Bioenergetics and the Dimensionality of Ecosystems

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1   Introduction

A major open topic in ecology is the understanding of the emergence and dynamics of diversity in ecosystems. Cascades of evolutionary branching in a DEB-community (where trade-offs in parameter values are well specified) are a possible explanation for an increase in diversity, but the maximal diversity is bound by the dimensionality of the environment (Meszéna and Metz, 1999). The purpose of this essay is to characterize a DEB-community (Kooijman, 2000, 352-356) subject to adaptive dynamics, from the point of view of dimensionality.

Since the dimensionality of the abiotic environment is exogenous to the biotic community, a persistent increase in diversity requires an increase in dimensionality in the biotic environment. A simultaneous increase in diversity and dimensionality can mean the branching (Geritz et al., 1997) of a primitive population into two populations, "genetically" and functionally isolated, such that a new resource has appeared.

The structure of the essay is as follows. In section 2 a DEB-mixotroph population in a homogeneous environment is summarily characterized, and in section 3 conditions for a persistent increase in diversity are discussed. In section 4 a discussion closes the paper.

2   Bioenergetics and natural selection

A DEB-individual (Kooijman, 2000, 65-120) is fully characterised through initial conditions and a set of two dynamic equations:

$$\frac{dl}{dt} = f(l, e, X; \Phi, \Psi) \, ;$$

$$\frac{de}{dt} = g(l, e, X; \Phi, \Psi) \, .$$

The state variables are l and e, respectively scaled volumetric length and scaled reserve density. X stands for the generalized resource, Φ stands for the set of traits of the individual and Ψ for the set of parameters of the environment (such as temperature or salinity, i.e., all properties of the environment that are not X).

Φ is the set of traits or "meta-parameters" of which the true DEB-parameters are a function of. For example, extensive parameters are linearly dependent on maximal body size while intensive parameters are independent. The functional response terms

(saturation coefficient and maximal ingestion rate) co-vary in a special relation, etc. The existence of these constraints (Kooijman, 2000, 267-270) reduces the set of traits to a number smaller than the set of DEB-parameters.

A structured DEB-population (Kooijman, 2000, 322-344) can be characterized by $\boldsymbol{r}$, the number of individuals in an infinitesimal interval in the phase-space of l, e, and a, age, and by the total size of the population, N:

$$\frac{d}{dt}\boldsymbol{r}(l,e,a) = p(l,e,a,X;\Phi,\Psi);$$

$$N(X,\Phi,\Psi) = \int \boldsymbol{r}\, dl\, de\, da.$$

To obtain these equations explicitly it is necessary to solve the McKendrick equations, which is by no means trivial (Gurney and Nisbet, 1998). But for the purpose of this essay we assume that these equations exist.

Until now we considered that the population was physiologically structured but that all its individuals shared the same set of parameters, Φ. Ignoring the specific mechanism of reproduction and assuming that mutations are rare and small, natural selection can be introduced as follows.

Let there be a resident population, x, exhibiting parameter or trait set Φ_x. Let there appear, by mutation, an invading population, y, exhibiting trait set Φ_y. In a first moment, the population size of the invader is small and so the environment is fully characterized by the resident population. If the growth rate of the invader in this environment is smaller than that of the resident, the invader cannot thrive and the invader trait goes extinct. If it is larger, than the invader grows and two situations are possible. When population x becomes rare, it cannot grow in the environment set by y, x becomes extinct and y establishes itself as the new resident. Otherwise, if when x is rare it can grow in the environment set by y, then both traits can be mutually invaded and both will survive, evolutionary branching has occurred (Geritz et al., 1997).

3   Discrete dimension of a small community

Consider a DEB-population of V1-morphs, with 1 life stage, such that the population dynamics are simply the dynamics of an individual scaled to the population size. Consider a spatially homogeneous environment closed to mass transfer and with input of one form of energy (e.g., light). Consider furthermore that the population is composed of mixotrophs, that can alternatively process the external inflow of energy, be heterotrophs (cannibals in this case) or decomposers, converting dead organic matter into non-organic materials (Mulder et al., 2001).

