, tend to diminish its productivity and/or diversity, just as 'random' changes in a machine designed for a function usually impair its execution of that function; (ii) humans strive to recreate properties of natural ecosystems to enhance productivity of artificial ones, as farmers try to recreate properties of natural soils in their fields; and (iii) productivity and diversity have increased during the Earth's history as a whole, and after every major biotic crisis.

Natural selection results in ecosystems organized to maintain high productivity of organic matter and diversity of species, just as competition among individuals in Adam Smith's ideal economy favours high production of wealth and diversity of occupations. In nature, poorly exploited energy attracts more efficient users. This circumstance favours the opening of new ways of life and more efficient recycling of resources, and eliminates most productivity-reducing 'ecological monopolies'. Ecological dominants tend to be replaced by successors with higher metabolism, which respond to more stimuli and engage in more varied interactions. Finally, increasingly efficient predators and herbivores favour faster turnover of resources.

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1. INTRODUCTION

Are ecosystems 'designed' to support high productivity and diversity, as organisms are 'designed' by natural selection (Dennett 1995) to survive and reproduce? Ecosystems, like human societies, are both functional wholes (Odum 1971) and arenas of competition among their members (MacArthur 1972). Smith (1759, 1776) argued that competition among individuals in human economies favours diversity of occupations and high production of wealth *if* appropriate rules of fair competition are correctly discerned and communally enforced. Does competition among plants and animals likewise enhance productivity of organic matter and diversity of species in natural ecosystems?

This paper answers the question above in two steps. First, we provide empirical evidence that ecosystems are organized for high diversity and productivity. In particular, we show that:

- (i) random changes in an ecosystem or in its environment tend to diminish its productivity or diversity;
- (ii) certain features of an ecosystem crucial to its productivity or diversity (such as the qualities of a forest soil) are those which knowledgeable farmers recreate to make their farms productive; and
- (iii) ecosystem diversity and productivity increases over

macroevolutionary time as a whole, and after each major extinction event.

Second, we analyse the causes of this phenomenon, outlining the evolutionary mechanisms that favour increased productivity and diversity.

2. ARE ECOSYSTEMS ORGANIZED FOR HIGH PRODUCTIVITY AND DIVERSITY?

(a) *Aristotle's approach: organized systems are disorganized by change*

Aristotle inferred that organisms are designed to survive and reproduce because abnormal organisms usually survive or reproduce less well than their normal counterparts ('On the Soul' 416b23–25 and 'Physics' 199b1–4 in Barnes (1984)). In (accidental?) accord with Aristotle, Fisher (1930) defined an organism as adapted to survive and reproduce in a certain environment, if changing either its phenotype or its environment usually diminished its prospects of survival or reproductive success. By analogy, we infer that an ecosystem is organized for high productivity and diversity if changes beyond the range with which its populations are adapted to cope tend to reduce its productivity or diversity. We give a few examples to show how this definition applies.

One expects unusually cool or dry conditions to reduce the productivity of a naturally evolved ecosystem, and, if they last long enough, its diversity as well. True, some rainforests are limited more by availability of light than of water (Wright & van Schaik 1994), so a very dry, sunny year increases their productivity (Wright *et al.* 1999), but

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such droughts also increase the risk of catastrophic fire (Leighton & Wirawan 1986; Piperno & Becker 1996), which may reduce subsequent productivity for some time to come. Unusually warm or wet conditions may enhance an ecosystem's productivity, but its productivity will not match that of an ecosystem adapted to these conditions. Moreover, unusually warm or wet conditions in a habitat that is normally cool or dry sometimes diminish productivity by favouring destructive pests or pathogens, which plants of habitats that are normally warm and wet are adapted to resist. If the climate stays warmer and wetter, new species better adapted to these conditions normally invade, and the ecosystem becomes different.

An extreme case of an environmental change that was disastrous to contemporary organisms, although it allowed much more productive ecosystems to evolve, is the oxygenation of the atmosphere by photosynthetic organisms. Oxygen poisoned that age's anaerobic world, even though the feasibility of aerobic respiration allowed organisms to evolve that could exploit energy far more effectively than their anaerobic predecessors (Margulis 1993; Niklas 1997).

The vulnerability of natural ecosystems to unaccustomed change is most evident when this change is induced by humans. Here, we consider several examples of how heedless human disturbance diminishes diversity and/or productivity. Humans are now fragmenting ecosystems into scattered parks. Conservation biologists fear the impact of global warming on these parks: will this warming injure natural ecosystems whose species can no longer migrate northwards with their appropriate climate? Reducing tropical forest to fragments separated by pasture, farmland or reservoir water lowers the diversity of plants and animals in the fragments, and impairs the function of their ecosystems (Lovejoy *et al.* 1986; Leigh *et al.* 1993; Terborgh *et al.* 1997; Laurance *et al.* 1998). Trees on fragment edges are exposed to drying winds from outside, and understory plants on fragment edges experience increased light and heat, and drier air and soil. Many of the trees in such fragments lack appropriate pollinators, dispersers or other needed mutualists. Tree diversity has dropped markedly on islands of less than a hectare in Panama's Gatun Lake which have been forested ever since their isolation in 1914 (Leigh *et al.* 1993). Newly isolated islets of Venezuela's Guri reservoir lack the agents that control leaf-cutter ants on the nearby mainland (Rao 2000). Leaf-cutter ant populations have therefore exploded on these islets, stringently limiting the abundance of recruiting plants and lowering plant diversity (Rao *et al.* 2001). Indeed, on these islets, angiosperm evolution appears to have reversed: diverse forest is being replaced by forest of much lower diversity, whose trees depend less on specific pollinators or dispersers, and presumably devote more energy to anti-herbivore defence than to growth (Terborgh *et al.* 2001).

