

Ecosystem development explained by competition within and between material cycles

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Ecosystems generally develop towards increased productivity and biomass, a decreased productivity/biomass ratio, and tighter nutrient cycles. These broad-scale trends are still lacking an explanation in terms of underlying ecological processes. Here I present a simple ecosystem model to show that resource competition between organisms in a material cycle (within-cycle competition) can explain successional and evolutionary changes in functional properties of ecosystems. Competition between organisms that are involved in spatially distinct cycles (between-cycle competition) constitutes another selective force that may lead to more productive and more closed ecosystems. However, these changes in ecosystem properties are only the indirect result of selection for different functional or demographic traits in the organisms involved. Within-cycle competition maximizes resource-use intensity, while between-cycle competition maximizes the basic reproductive rate. Therefore, the two levels of competition may operate in partly contradictory directions, a complication that is ignored by holistic 'maximum principles' in ecology.

Keywords: ecosystems, nutrient cycling, succession, evolution, interspecific competition

1. INTRODUCTION

A number of phenomenological, holistic theories (Margalef 1963; E. P. Odum 1969; H. T. Odum 1983; Ulanowicz & Hannon 1987; Schneider & Kay 1994) have been proposed to account for empirical trends in ecosystem development during succession. These generally include increased productivity and biomass, a decreased productivity/biomass ratio, and increased nutrient cycling (E. P. Odum 1969; H. T. Odum 1983; Begon *et al.* 1990). Although the successional trend towards increased nutrient conservation has been debated (Vitousek & Reiners 1975), Finn (1982) clarified the issue and reasserted the trend toward higher nutrient cycling efficiency during succession. Similar trends, in particular maximization of energy flux or net productivity, have also been postulated in the evolution of ecological systems (Lotka 1922; Odum & Pinkerton 1955; Odum 1983). However, the mechanistic basis for these trends is still unclear.

Material cycles are likely to play a critical role in the organization of ecosystems, as are hypercycles in the emergence of life (Eigen & Schuster 1979). Nutrient cycling has usually been viewed under its immediate aspect, i.e. simply as a process by which the mineral elements necessary for primary production are renewed. But its main significance may lie elsewhere, particularly as the driver of a circular causal chain that transmits indirect effects to all ecosystem components, thereby modifying the nature of the interactions between species and the dynamics of food webs (Ulanowicz 1990; DeAngelis 1992; Loreau 1995). Yet theoretical investigations of its implications for the development and evolution of ecosystems are virtually non-existent (Higashi *et al.* 1993).

I present here a simple model of material cycle, and analyse how competition between species or genotypes drives ecosystem development. Interspecific competition has been used successfully to partly explain successional changes in community structure (Tilman 1988); here I concentrate on its impact on ecosystem processes. I consider two levels of competition: (1) within-cycle competition, defined as competition between organisms that are involved in the same (spatially homogeneous) material cycle; and (2) between-cycle competition, defined as competition between organisms that are involved in spatially distinct cycles. I show that within-cycle resource competition provides a simple mechanistic explanation for successional and evolutionary changes in functional properties of ecosystems. But between-cycle competition for space may also drive ecosystems in a broadly similar direction. Since changes in ecosystem properties are only the indirect result of selection for different functional or demographic traits in the organisms involved, the two levels of competition may be partly in conflict, a complication that is ignored by holistic 'maximum principles' in ecology.

2. A SIMPLE MODEL OF MATERIAL CYCLE

The simplest possible material cycle involves plants (autotrophs) and decomposers (heterotrophs). The model presented in figure 1 captures the essence of such a cycle. The reciprocal plant–decomposer interactions are donor-controlled (consumption of plant material by decomposers does not involve control of plant biomass by decomposers and similarly for uptake by plants of inorganic nutrient released by decomposers), but only indirectly, through the mediation of the inorganic nutrient pool and the litter (or