Without natural selection, a functional community may arise (Kooijman, 2000, 352-356), exhibiting cyclical fluctuations, since originally autotrophs thrive but as inorganic matter is exhausted growth must halt. Heterotrophism and decomposition become feasible, when organic mass is abundant. Hence, under some conditions, defined by the DEB-parameters, it is possible that a three-stage community arises. Each stage processes a different type of resource (environmental dimension). Autotrophy is supported by the abiotic environment (either the external energy source or inorganic matter) and decomposition is supported by the first biotic dimension (biomass). The number of heterotrophic levels depends on the number of different

preys, which is one in the absence of natural selection, since all individuals are identical.

Assume that different individuals take different specializations and do not change it throughout their lives. Natural selection, through trait change, turns functional diversity into genetic divergence, since the traits that are more advantageous for each specialization are different. Loss of metabolic plasticity is advantageous for prokaryotes since it allows for a reduction in DNA size and hence an increase in population growth rate, which favours specialization, if the environment is stable (Kooijman, 2000, 294-295). The emergence of genetically isolated populations allows in turn the coevolution of preys and predators, leading to stabilization of traits (Doebeli and Dieckmann, 2000). Thus, specialization of several consumer levels is expectable.

Specialization at the bottom and at the top of the ecosystem are not so plausible. The energy source is assumed to be unique and even though the decomposers can also specialise in structure or reserves, or the corpses of some particular "species", structural homeostasis implies that species that are genetically similar are also biochemically similar (Kooijman, 2000, 30) – hence leaving little room to specialization.

Assume that each evolutionary branching occurs at a time, since mutations are rare. Then the adaptive dynamics of a new trait y in a population x are described in the (Φ_x, Φ_y) phase-space, by the sign of the invasion exponent, $s_x(y)$, which is the growth rate of a rare mutant y in an environment set by population x (Geritz et al., 1997). The invasion exponent is a function of X, Φ_x and Ψ. Now X is the vector of different resources (the environment), which is $1 + n$ dimensional, where n is the number of isolated populations in the community. Ψ is a set of $1 + n$ sets of parameters, containing the parameters of the abiotic environment plus the sets of traits of each isolated population.

If the dimensionality of the environment is measured discretely, the complexity of the problem grows in direct proportion to the number of different coexisting populations. In a DEB-model, where mass and energy conservation are explicitly considered, the maximal number of coexisting populations (hence the dimensionality of the environment) is constrained by the energy available to fuel the ecosystem, and only a finite (and expectably small) number of coexisting species is possible.

4 Discussion

In this essay the evolutionary dynamics of a DEB-community in a closed environment were characterized, from the point of view of dimensionality. It was argued that a cascade of evolutionary branching occurs simultaneously with a stepwise increase in the dimension of the environment. This may lead to substantial modelling complexity, even for a small cascade.

The dynamics of diversity in the real world, of course, are not explained only through the simple mechanism sketched above. There is an intrinsic dimensionality of the environment arising from spatial heterogeneity (Kareiva and Tilman, 1997), seasonality, diversity of mass fluxes, etc. Moreover, the action of biota leads to further structuring of the abiotic environment (O'Neill et al., 1996). Besides, no ecosystem is closed, species migrate and go extinct (the McArthur-Wilson theory of biogeography) and ecosystems themselves expand or contract.

However, an important question that might be asked in a very simple context as this is how does energy availability relate to the carrying capacity for biodiversity. Two large scale patterns are apparent worldwide: the validity of species-area relationship, even at a continental scale (Brown, 1995), and a decrease in biodiversity from the Equator to the Poles. If homeostasis at the individual level is assumed (Kooijman, 2000, 30), low temperature, seasonality or nutrient scarcity ultimately imply higher energy costs, due to the need to dissipate more heat (Kooijman, 2000, 92-94) or to storage reserves for the low season or to buffer the availability of critical nutrients (Kooijman, 2000, 37-39). Hence, the empirical evidence (species-area and Latitude-diversity correlations) seems to support the idea that energy availability is correlated with the ultimate limit to biodiversity. In the context of the closed environment described above, changing the availability of inorganic compounds and energy inflow suffices to test this hypothesis.

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