The problem here is the *change* in degree of fragmentation. Ecosystems, like their member species, are adapted to the conditions in which they evolved. In regions of Belize, where forest fragments have occurred in the savanna for thousands of years, a 0.9 ha forest fragment was found to contain 56 species among its trees (≥ 10 cm diameter at breast height), whereas three 1 ha plots of continuous forest from areas in Belize with the same rainfall

as the fragment averaged 55 tree species apiece (Kellman *et al.* 1994). Moreover, 'edge effects' in these natural fragments are minimal, compared with those in fragments recently isolated by human activity.

Newly arrived human hunters with stone-tipped weapons killed off Beringia's mammoths and other megaherbivores at the end of the Pleistocene, inducing a productivity-reducing replacement of grassland by moss tundra (Zimov *et al.* 1995). Climate change did not kill the mammoths: they survived on Wrangel Island, north of Siberia until humans arrived in 1700 BC. Trampling and grazing by megaherbivores prevents moss from replacing the grassland. When the herbivores disappeared, the mosses took over. The mosses' low transpiration led to a waterlogged soil. Mosses, unlike grasses, bind nutrients into compounds that resist recycling, and thus impair soil fertility. The replacement of grassland by moss tundra thus caused a major drop in ecosystem productivity (Zimov *et al.* 1995).

Planting exotic pasture grasses in deforested areas where large herbivores have disappeared, or clearing land where aggressive grasses can colonize, often enables monospecific grassland to spread where diverse tropical forest once grew (D'Antonio & Vitousek 1992). *Saccharum spontaneum*, an aggressive grass native to southeast Asia, was accidentally introduced to the Panama Canal Area around 1970. This grass readily colonizes bare ground, forming thick monospecific stands. Among Panamanian vertebrates, only capybaras eat full-grown *Saccharum*, and that only near open water. This grass burns readily in dry seasons (alas, there are always people ready to set fire to it). These fires block forest succession by killing tree seedlings, and slowly spread the grassland at the expense of neighbouring forest. This grass has transformed reforestation of abandoned clearings from an automatic process to a difficult achievement (Dalling & Denslow 1998, pp. 675–676). Similarly, abusive land practices in Indonesia have transformed vast areas of luxuriant forest into monotonous, useless stands of the grass *Imperata cylindrica*, inhospitable to birds and mammals (Whitmore 1984, p. 207), which is spread further every dry season by fires (D'Antonio & Vitousek 1992). However, in Nepal, grassland dominated by *S. spontaneum* and *I. cylindrica* supports a diverse array of vertebrate herbivores (Karki *et al.* 2000). In general, where herbivores crop most of a grassland's production, fires are rarer and less damaging to nearby forest (Dublin 1995). These monospecific grasslands spread due to a combination of careless land use and the elimination of vertebrate grazers.

The near extinction of sea otters from the northern Pacific in the 1800s allowed their favoured prey, sea urchins, to multiply. These urchins grazed down highly productive kelp beds, causing them to be replaced by a pavement of crustose coralline algae. When hunting of the sea otters ceased shortly after 1900, the remaining sea otter populations recovered, but they failed to recolonize many islands where they had formerly lived. Where the otters have recovered, offshore kelp beds have reappeared, which harbour a multitude of crustaceans, fishes and squids. Where the otters are absent, kelps and harbour seals are rare and bald eagles absent (Estes & Palmisano 1974), and both primary and secondary productivity much lower (Duggins *et al.* 1989). In the 1990s, killer

whales have begun eating sea otters—apparently because overfishing in the nearby open ocean has deprived them of their normal diet. Where killer whales can reach the otters, sea urchins are spreading again, destroying the kelp and reducing nearshore productivity (Estes *et al.* 1998).

(b) D'Arcy Thompson's approach: analogies with human design

D'Arcy Thompson defined organismic adaptation in terms of 'mechanical fitness for the exercise of some particular function or action which has become inseparable from the life and well-being of the organism' (Thompson 1942, p. 958). Similarly, one can recognize features of an ecosystem that seem designed to enhance its productivity or diversity.

A forest's health depends on the qualities of its soil. A good soil has remarkably contradictory properties. It is soft enough for roots to penetrate but cohesive enough to stay put. It prevents nutrients and much of the water it receives from draining or leaching away, but leaves them accessible to plant roots. Even when well watered, natural soil is usually so porous that oxygen and carbon dioxide circulate freely through it (Bruenig 1996; Marshall *et al.* 1996). These properties develop 'naturally' in the soils of most undisturbed forests but are impaired or destroyed by the heedless logging or deforestation usual in tropical settings (Bruijnzeel 1990; Stallard *et al.* 1999). Skilful farmers seek, often successfully, to preserve these same soil properties (Bruijnzeel 1990), but this is a deliberate achievement that does not happen by accident.