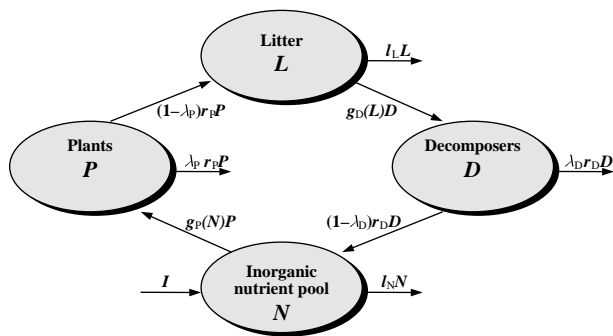


Figure 1. Flow diagram of the material-cycle model.

other forms of dead organic matter). Explicit representation of these non-living compartments is essential, because simple donor-controlled interactions do not allow within-cycle competition between different plant or decomposer species or genotypes. In the system depicted in figure 1, plants and decomposers eventually control the inorganic nutrient pool and the litter, respectively.

The ecosystem is assumed to be limited by a single nutrient; accordingly, all compartment sizes and fluxes correspond to nutrient stocks and fluxes. The inorganic nutrient pool (of size N) is supplied by a constant input I of nutrient per unit time. Plants and decomposers have nutrient stocks P and D , respectively. Their resource uptake depends on their respective stocks and functional responses to resource availability. The latter are represented by the functions $g_P(N)$ and $g_D(L)$, which may have any form provided that they be monotonic increasing. Examples are the classical Holling type 1, type 2 or type 3 functional responses. Plants and decomposers release nutrient (by mortality, excretion, etc.) at rates r_P and r_D per unit time, respectively; these are equal to the turnover rates of plants and decomposers at steady state. A fraction λ_P or λ_D of these flows is lost from the system, the rest ($1 - \lambda_P$ or $1 - \lambda_D$) being cycled within the system as litter (of stock L) or in inorganic form. Nutrient also lost from the inorganic nutrient pool and the litter (by leaching, export, etc.) at rates l_N and l_L per unit time, respectively.

The diagram translates into mathematical equations simply by setting the time derivative of compartment size equal to the sum of inflows minus the sum of outflows for each compartment, thus providing the following set of equations:

$$\frac{dN}{dt} = I - l_N N - g_P(N)P + (1 - \lambda_D)r_D D \quad (1a)$$

$$\frac{dP}{dt} = g_P(N)P - r_P P \quad (1b)$$

$$\frac{dL}{dt} = (1 - \lambda_P)r_P P - l_L L - g_D(L)D \quad (1c)$$

$$\frac{dD}{dt} = g_D(L)D - r_D D \quad (1d)$$

At steady state, the time derivatives in equations (1) vanish; in other words, inflows balance outflows for each compartment. Solving these mass-balance equations

provides the steady-state nutrient stocks, denoted by an asterisk:

$$N^* = g_P^{-1}(r_P) \quad (2a)$$

$$P^* = \frac{S_N^*}{r_P \Lambda} \quad (2b)$$

$$L^* = g_D^{-1}(r_D) \quad (2c)$$

$$D^* = \frac{S_L^*}{r_D \Lambda} \quad (2d)$$

where:

$$S_N^* = I - l_N N^* - (1 - \lambda_D)l_L L^*, \quad (3a)$$

$$S_L^* = (1 - \lambda_P)(I - l_N N^*) - l_L L^*, \quad (3b)$$

$$\Lambda = \lambda_P + (1 - \lambda_P)\lambda_D, \quad (4)$$

and g^{-1} denotes the inverse function of g , the functional response to resource availability.

S_N^* is the excess of inflow of inorganic nutrient over outflows from the non-living compartments, where the loss from the litter is multiplied by the fraction $1 - \lambda_D$ of nutrient that is cycled by the decomposers; therefore it represents the net supply of nutrient in inorganic form at steady state. S_L^* is interpreted similarly as the net supply of nutrient in the form of dead organic matter, while Λ represents the fraction of nutrient lost from the living compartments over a complete cycle.

The steady state can be shown to always verify the Routh-Hurwitz criteria for local stability, hence to be qualitatively stable (Puccia & Levins 1985).

