

Cell size as a master functional trait of microorganisms: Emerging trade-offs and community structure¹

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Introduction

One of the major challenges in ecology is to find general principles under which ecological communities are structured. It has been argued for a long time whether any deterministic “rules” or stochastic forces shape ecological communities [2, 3, 6]. Recent studies suggest that, although species composition in communities may be contingent on stochastic events, trait-based functional groups are deterministically selected for by the environmental conditions [5]. Hence “rules” may be adopted to trait groups instead of species, and the trait-based approach is increasingly common among community ecologists in recent years [7, 11].

In the trait-based approach, species are defined by a point or distribution of multidimensional trait space instead of the nomenclature. Resource competition, predation, dispersal, and adaptation/evolution structure communities of trait groups along environmental gradients. The theoretical framework of this approach is adaptive dynamics of continuous traits [7, 10], with which we seek for a set of species such that all members stably coexist and others cannot invade (Evolutionary Stable Strategy, ESS).

Adaptive dynamics has been successful in proposing novel mechanisms of evolution, coevolution, and sympatric speciation along one dimensional trait space or arbitrary trade-off curves (typically linear) in multidimensional trait space [4]. However, there are more than one functional traits that significantly influence ecological interaction, and outcomes of the interaction can strongly depend on the shape of trade-off curves [12]. Therefore we need to sort out a set of influential functional traits, and to derive trade-offs between traits from first principles or from empirical observation.

Cell size as a master trait

In aquatic environments, unicellular organisms (bacteria and phytoplankton) compete for resources such as inorganic nutrients and organic matter. The limiting factor for growth often being resource availabilities, Functional traits relating to the uptake and synthesis are considered to be crucial in shaping communities.

Both theories [1] and experiments [8] indicate that nutrient uptake traits can be scaled by cell by a power-law:

$$X = \alpha V^\beta$$

¹This work was supported by the Global Environmental Research Fund (Fa-084) by Ministry of the Environment, Japan.

where X is a trait value, V is cell volume, and α and β are coefficients. For example, transport rate of nutrient molecules to the cell surface is proportional to cell radius ($r \propto V^{1/3}$), and uptake rate at membrane surface is proportional to r^2 ($\propto V^{2/3}$) for a spherical cell in theory [14]. Storage capacity of nutrients should be proportional to the volume of storage, and empirical evidences support the argument [8].

Functional traits that relate to loss processes, such as predation, infection, and sinking also depend on cell size. This implies that cell size strongly affects the fate of unicellular organisms. For example, small phytoplankton are mostly consumed by smaller zooplankton in the surface layer, fueling microbial loops. Medium-sized phytoplankton, on the other hand, are consumed by larger zooplankton, and energy and matter are transferred up to the classical food chain. Larger phytoplankton are not consumed in the surface layer, instead, directly sink to the deep ocean, being an effective biological pump. Therefore cell size is one of the most important traits of bacteria and phytoplankton from an ecological point of view, as well as being a master trait that influences most functional traits that are crucial in determining community structure.

Adaptive dynamics of cell size

Assuming theoretical and/or empirical scaling relationships [1, 8, 14], dimension of trait space is reduced to one. Each trait is a function of cell size, and species evolve along a curve expressed parametrically by cell size. Recent theoretical studies analyzed adaptive dynamics of cell size in the reduced trait space [9, 13, 14].

The curve in trait space is derived theoretically or empirically, and do not explicitly assume trade-offs between functional traits, prerequisites for stable coexistence of species. Two studies [9, 14] showed coexistence of different-sized cells, implying that the scaling relationships embrace trade-offs between functional traits.

In [14], Yoshiyama & Klausmeier employed theoretical scaling relationships between cell size and resource uptake traits, and analyzed a resource competition model. They proved that an optimal cell size increases with decreasing resource molecular weight, and that different-sized cells can coexist on two different-sized resource molecules. A trade-off emerges between utilizing resources of different molecular weights, which was derived from first principles of biophysics. However, the trade-off is not sufficient enough for a coalition of different-sized cells to be evolutionary stable.

In [9], Litchman and colleagues parameterized a resource competition model of phytoplankton using empirical relationships between cell size and resource uptake traits. The aim was to explain observed difference in size distributions of diatoms between marine and freshwater environments. They considered four environmental settings: either nitrogen or phosphorus is the limiting nutrient under constant or fluctuating supply (Table 1). When phosphorus is the limiting nutrient, as usually observed in freshwater environments, being small is the ESS, and

| | Constant input | Short | Fluctuating input Intermediate | Long |
|--------------|----------------|------------|-------------------------------------------|------------|
| N limitation | Small cell | Small cell | <i>Coalition of small and large cells</i> | Small cell |
| P limitation | Small cell | Small cell | Small cell | Small cell |

Table 1: Four environmental settings and the corresponding ESS. Created from results of [9].

large cells cannot persist regardless the regime of nutrient supply. In contrast, under nitrogen limitation, as usually observed in marine environments, ESS cell size grow larger with an increasing period of nutrient input, and an evolutionary stable coalition was achieved at input frequency of 30 to 40 days (see Fig. 2 of [9]). Such intermediate frequency in nutrient input is typically observed in marine environments, rarely in freshwater environments. In this case, a trade-off emerged between better growth at low nutrient conditions and storing nutrients from the empirical scaling relationships. However, it was realized only under nitrogen limitation and fluctuating nutrient input. Unlike the previous example, the trade-off is strong enough such that two species can coexist as an ESS, and evolutionary dichotomy can be achieved.

Concluding remarks

Current focus of community ecology is shifting to trait groups and the interaction with environments. Trait-based approach of community ecology tries to find assembly rules of trait groups, and to forecast how the assemblages shift under rapidly changing environments. Because trait groups are distributed in trait space that is essentially multidimensional, the most important task is to reduce the space by selecting a couple of functional traits or by choosing a few master traits that relate to other functional traits.

For unicellular organisms, cell size can be a master trait with which other functional traits are expressed by allometric relationships, and evolution of the community structure is adequately analyzed by adaptive dynamics of cell size. Future theoretical challenges are to incorporate cell growth cycle, multiple limiting resources, size-selective predators, and spatial structure that may significantly modulate the community structure.

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