(c) Trends in the fossil record: diversity and productivity increase during evolution

In general, diversity has increased over evolutionary time, on sea and on land (Milne *et al.* 1985, pp. 35–50). This increase of diversity reflected a series of evolutionary innovations that 'resulted in: (i) a progressively more efficient utilization of available energy; (ii) a progressively wider use of available materials (nutrients); and (iii) a progressive spread of organisms to a wider range of environments' (Fischer 1984, p. 146). These innovations include photosynthesis, aerobic respiration, nitrogen fixation (using energy from carbohydrates to obtain needed NH_3 from N_2), nitrate reduction (obtaining energy by turning NO_3-N into N_2), sulphate reduction (the use of sulphate, SO_4^{2-} by anaerobic bacteria as an oxygen source for oxidizing carbohydrates), some kinds of bacteria becoming endosymbionts within others to form eukaryotes, other endosymbioses combining complementary specialties in one individual, using calcium and silica to make skeletons, multicellularity, various modes of locomotion, burrowing in search of buried organic matter, predatory habits, herbivory, and social behaviour (Fischer 1984; Maynard Smith & Szathmáry 1995). These innovations all increased ecosystem productivity and diversity. Some, like aerobic respiration, nitrate and sulphate reduction, and burrowing in search of organic carbon, employ previously unusable wastes to obtain energy, some of which, like oxygen, were toxic to preceding organisms. Sulphate-reducing bacteria 'saved the world from accumulating a skin of gypsum' (Fischer 1984, p. 147). Nitrate reduction averted the conversion of the oceans into nitrate brines

and prevented nitrogen-fixing bacteria from depleting the atmosphere's nitrogen (Fischer 1984).

From the Cambrian period onwards, the biomass, diversity and level of activity of marine consumers increased (Bambach, 1985, 1993; Kidwell & Brenchley 1996; Martin 1996), implying an increase in marine productivity also (Vermeij 1999). Increased consumer biomass is reflected by the increased thickness of fossil shell beds and the increased proportion of shell beds over 30 cm thick: 10% in the Ordovician and Silurian, 34% in the Jurassic, and 60% from the Miocene onwards. In the Cambrian, most shell beds are thin and consist largely of trilobite skeletons. In the Ordovician and Silurian, shell beds dominated by brachiopods are somewhat thicker. From the Jurassic onwards, the increasingly thick shell beds are dominated by bivalves and barnacles (Kidwell & Brenchley 1996).

Marine diversity of local communities, and of the seas as a whole, increased sharply from the mid-Cambrian to the mid-Ordovician, levelled off, decreased towards the end of the Palaeozoic, then increased rapidly from the Triassic onwards (Bambach 1985; Signor 1990).

Increased activity levels, more effective recycling of resources, and faster turnover of these resources reflect higher productivity. Faunal dominants generally give way to successors with relatively more massive and elaborate soft parts and higher basal metabolism (Bambach 1993), as in the replacement of brachiopods by bivalves (Rhodes & Thompson 1993), cyclostome by cheilostome bryozoans (McKinney 1995), and slower shell-bearing cephalopods by fast-swimming squids and fishes (Vermeij 1999). Activity increased in the Early Cambrian when trilobites and other arthropods appeared, again in the Devonian when bony fishes and malacostracan crustaceans appeared, in the later Mesozoic when bivalves diversified and decapod crustaceans and teleost fishes appeared, and yet again from the Miocene onwards when new groups of energetic, predaceous gastropods, crustaceans and fishes appeared. Relatively energetic groups usually appeared first in productive nearshore settings and only invaded less productive habitats later (Jablonski *et al.* 1983), seemingly when these habitats became productive enough to support them. Increases in activity levels tended to occur when the earth was warm, the oxygen levels were increasing (as if the plants were 'getting ahead' of the animals) and sea levels rising (Vermeij 1987); that is to say, when resources were becoming more readily available (Vermeij 1995).

Increased activity allowed more effective recycling. In the Cambrian period, burrowing animals began to rework and aerate surface sediments, allowing aerobic microbes to recycle buried carbon. The depth and intensity of reworking increased in several stages thereafter (Thayer 1979, 1983; Signor 1990, pp. 523–524). For example, bivalves evolved as shallow-burrowing suspension feeders in the Cambrian, while deposit-feeding bivalves evolved in the Ordovician (Stanley 1975). Lucinid clams were burrowing more deeply in the Devonian, and other bivalves were burrowing a metre deep by the Permian. Trigoniid clams, suspension feeders that burrowed so rapidly that they could live on a sea bottom of shifting sand, diversified rapidly from the Jurassic onwards. After the Late Cretaceous crisis nearly wiped them out, cardiid clams, even

faster burrowers, diversified in their place, and other bivalves evolved which burrowed both rapidly and deeply. Older, slower lineages of bivalves usually survived the appearance of these newcomers, so diversity increased (Stanley 1975, 1978).