In what follows I assume that plant and decomposer biomasses are proportional to their nutrient stocks, after multiplication by a suitable carbon/nutrient ratio. Similarly, the steady-state primary productivity, Φ_P^* , and secondary productivity, Φ_D^* , are assumed to be proportional to the corresponding nutrient inflows, i.e.

$$\Phi_P^* = g_P(N^*)P^* = \frac{S_N^*}{\Lambda} \quad (5a)$$

$$\Phi_D^* = g_D(L^*)D^* = \frac{S_L^*}{\Lambda} \quad (5b)$$

Thus, the primary and secondary productivities are given by simple ratios between net supplies of nutrient and the fraction of nutrient lost from the material cycle. A distinctive feature of cyclic systems is that the productivities are coupled, so that any parameter change has similar qualitative effects on all of them.

3. WITHIN-CYCLE COMPETITION AND ECOSYSTEM PROPERTIES

Now assume that several plant and decomposer species or genotypes are present within such a cycle. A well-known result from competition theory is that when several species are limited by the same resource, the species with the lowest steady-state resource level eventually outcompetes all the others (Tilman 1982,

1988). Thus, the plant species with the lowest N^* will displace all other plant species; similarly, the decomposer species with the lowest L^* will displace all the others. Thus, competition maximizes resource-use intensity, which is measured conveniently by the inverse of N^* or L^* .

A corollary of this law is that competition for non-living resources also results indirectly in maximization of productivity. To show this, consider the steady-state primary and secondary productivities in the present model ecosystem (equations (5) and (3)). As competition minimizes the steady-state levels of the non-living compartments, N^* and L^* , it also minimizes the nutrient losses from these compartments; therefore, it maximizes the net nutrient supplies, and hence the primary and secondary productivities. Note that this result is also valid for non-cyclic systems, which are recovered as a particular case of the present system where $\lambda_D=1$. It is valid for any consumer–resource system where the resource is renewed by external processes, i.e. where the resource is non-living. What generates the potential for the overexploitation of biological resources (implying a non-monotonic relationship between the productivity and resource-use intensity of consumers) is their self-reproduction. However, as noted above, cyclic systems have the additional property that all productivities are coupled. Therefore, competition between decomposers tends to increase not only their own productivity, but also primary productivity.

How does this relate to ecosystem development? On an ecological time-scale, succession generally involves the progressive replacement of species with high colonization abilities and growth rates by species of greater size and life spans (Odum 1969; Tilman 1988), two factors that contribute to decrease biomass turnover rate. This in turn contributes to increase resource-use intensity: since the plant functional response $g_P(N)$ is a monotonic increasing function of N , $N^*=g_P^{-1}(r_P)$ is an increasing function of the turnover rate r_P , all other things being equal. A similar argument holds for decomposers. Provided that the colonization abilities and growth rates of the successive species are different enough, succession may be approximated by a shifting trajectory of steady-state communities (Tilman 1988). Therefore, interspecific competition makes ecosystems develop towards increasing resource-use intensity, i.e. move to the right along the x axes in figure 2. As a result, both primary and secondary productivities increase. Because the productivity/biomass ratio of a compartment is simply equal to its turnover rate at steady state, this ratio tends to decrease (figure 2), which means that biomass not only increases, but it increases faster than productivity. Finally, the ecosystem's cycling efficiency increases (figure 2), because productivity increases while the input of nutrient is constant, which implies that a greater proportion of fluxes is due to internal cycling.

In short, the dynamics of resource competition within material cycles is able to explain all the trends in the basic functional properties of ecosystems during their development. This conclusion applies *a fortiori* to ecosystem development on an evolutionary time-scale, since in that case transient dynamics can be ignored safely and new genotypes can only invade if they have a greater resource-use intensity.

