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Competitive exclusion and limiting similarity: A unified theory

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Abstract

Robustness of coexistence against changes of parameters is investigated in a model-independent manner by analyzing the feedback loop of population regulation. We define coexistence as a fixed point of the community dynamics with no population having zero size. It is demonstrated that the parameter range allowing coexistence shrinks and disappears when the Jacobian of the dynamics decreases to zero. A general notion of regulating factors/variables is introduced. For each population, its *impact* and *sensitivity* niches are defined as the differential impact on, and the differential sensitivity towards, the regulating variables, respectively. Either the similarity of the impact niches or the similarity of the sensitivity niches results in a small Jacobian and in a reduced likelihood of coexistence. For the case of a resource continuum, this result reduces to the usual "limited niche overlap" picture for both kinds of niche. As an extension of these ideas to the coexistence of infinitely many species, we demonstrate that Roughgarden's example for coexistence of a *continuum* of populations is structurally unstable.

Keywords: Population regulation; Competitive exclusion; Coexistence; Limiting similarity; Niche

1. Introduction

We expect the struggle for life between the kinds attempting to occupy the same niche and peaceful coexistence between the species established in different niches (Gause, 1934). This principle of "competitive exclusion" has become a cornerstone of ecological thinking while at the same time it has remained highly controversial. The basic models were introduced by MacArthur and Levins in the mid-1960s both for discrete and for continuous resources. These models differ considerably in their mathematical setup and sophistication.

The discrete models (MacArthur and Levins, 1964; Tilman, 1982) consider competition for a finite number of distinct resources and state that the number of coexisting species should not exceed the number of resources they compete for. This conclusion has a sound mathematical foundation: to have a structurally stable solution, i.e., a solution that does not disappear on the slightest change of the model specification, the number of equations describing the population dynamical equilibrium should not exceed the number of unknowns.

With some risk of becoming tautological, we can relax the assumption of resource competition by counting all the factors behaving like resources (Levin, 1970; Armstrong and McGehee, 1980; Heino et al., 1997). Limited practical usefulness is the price for theoretical robustness. It is a rare biological situation where the resources, or the regulating factors, are easy to count and low in number. In most cases, very many environmental factors that are potentially regulating are present. Which are the really important ones? Which of them should be considered as distinct from the others (cf. Abrams, 1988)? On the other hand, if only

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the limiting resources are counted, their number often turns out to be too low to explain species diversity in a constant environment (Hutchinson, 1959).

The classical continuous model (MacArthur and Levins, 1967) studies the partitioning of a continuous scale of resources, e.g., seeds of different sizes. In this case, strictly speaking, an infinite number of different resources are present, i.e., each seed size has to be considered as a different resource. Consequently, the argument used for the discrete situation cannot be applied to bound the number of species in the continuous case. Still, we do not expect an infinite number of species to coexist. The classical concept of "limiting similarity" (Hutchinson, 1959), based on the study of the Lotka–Volterra competition model (MacArthur and Levins, 1967), states that the resource scale is partitioned between the species. The width of the "resource utilization function" of a species is expected to set the width of a single partition, referred to as the "niche breadth". The allowed similarity of the coexisting species is limited and their number is bounded by the number of possible partitions. It seems to be reasonable to consider one partition of the resource scale as a single resource, distinct from the rest. Unfortunately, no mathematical theory has appeared as yet that fully captures this intuition in a general way: again, the question is, to what extent should the resources differ to be counted as different? Neither has any general conclusion emerged when the later studies went beyond the original Lotka–Volterra framework. These studies actually resulted in a fading away of the hope of finding a model-independent lower bound to similarity (Abrams, 1983).

The status of the limiting similarity principle is unclear even for the original Lotka–Volterra model. May (1973, p. 158) found that the limit of similarity of two coexisting species can be arbitrarily small if their respective carrying capacities are chosen to be sufficiently similar. Yodzis (1989, p. 125) states that, contrary to the two species case, there is a strict lower bound to similarity for three species. Probably, the most drastic blow against limiting similarity occurred when Roughgarden (1979, pp. 534–536) provided an example of coexistence of a *continuum* of types in the Lotka–Volterra model. While the example was intended to describe the phenotype distribution within a single species, it can be interpreted in the context of species coexistence. An infinite number of different resources *does* allow coexistence of an infinite number of species. The example thus seems to violate the whole idea of limiting similarity (Maynard Smith and Szathmáry, 1995).

Even though limiting similarity and resource partitioning failed to earn the status of a mathematical theory, they have remained widely accepted concepts in ecology (Begon et al., 1996, p. 300). However, if limiting similarity were just an artifact of some specific mathematical models, we would not be allowed to use it as a basis of biological reasoning. Without limiting similarity, the practical relevance of competitive exclusion would be constrained to the simplest cases of population regulation (Rosenzweig, 1995, p. 127). If we could not safely assume competitive exclusion between the variants of the same species, even the Darwinian concept of natural selection would lose its basis. The goal of the present paper is to carry out the mathematical step from the solid ground of competitive exclusion in the discrete case to establish the general existence of limiting similarity in a well-defined sense.

The key issue of species coexistence is the necessity for mechanisms stabilizing it (Chesson, 2000b). This vantage point allows us to investigate the problem independent of specific model assumptions. We start from May's observation (May, 1973, 1974) that the more similar the two species are, the more narrow the range of K_1/K_2 permitting coexistence (May, 1973; K_1 and K_2 stand for the two carrying capacities. See also a similar analysis by Vandermeer, 1975, which uses the intrinsic growth rates, instead of the carrying capacities as a reference.) We generalize this statement beyond its original framework of a Lotka–Volterra-type model and to an arbitrary number of species. Limiting similarity is interpreted as a shrinking likelihood of coexistence with increasing similarity. Especially, we demonstrate that the Roughgarden type of continuous coexistence, as it is called, generally becomes impossible on the slightest change of the model. To relate limiting similarity to resource usage, or to the regulating factors, and to the concept of niche, we will apply Leibold's (1995) distinction between the two legs of the population–environment interaction. We restrict our mathematical analysis to fixed-point attractors in a constant environment.

The theory is presented in several steps. After introducing our central notions in Section 2, we demonstrate the basic issues of limiting similarity and establish the connection between the discrete and the continuous cases via a linear model in Section 3. Then, in Section 4, the nonlinear, model-independent generalization is presented. Finally, we discuss the wider context of our work, in Section 5. Background mathematics are summarized for the convenience of the interested reader in the appendix.

2. Basic concepts

2.1. The notion of robust coexistence

Populations coexist when the long-term growth rates of all of them are simultaneously zero, i.e., the births just compensate for the deaths in each of them. Coexistence of any given set of populations can be achieved in many parameter-rich models by adjusting the parameters. The problem of coexistence becomes non-trivial only when one rejects parameter fine-tuning and requires the population dynamical equilibrium point to exist for a considerable range of the parameters. In a given environment, the wider this range, the more likely the coexistence. We will refer to this property as *robustness* of coexistence. Robustness of coexistence is measured by the volume of the set of parameter values permitting coexistence. In special, but