Turnover of living matter also increased. At first, most macroscopic plants, both marine and terrestrial, decomposed. In the sea, true herbivores evolved dozens of times from detritus eaters and predators from the Mesozoic onwards (Vermeij & Lindberg 2000). Herbivores enhance productivity by reducing the time between production and recycling of vegetable matter, increasing the turnover rate of these resources.

Similar developments indicate a parallel increase in terrestrial productivity. Ever larger plants appeared, from Ordovician mosses to Carboniferous trees (Shear 1991). Early forests, like the swamp forests of the Carboniferous period, were dominated by slow-growing trees full of lignin (Robinson 1990). In the Carboniferous, oribatid mites were decomposing wood of all kinds of trees (Labandeira 1998, p. 346), but most plant matter was still buried unused. Although insects that sucked plant juices evolved earlier, few insects were actually eating live plants before the Late Carboniferous, by which time stem-boring and gall-making insects had also appeared. By the Permian, however, insects had evolved an abundance of effective herbivores, and vertebrate herbivores also appeared (Labandeira 1998). During the Mesozoic, an abundance of large dinosaurs—'animated compost heaps' capable of dealing with most plant poisons (Coe *et al.* 1987, p. 241)—were feeding on live plants. Fungal decomposers evolved by the Permian (Visscher *et al.* 1996) and termites in the Mesozoic, and recycling of the resources in dead plants was finally assured.

Two major changes in terrestrial vegetation have occurred since the Jurassic: have these changes increased ecosystem productivity or diversity? The first change resulted from the evolution of angiosperms. Angiosperms appeared in the earliest Cretaceous period as fast-growing weeds of disturbed sites (Wing & Boucher 1998). Over 100 Myr ago, angiosperms evolved features attracting 'faithful' pollinators seeking flowers from other plants of the same species (Crepet 1984; Wing & Boucher 1998). Such pollinators allowed their plants to persist when rare. These plants could therefore escape specialist herbivores by being too rare to find rather than investing heavily in anti-herbivore defences (Regal 1977). As there is a trade-off between growth rate and level of anti-herbivore defence (Coley *et al.* 1985), the evolution of flowers attracting faithful pollinators triggered a rapid diversification of rare, fast-growing angiosperms, especially in the tropics (Wing & Boucher 1998), where pest pressure is most intense today (Leigh 1999). In tropical climates, diverse fast-growing angiosperm forest had replaced less diverse, more heavily defended forests of wind-pollinated gymnosperms by the Eocene (Wing & Boucher 1998; Leigh, 1999). As the long-lasting defences of gymnosperm leaves hinder litter decomposition and acidify the soil (Waring & Schlesinger 1985), their replacement by angiosperms improved the soil, further enhancing ecosystem productivity.

The second change was the evolution of grassland. In North America, short-grass prairie and a suite of grazing

mammals appeared in areas with 400 mm or less rainfall per year about 15 Myr ago (Retallack 1997a). Six or seven million years ago, tall-grass prairie dominated by C₄ grasses replaced woodland in regions with 400–750 mm rain yr⁻¹ (Retallack 1997a). Did the evolution of grassland create ecosystems with higher productivity and diversity than their predecessors?

Grasses evolve to support a herbivore load that destroys their competition. This accords with simple predator–prey theory, which shows that harvesting prey diminishes the predator population (Volterra & Ancona 1935, p. 30), implying that increased prey efficiency increases the number of predators. Trees, however, evolve to deter herbivores. In the biggest nearly natural grassland ecosystem left, East Africa's Serengeti (Sinclair & Arcese 1995), chewing herbivores consume 66% of the annual above-ground production, whereas herbivores consume 10% or less of a tropical rainforest's leaf production (McNaughton 1985). Moreover, herbivores increase the above-ground productivity of Serengeti grasslands by an average of 86% (McNaughton 1985): tropical forest receives no such benefit from its herbivores. The Serengeti, which averages 800 mm rain yr⁻¹, supports over 8 tons km⁻² of large herbivores, and the nearby Ngorongoro Crater, with 630 mm rain yr⁻¹, supports 11 tons km⁻² (Runyoro *et al.* 1995, table 7.3). The forest of Barro Colorado Island, Panama, with 2600 mm rain yr⁻¹, supports 4.5 tons km⁻² of mammals of all kinds (Leigh 1999). Tree leaves are more heavily eaten in drier climates, because the leaves of deciduous dry forest trees do not live long enough to pay for adequate anti-herbivore defences. Accordingly, dry forest supports a higher biomass of herbivores than wetter forest (Leigh 1999). Apparently, grasses spread by using herbivores to enhance their competitive ability, even though, in places where herbivores have been hunted out, fires often spread grassland at the expense of neighbouring forests.

We lack data to compare diversity or productivity of Serengeti grasslands with its woodlands. Clearly, grassland relies more on fast growth than defence, even though Serengeti grasses fill their roots and root crowns with silica to deter overgrazing (McNaughton *et al.* 1984), and turnover of vegetable matter is much faster in grasslands than in forest. Therefore, Serengeti grassland should be more productive than adjoining woodland. This grassland also supports an extraordinary diversity of mammals and birds (Sinclair & Arcese 1995).