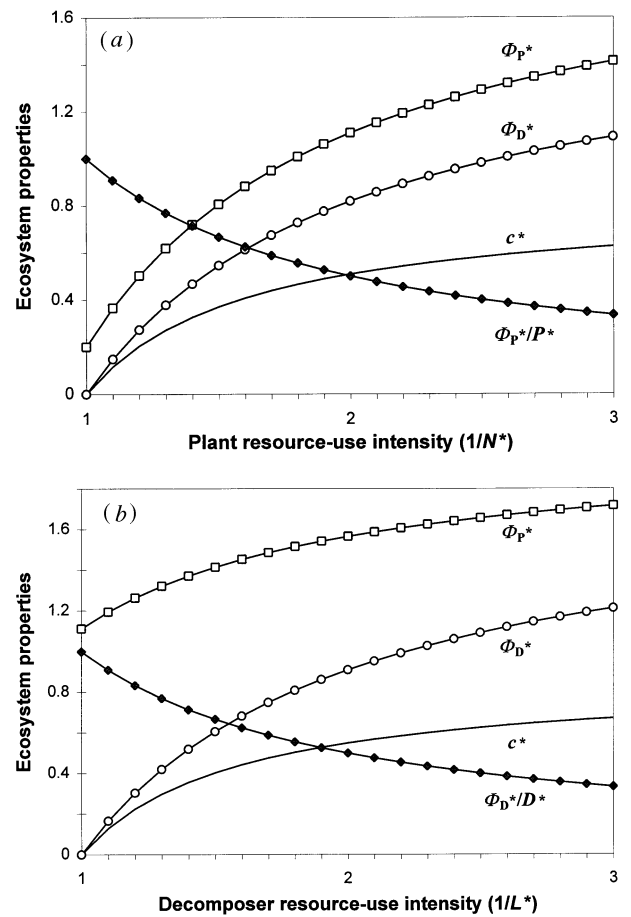


Figure 2. Primary productivity (Φ_P^*), secondary productivity (Φ_D^*), plant productivity/biomass ratio (Φ_P^*/P^*), decomposer productivity/biomass ratio (Φ_D^*/D^*), and cycling efficiency (c^*) as a function of resource-use intensity of plants ($1/N^*$, in (a)) or decomposers ($1/L^*$, in (b)) in the model ecosystem of figure 1 at steady state. In both cases, productivity and biomass of both plants and decomposers increase; the productivity/biomass ratio of either plants (in (a)) or decomposers (in (b)) decreases, while the other is constant; and cycling efficiency increases. Cycling efficiency (multiplied by 2 on the graphs) is measured by the recycled fraction of inflows to the nutrient inorganic pool. Because there is a single cycle in this system, this measure can be shown to be equivalent to the probability that a molecule of nutrient completes a full cycle, and to Finn's (1980) cycling index. Simple Lotka–Volterra functions were used for resource uptakes, the corresponding functional responses being $g_P(N) = \alpha_P N$ and $g_D(L) = \alpha_D L$. Only the nutrient release rates r_P (in (a)) and r_D (in (b)) were variable; the other parameters were set at the following values: $I=1.2$; $\alpha_P = \alpha_D = l_N = l_L = 1$; $\lambda_P = 0.1$; $\lambda_D = 0.5$; $r_D = 0.18$ in (a); $r_P = 0.0889$ in (b).

4. BETWEEN-CYCLE COMPETITION AND ECOSYSTEM PROPERTIES

Resource competition, however, selects directly only for greater resource-use intensity; it is insensitive to other traits of plants and decomposers that may affect ecosystem properties. In particular, any trait that would act to reduce rates of nutrient loss from the system (by reducing λ_P , λ_D , l_N or l_L) would have a strong positive effect on primary and secondary productivities, plant and decomposer biomasses and ecosystem cycling efficiency, as equations (3)–(5) and figure 3 show. (This is true at least

as long as the ecosystem is nutrient limited. In ecosystems where competition for light becomes more important than competition for nutrients as succession proceeds, the pressure to conserve nutrients may be low.)

There are many examples of such traits in plants. Thus, plants may produce litter of different qualities, thereby controlling patterns of nutrient cycling (Hobbie 1992); they may modify soil structure, which in turn strongly affects nutrient retention (Wood *et al.* 1984); or they may recycle some limiting nutrients internally via biochemical pathways (Switzer & Nelson 1972). Traits that increase nutrient conservation may have an associated cost to the genotypes that express them, whereas they may benefit all genotypes indiscriminately in a homogeneous environment. Therefore, their selection is analogous to that of altruistic traits. Positive selection for such traits is known to require sufficient spatial heterogeneity of interactions (Wilson 1980).

The spatial scale at which the cycling of most nutrients takes place is limited—in some cases it may be as small as that of the individual plant (Abbadie *et al.* 1992). This spatial structure tends to generate competition between organisms involved in spatially distinct cycles. The latter constitutes a potential selective force for traits that increase productivity even in ‘climax’ ecosystems. As an extreme, if not completely unrealistic, case of pure between-cycle competition, consider a perfectly structured environment in which each individual plant occupies an isolated site during its lifetime and is associated with a single decomposer individual or colony. Assume that sites become vacant when previous occupants are extirpated by natural death or disturbance, and establishment of both plants and decomposers in vacant sites obeys a ‘competitive lottery’ (Sale 1977; Chesson & Warner 1981). On this hypothesis, the various species or genotypes of either plants or decomposers have approximately equivalent competitive abilities, so that direct competitive displacement in a site is negligible. Finally, assume that the probability of a genotype’s successful establishment in a site is proportional to its total production in all other sites, because higher production means production of more propagules of a higher quality.

The dynamics of site occupancy by plants then obeys the following equation:

$$\begin{aligned} \frac{dS_{Pi}}{dt} &= \alpha_{Pi} \sum_j \Phi_{Pij} \left(1 - \sum_k S_{Pk} / T \right) - m_{Pi} S_{Pi} \\ &= S_{Pi} (r_{Pi} V_P - m_{Pi}) \end{aligned} \quad (6)$$

where

$$r_{Pi} = \alpha_{Pi} \sum_j \Phi_{Pij} / S_{Pi} \quad (7)$$

$$V_P = 1 - \sum_k S_{Pk} / T \quad (8)$$

In this equation, T is the total number of sites available, S_{Pi} is the number of sites occupied by plant genotype i , m_{Pi} is plant genotype i ’s mortality rate, Φ_{Pij} is plant genotype i ’s productivity in site j , and α_{Pi} is plant genotype i ’s reproductive efficiency, a constant of proportionality which incorporates both the allocation of plant genotype i ’s production to