As we have seen, herbivores prompted the evolution of two major ecosystems: flowering forests and grasslands. Both innovations enhanced plant productivity and vertebrate diversity. By contrast, domestic herbivores often overgraze their habitats, as anyone knows who has seen domestic goats denude a Near Eastern hillside and diminish its biodiversity. The monospecific grasslands that revegetate carelessly cleared land in the moist tropics support few birds or mammals (Whitmore 1984). Fragmentation of tropical forest by reservoirs eliminates predators, allowing herbivores to diminish the diversity and productivity of these fragments' plants (Terborgh *et al.* 1997, 2001; Rao *et al.* 2001). The tendency of heedless human activities to reduce productivity and diversity—so unlike long-term evolutionary innovations—indicates that evolution is 'cleverer' than we are (Hammerstein 1996).

The evolution of productivity and diversity recurs after each major biotic crisis (Erwin 1998). The Permian Period ended 251 Myr ago with an event that killed 82% of the world's marine genera, leaving the sea with simple communities of widespread generalists. Although it took millions of years, marine diversity eventually recovered (Erwin 1998). This crisis also wiped out the world's forests, prompting a gigantic bloom of fungi to decompose this mass of dead vegetation and drastically reducing terrestrial productivity and diversity (Visscher *et al.* 1996; Looy *et al.* 1999; Retallack 1999; Ward *et al.* 2000). Herbaceous lycopods, quillworts and their allies, replaced the killed trees, and no coals formed for 6 Myr. Only afterwards did forest begin to recover, but within *ca.* 10 Myr of the crisis, diverse forest ecosystems had evolved again, and had even reoccupied demanding swamp habitats (Retallack *et al.* 1996; Retallack 1997b; Looy *et al.* 1999).

The Cretaceous period ended 65 Myr ago when a large bolide struck Yucatan, Mexico, causing devastating extinctions on land and sea. Marine phytoplankton, the ocean's major primary producers, recovered quickly, perhaps within a few years. Zooplankton and deepwater biotas recovered much more slowly, but 3 Myr after the crisis, marine ecosystems had evolved back to normal (D'Hondt *et al.* 1998). In New Mexico, a diverse flora of palms and many dicots were destroyed, and forest recovery was an evolutionary analogue of forest succession on Krakatau after that volcano's explosion (Wolfe & Upchurch 1987). First ferns appeared, then a low-diversity assemblage of trees resembling the pioneers that now colonize large clearings in the tropics, and finally, increasingly diverse mature forests. The vegetation took 1.5 Myr, however, to evolve half the pre-impact diversity (Wolfe & Upchurch 1986, 1987). A more complete story is being assembled from North Dakota, USA. There, the impact killed 80% of the plant species and all specialized plant-eating insects. Herbivory levels declined. Specialized insect pests reappeared and plant diversity recovered fully only during the Early Eocene warming, 10 Myr after the impact (Labandeira *et al.* 2002). The impact's consequences also wiped out the world's dinosaurs, including the leaf-eaters. Large leaf-eating mammals only evolved 8 Myr later, in the Late Palaeocene, and they only became common and diverse in the Early Eocene (Janis 2000).

3. WHAT MECHANISMS ORGANIZE ECOSYSTEMS FOR HIGH DIVERSITY AND PRODUCTIVITY?

A central problem of ethology concerns animals living in groups whose members depend on each other for various services (Leigh 1999, p. 214). Natural selection is a competitive process, and a group's members are each other's closest competitors for food, mates or shelter. What keeps competition among them from preventing cooperation or destroying its fruit? Such competition would annihilate their common interest in living together? In his *Politics*, Aristotle argued that those human societies whose political organization best served the common good were least liable to revolutionary overturn, for they had the fewest members that would benefit from a revolution. How to design a human society so that each member's advantage mostly coincides with the common good, however, has preoccupied philosophers since the days of Plato and

Aristotle. The analogous problem for ecosystems is equally challenging. Presumably, an ecosystem serves more members better by harbouring more species and producing more vegetable matter to support them. Even so, how can ecosystems become organized for high diversity and productivity when each species evolves in response to the advantage of the individuals in the ecosystem?

At any level of biological organization, certain forms of competition among the parts can impair the good of the whole. How might such competition be suppressed? Among honeybees, for example, the whole hive depends on an appropriate division of labour among its inhabitants (Seeley 1995). Nevertheless, a worker bee can profit by laying unfertilized eggs *if* they produce males able to mate. Honeybee queens minimize the success of worker-laid eggs by mating with many males, thereby ensuring that most of a worker's colleagues are half-sisters, more closely related to the queen's eggs than to her own. If a worker's eggs are found by a half-sister, the half-sister eats them, thereby enforcing the workers' common interest in helping their queen reproduce (Ratnieks & Visscher 1989; Halling *et al.* 2001).

At least six mechanisms can reconcile an individual's advantage with the good of its group: (i) reciprocal altruism (Trivers 1971; de Waal 1996); (ii) the attractiveness to potential mates or collaborators of altruistic behaviour (Zahavi & Zahavi 1997); (iii) kin selection (Hamilton 1964); (iv) selection among discrete groups (Crow & Aoki 1982; Leigh 1983); (v) 'trait-group' selection (Wilson 1980); and (vi) competition in the context of mutual policing (Smith 1759). Of these, the last two are most likely to influence the organization of ecosystems.

(a) *Competition, mutual policing and productivity*

Can the economics of Adam Smith (1759, 1776) help us understand what mechanisms promote the productivity and diversity of ecosystems? Of course, economics differs from ecology. Economics is concerned with beings that can reason, and ecology, primarily with beings that cannot reason. Economics studies relationships within a single species; ecology, relationships among many species. Humans often choose their occupations (within limits); plants and animals inherit their parents' ways of life. Nonetheless, economists and ecologists ask similar questions. Both are concerned with productivity. Economists monitor a country's 'gross domestic product', the total monetary value of the goods and services its inhabitants produce in a year; ecologists measure an ecosystem's 'net productivity' by totalling the organic matter (measured by its caloric content) produced by its animals and plants in a year, whether or not it is consumed or discarded before the year ends. Ever since Smith, economists have known that diversity of occupations reflects a division of labour that promotes a country's enrichment, while biodiversity is a central concern of ecologists. What makes economics—especially classical economics of the days before multinationals—so useful a model for ecologists, is that competition for the resources to survive and reproduce is a fact of life in both human economies and natural ecosystems.

Smith (1776) argued that *fair* competition among a society's members for the means to procure the necessities and luxuries of life, promotes diversity of occupations and production of wealth to the extent permitted by the

resources available and the prevailing degree of economic and political stability. Economic expansion is fuelled by increased income, which increases the tempo of economic activity; expanded trade relationships, which facilitate division of labour on a wider scale, permitting more efficient exploitation of the resources available; and technological innovation enabling the exploitation of new energy sources or improved exploitation of existing ones (Smith 1776; Vermeij 1995, p. 142). Forms of competition which obstruct one of these desiderata are deemed unfair. Monopolies are unfair when they sequester resources from those best able to exploit them or block trade promoting more effective division of labour. Other forms of competition, such as robbery or slavery, are deemed unfair because they destroy the relationship between an agent's contribution to the commonwealth and the reward he derives from it.

Smith (1759) assumed that observers of unjust competition would organize communal action to suppress it. In most human civilizations, however, powerful individuals or organizations often escape punishment when they compete in ways that diminish their society's productivity, directly or by the discord such unfairness promotes. Does Adam Smith's theory work better for natural systems? Why should this be so? Is this another instance where evolution is 'cleverer' than we are (Hammerstein 1996, p. 529)?

Adam Smith's theory is illustrated by the genes of a genome. An organism's genes share a common stake in the success of their carrier and its descendants (Leigh 1999, p. 216). Unbiased meiosis ensures that alleles spread only if they benefit their carriers. Nevertheless, at a few loci, 'segregation-distorter' alleles spread a phenotypic defect through a population by biasing meiosis in their own favour (Crow 1979). Alleles at unlinked loci cannot 'ride the coat-tails' of such distorters, but are compromised by the phenotypic defect they spread (Prout *et al.* 1973). At unlinked loci, therefore, selection favours mutants that suppress the segregation distortion. Such mutants restore unbiased meiosis, thereby sparing some of their descendants from the distorter's phenotypic defect. The more unlinked loci there are, the more likely a mutant shutting down distortion is to arise. Here, communal enforcement of unbiased meiosis, the rule defining fair competition among alleles at a locus, assures that selection favours alleles benefiting the individual carrying them (Leigh 1991).

What keeps competition in ecosystems fair? The tendency of unexploited energy to find users serves as a productivity-enhancing form of mutual policing. This tendency serves to undermine the natural counterparts of market-distorting monopolies, which Smith (1776) considered the most prevalent form of unfair competition in human societies. Thanks to their governmental structures and their capacity for large-scale organization, humans can design and defend monopolies more easily than any other organism: in nature, monopolies are rarer and usually shorter-lived. A savage plant-ant that attacks herbivores and destroys leaves and growing tips of vines encroaching on their host-plant and seedlings growing nearby, sometimes enables relatively inefficient host-plants to monopolize space. Thus ants of the genus *Myrmelachista* enable stands of the melastome *Tococa occidentalis* to monopolize

a fraction of the tree-fall and landslide gaps occurring in Peruvian Amazonia. These monopolies, however, are temporary. If the crowns of trees around the gap do not grow and shade out these light-demanding ant-plants, they eventually die off, as if by disease (Morawetz *et al.* 1992). In the eucalyptus forests of southeast Australia, a colony of 30 g birds, bell miners, sometimes monopolizes tracts of forest heavily infested by psyllids, defending them against all other species of canopy birds. For more convenient feeding, the bell miners allow psyllid populations to build up to levels which eventually kill the trees they infest, especially because these birds often eat the psyllids' sugary covers without taking the animals themselves. If the bell miners are removed, other birds move in and eat the psyllids, and the trees recover (Loyn *et al.* 1983). In fact, bell miner colonies are relatively rare.