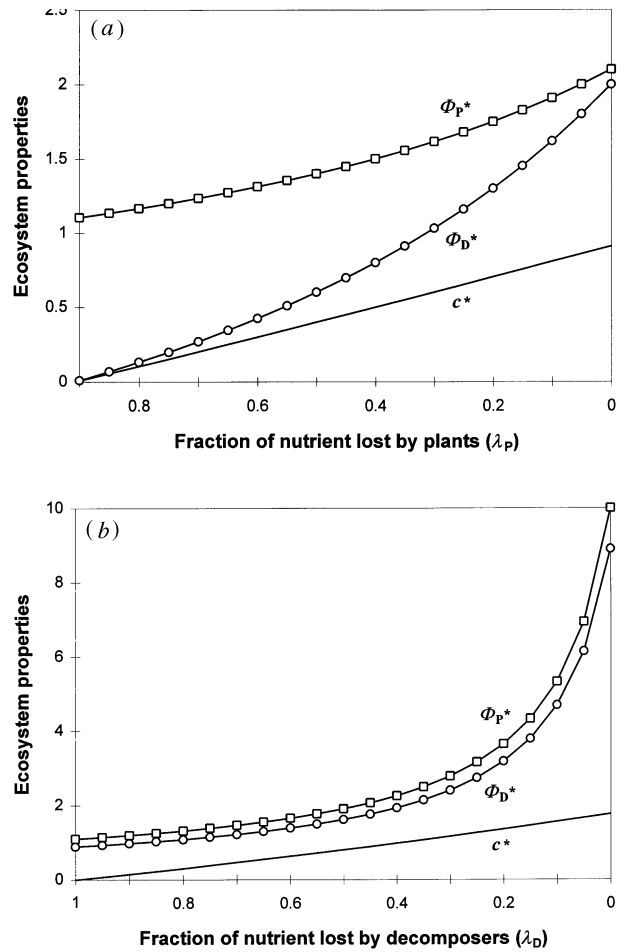


Figure 3. Primary productivity (Φ_P^*), secondary productivity (Φ_D) and cycling efficiency (c^*) as a function of the fraction of nutrient released by plants (λ_P , in (a)) or decomposers (λ_D , in (b)) that is lost from the ecosystem, in the model of figure 1 at steady state. In both cases, the productivity and biomass of both plants and decomposers, as well as cycling efficiency, increase when λ_P or λ_D decreases (note the inverted scales). Productivity/biomass ratios are not affected. Cycling efficiency is multiplied by 2 on the graphs. Parameters values are as follows: $I=1.2$; $l_N N^* = l_L L^* = 0.1$; $\lambda_D = 0.5$ in (a); $\lambda_P = 0.1$ in (b).

reproduction and its ability to disperse and establish in new sites. The aggregated parameter r_{Pi} , which is plant genotype i ’s average productivity multiplied by its reproductive efficiency, then represents a potential reproduction rate, reproduction being considered here to have been completed after the establishment of offspring in new sites. Lastly, V_P is the fraction of vacant sites; only dispersal to vacant sites leads to successful reproduction. Equation (6) is analogous to Levins’s (1969) classical model of metapopulation dynamics, with two major differences: it is applied to a spatially structured population of individuals instead of a metapopulation (Tilman 1994), and it is extended to multi-species or multi-genotype competition for space.

An equivalent equation holds for decomposers, with a mere change in subscripts:

$$\begin{aligned} \frac{dS_{Di}}{dt} &= \alpha_{Di} \sum_j \Phi_{Dij} \left(1 - \sum_k S_{Dk} / T \right) - m_{Di} S_{Di} \\ &= S_{Di} (r_{Di} V_D - m_{Di}) \end{aligned} \quad (9)$$

The outcome of this competition for vacant sites between species or genotypes is straightforward. At steady state, when the time derivative in equations (6) or (9) vanishes, the fraction of vacant sites, V_X^* , must satisfy:

$$V_X^* = m_{X_i}/r_{X_i} \quad (10)$$

where $X = P$ or D . This relation can only be satisfied by a single species or genotype. Therefore V_X^* here plays a role analogous to that of the steady-state resource level in classical resource competition (Tilman 1982, 1988), and the species or genotype with the lowest V_X^* eventually outcompetes all the others.

This result has a simple demographic interpretation. Define the dimensionless quantity R_{X_i} as:

$$R_{X_i} = r_{X_i}/m_{X_i}. \quad (11)$$

R_{X_i} is genotype X_i 's potential reproduction rate, r_{X_i} , multiplied by $1/m_{X_i}$, which is its average life span. Thus, R_{X_i} represents the average number of successfully established offspring that is produced by an X_i individual over its lifetime in a nearly empty habitat ($V_X=1$). This quantity is known as the basic reproductive rate in epidemiology (Anderson 1981). As equation (10) shows, V_X^* is simply the inverse of R_{X_i} . Therefore, the genotype with the highest basic reproductive rate is selected in the competition for site occupancy, both among plants and among decomposers.

In the simplest case where plants and decomposers disperse independently and their effects on their local environment are additive, the outcome of this dual selective process is the selection of that material cycle which combines the plant and decomposer genotypes with the highest basic reproductive rates. (This selection would be strengthened by any spatial association between plant and decomposer genotypes with high basic reproductive rates, or by more than additive interactive effects between these genotypes in a site, but would be counteracted under opposite conditions.) Now, the basic reproductive rate of a genotype is proportional to its average productivity in a site (equations (11) and (7)), all other things being equal. If the dynamics of site occupancy are slow compared with the dynamics of the cycles within sites, the latter will approach their steady state, so that traits that contribute to increase steady-state productivities may be selected for. In particular, selection for increased nutrient conservation is possible, leading to enhanced ecosystem properties, namely, increased primary and secondary productivities, plant and decomposer biomasses, and ecosystem cycling efficiency.