A few natural monopolies and oligopolies persist. On some sandy soils in the eastern USA, flammable pines grow. The fires they fuel destroy their competitors and ruin the soil (Givnish 1981), creating a 'pine barren', much less productive than the forest that replaces it when fires are prevented. A *Casuarina-Eucalyptus* counterpart grows in certain parts of eastern Australia. The monodominant stands of *Gilbertiodendron dewevrei* in the forests of tropical Africa may also be productivity-reducing monopolies: their litter arthropods are fewer and less diverse, and decomposition of their litter and the recycling of its nutrients are slower (Torti *et al.* 2001).

Monopolies are 'unfair' because they protect their plant and animal beneficiaries regardless of their efficiency or competitive ability. If different monopolies with major effects on ecosystem function evolved in different biogeographic realms, lowland tropical forests on different continents might differ greatly in leaf production, light use or the amount of wood used to place their leaves in the sun. In fact, different rainforests of the lowland tropics resemble each other in these features (table 1). Moreover, leaf-eating insects suffer similar predation pressure in different forests. Birds consume similar quantities (measured by dry weight) of leaf-eating insects in different forests—28 kg ha⁻¹ in Sarawak, 30 kg ha⁻¹ in mainland central Panama, 24 kg ha⁻¹ on Barro Colorado Island, and 20 kg ha⁻¹ in Amazonian Peru (Leigh 1999, table 7.18).

Suppression of monopolies, and effective exploitation of the environment, presupposes diversity. Bell miners would be unable to monopolize sugar-producing psyllids in the lowland tropics, because they could not keep ants from eating the sugar (Greenberg *et al.* 1993). In Hawaii, cloud forest productivity declines as the volcanic soil ages, partly because on those distant islands there is too little dust in the air to replace the phosphorus leached from the soil (Chadwick *et al.* 1999), but partly because the depauperate flora cannot prevent, or cope with, the formation of a hardpan in the soil that blocks root penetration and causes waterlogging near the soil surface (Kitayama *et al.* 1997).

Thanks to the relative freedom of natural ecosystems from monopolies, competition tends to increase their productivity and diversity. Competition is inherently an unequal business, which is why two species must occupy different ways of life, that is to say, be limited by different factors in order to coexist (Gause 1935). Usually, the winner is larger, has a higher metabolism, responds to more different kinds of stimuli, engages in a greater variety of

Table 1. Ecological characteristics of selected lowland tropical rainforests.

(Leaf-fall, tons dry weight ha⁻¹; leaf area index, ha leaves ha ground⁻¹; light, per cent incoming solar radiation reaching the forest floor; gross production, tons carbohydrate ha⁻¹ yr⁻¹; and basal area, total cross-sectional area of tree trunks 10 cm or more diameter at breast height (m²) ha⁻¹. Data for leaf-fall and basal area from Leigh (1999, table 6.1), except basal area for Gabon which is from Hladik (1982). Data for leaf area index from Leigh (1999, table 6.1); data for light from Leigh (1999, table 6.10) except for Barro Colorado Island and La Selva, which are from Engelbrecht (1998, table 5.1). Gross production for Pasoh from Kira (1978, p. 578) and for Manaus from Malhi *et al.* (1998), multiplied by 2.5 to convert from C to carbohydrates.)

	leaf-fall	leaf area index	light	gross production	basal area
Pasoh, Malaysia	6.6	8.0	0.4	77.2	31.4
Gabon, Africa	6.5	—	3.0	—	34.8
Manaus, Brazil	6.0	5.7	1.1	75.0	24.8
Barro Colorado Island, Panama	6.4	7.3	1.6	—	28.5
La Selva, C. Rica	6.6	—	3.2	—	24.7

interactions, and performs more functions at a higher level than does the loser (Vermeij 1999). The replacement of a dominant, which usually results from developing a more effective way to exploit available resources, therefore tends to increase energy flux, not only among the dominants but in the ecosystem as a whole (Bambach 1993), and the number and variety of interactions among species (Vermeij 1999). Competition among species thus promotes the ecological equivalent of technological innovation, increased income, and wider trade networks. When a dominant is replaced, the loser may survive, either in less productive settings or by living off the scraps from the new master's table. Thus the advent of a new dominant often enhances diversity (Vermeij 1999).

Insofar as new dominants are more energetic, adaptable, responsive and intelligent than their predecessors, they are also likely to use more subtle and varied criteria for choosing mates. They are capable, therefore, of a more discriminating choice of mates and are accordingly more susceptible to sexual selection. This susceptibility facilitates speciation and diversification (Darwin 1871). It appears, moreover, that in most species, individuals choose mates on the basis of good health or good genes (Zahavi & Zahavi 1997). In these species, sexual selection reinforces natural selection.

(b) *Pest pressure and mutualism among tropical trees*

A form of group selection, 'trait-group' (Wilson 1975) or 'neighbourhood' (Leigh 1994) selection, can also enhance ecosystem productivity. Neighbourhood selection is best illustrated by fig-pollinating wasps (Herre 1985). One to six mated female wasps enter a fig 'fruit' or syconium (a ball lined on the inside with flowers), pollinate the flowers, and lay eggs in some of their ovules. When mature, this fruit's young wasps mate among themselves, and mated females fly off to find other figs to pollinate. Two levels of selection affect these wasps. Within-neighbourhood selection, selection among one fruit's pollinators, increases a pollinator's share among the genes in this fruit's, this neighbourhood's, mated daughters. Its effectiveness is proportional to the genetic variation among the fruit's pollinators, being zero in one-pollinator fruits and greater in fruits with more pollinators. Selection among neighbourhoods increases the number of mated daughters per fruit. Within-neighbourhood selection fa-

vours a 50 : 50 sex ratio among a pollinator's young, giving it the maximum share among the genes in the neighbourhood's mated daughters, regardless of its competitors' sex ratios. Neighbourhood selection, however, favours only enough sons to fertilize the daughters. Therefore, the young of a fruit's only pollinator are nearly all female, while the proportion of males among a neighbourhood's young is closer to one-half, the more pollinators that fruit has (Herre 1985). Such two-level selection occurs in any kind of organism whose reproductive output is limited, like a tree's, by competition with a few fixed neighbours, but whose young disperse far beyond their parents' competitive reach, creating selection among neighbourhoods (Wilson 1975).

Trees dominate forest ecosystems, so neighbourhood selection among trees affects their whole ecosystem. Insofar as pests and pathogens favour effective seed dispersal, they favour neighbourhood selection among their host trees (Leigh 1994). This neighbourhood selection acts even if a tree's neighbours are different species. Within-neighbourhood selection favours features increasing a tree's share of its neighbourhood's reproduction, whether these neighbours are the same or different species; selection among neighbourhoods favours increasing a tree's absolute reproductive output, even if it means increasing its neighbours' reproduction.

As a tree has several neighbours, within-neighbourhood advantage easily overrides the neighbourhood's good. Nonetheless, trees often face several nearly equally advantageous solutions to a problem. A tree may deploy leaves and roots in ways that also benefit its neighbours, or in ways that enhance its growth at their expense (Horn 1971; King 1993). It may defend its leaves with short-lived chemicals, so that fallen leaves decay rapidly, or with long-lived poisons that slow decomposition of fallen leaves and injure the soil (Hobbie 1992). Neighbourhood selection makes it more likely that the best solution for the neighbourhood prevails.

Indeed, trees benefit their neighbours in various ways. Some lift water from the subsoil, some of which becomes available to neighbouring plants (Dawson 1993) and to soil organisms that improve the soil's water-holding capacity, penetrability and fertility (Joffre & Rambal 1993, p. 571). Others form root grafts with neighbours that help the neighbourhood avoid windthrow during hurricanes (Basnet *et al.* 1993).

Effective seed dispersal is needed, however, to favour solutions that are good for neighbours. In the New Jersey pine barrens, selection favours the non-neighbourly behaviour of flammable pines that create fuel for fires, killing competing oaks and ruining the soil (Bond & Midgley 1995), because fires spread much further than a tree's seeds: these seeds cannot escape their parents' competitive reach. The seeds of the monodominant tree *G. dewevrei* seldom disperse far (Hart *et al.* 1989). These trees are accordingly poor neighbours. They drop a thick decay-resistant litter, reducing the abundance and diversity of litter arthropods and slowing the recycling of nutrients, and create an even canopy casting far deeper, more uniform shade than the uneven canopy of adjacent mixed forest, greatly reducing the abundance of saplings and poles 2.5–25 cm in stem diameter (Hart *et al.* 1989; Torti *et al.* 2001).

4. CONCLUDING REMARKS

We find that, indeed, ecosystems are organized to support high productivity and diversity in the settings where they evolved, as organisms are designed, thanks to natural selection, to survive and reproduce in the locales they inhabit. Evolution tends to increase productivity and diversity. Sudden changes to which an ecosystem's populations are not adapted, diminish its productivity and diversity in the short term even if, like the oxygenation of the atmosphere, these changes eventually allow other, more productive and diverse, ecosystems to evolve.

How are ecosystems organized for these functions? When one dominant replaces another, the new dominant tends to have higher metabolism, respond to more stimuli, carry out more functions quicker, and engage in more varied interactions than its predecessor. New dominants usually manipulate their ecosystem in ways that promote its productivity. High productivity generates an abundant supply of resources from which the ecosystem's members, producers and consumers, all benefit. If they generate resources at a reasonably steady rate, more productive economies usually support greater division of labour by allowing specialization to more specific tasks and by opening up new occupations. In ecosystems, diversity can be quantified by the number of its species, or by the number of distinct ways of life it supports. Diversity and productivity do not increase in lock-step, but usually, higher productivity supports higher diversity. Diversity begets diversity: more interactive species capable of responding to more stimuli can use more criteria to choose mates, and are therefore more susceptible to sexual selection, which greatly increases speciation rate, and reinforces natural selection for higher metabolism, responsiveness to more stimuli and more effective function. Increasing the number of species, moreover, increases the number of opportunities for specialized parasites, pathogens and mutualists. Natural and sexual selection on its component species should therefore increase an ecosystem's productivity and diversity to the extent its environment, and the properties of the available colonists, permit.

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