A noteworthy feature of this model is that material cycles within sites behave like 'superorganisms' (Wilson & Sober 1989), where genotypes play the role of alleles at the plant and decomposer 'loci', and the basic reproductive rate is the measure of fitness. Like organisms, these cycles have a temporary existence; their properties result from the random assortment of their constituent genotypes, and the unit of selection is the genotype. Selection of traits advantageous to the cycle is then just as natural as selection of traits advantageous to the individual organism in the classical theory (Wilson & Sober 1989).

5. DISCUSSION: ON SOME MAXIMUM PRINCIPLES IN ECOLOGY

It is clear that within-cycle competition in a perfectly homogeneous environment and between-cycle competition in a perfectly spatially structured environment are two ideal extremes, between which reality should most often lie. Intermediate situations where the two levels of competition act together can be dealt with easily in the frameworks of the structured-deme theory (Wilson 1980) or kin-selection theory (Hamilton 1975; Frank 1994). We are currently developing a more complex model, including two distinct spatial scales, that accounts for the combined dynamics of within- and between-cycle competition. Selection then hinges on the balance achieved between the selective forces that act within and between cycles, this balance in turn being governed by the degree of between-cycle environmental heterogeneity (C. de Mazancourt & M. Loreau, unpublished data).

Both levels of competition work towards increasing ecosystem productivity, biomass and cycling efficiency, thus contributing to the same successional and evolutionary trends in ecosystem development. However, they do so only indirectly, and through different pathways: within-cycle resource competition directly maximizes resource-use intensity of both plants and decomposers. On the other hand, between-cycle competition maximizes their basic reproductive rate. Although productivity is correlated with each of these traits when all other parameters are equal, there may be trade-offs between traits that act to weaken or destroy these correlations. For instance, the basic reproductive rate is determined by the way energy and nutrients are allocated to growth, reproduction, and survival (equations (11) and (7)). These traits are subject to well-known trade-offs (Stearns 1992), so that the basic reproductive rate need not be related in a simple way to productivity. There may also be trade-offs between traits that increase resource-use intensity and other traits that increase productivity, e.g. through improved nutrient conservation. Although I know of no empirical example of such trade-offs, they are likely, theoretically, if traits that increase nutrient conservation have an associated cost in terms of energy or nutrients so that the latter may be diverted from structures and processes that ensure an intensive resource utilization. In such cases, the two levels of competition may operate in partly contradictory directions.

Lotka (1922) postulated that natural selection tends to maximize the energy flux through ecosystems. He gave two informal arguments to support his principle: (i) that natural selection favours organisms that are able to exploit the residue of untapped available matter and energy; and (ii) that natural selection favours groups of organisms that increase the rate of circulation of matter in the ecosystem. His first argument is supported by the present analysis of within-cycle competition; his second argument is partly supported by the present analysis of between-cycle competition (with the qualifications that increasing the rate of material circulation is only one possible way of increasing nutrient conservation, and the latter is only indirectly related to the basic reproductive rate that determines fitness). But he overlooked the possibility of a conflict between the two levels of selection. Therefore, his 'principle' can only be correct in so far as

the broad trends in the development and evolution of ecosystems are concerned.

Odum later proposed that biological and ecological systems obey a 'maximum power principle' (Odum & Pinkerton 1955; Odum 1983), while Brown suggested recently that it is more specifically 'reproductive power' that is maximized (Brown *et al.* 1993; Brown 1995). These principles emphasizing total productivity or reproductive output receive some support from the present analysis of competition in a spatially structured environment. However, productivity or reproductive power are only one component in the basic reproductive rate. It is this inclusive demographic parameter that determines fitness in a spatially structured environment, in agreement with claims that an energetic definition of fitness has to be rooted in demography (Kozlowski 1996; Blackburn *et al.* 1996; Chown & Gaston 1997). Furthermore, the trait that is maximized by competition in a homogeneous environment is the intensity of resource exploitation, which is more distantly related both to reproductive power and to simple demographic parameters.

To be of any explanatory or predictive power, ecological 'principles' must be based on underlying ecological mechanisms. The theory presented here seeks to explain ecosystem properties in terms of lower-level processes, and accordingly helps reveal some of the selective forces at work, identify the conditions under which they operate, and formulate more testable predictions on ecosystem development.

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