

1 Introduction

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“Not until we reach the extreme confines of life, in the arctic regions or on the borders of an utter desert, will competition cease. The land will be extremely cold or dry, yet there will be competition between some few species, or between individuals of the same species, for the warmest or dampest spot.”

Charles Darwin, *The origin of species* (1859)

Many ecologists consider competition as one of the most important ecological processes causing pattern in species composition and biodiversity. For the past century, various theoretical, laboratory and field studies have sought to understand how species that compete can coexist. In the early 1980s, two influential reviews (Schoener 1983; Connell 1983) demonstrated that, at least in published studies, interspecific competition appears to be frequently important. At the same time, there was little evidence for competitive exclusion, that is, the local extinction of species due to competition (Schoener 1983; Connell 1983). These empirical results were complemented by major theoretical advances that sought to create a coherent body of competition theory. These efforts culminated in the publication of several books on the issue (Keddy 1989; Tilman 1982, 1988; Grace and Tilman 1990). Today, we consider it timely to write a new volume, as experimentation and modelling of competition-coexistence relationships have well advanced beyond the milestone books of the 1980s. In addition to this, the global loss of biodiversity has led to a renewed interest in mechanisms that explain spatial differences and temporal change of diversity. The academic interest of the previous period is now being supplemented by the practical interest of safeguarding biodiversity against further losses. By integrating the latest theoretical and empirical advances in the field, we hope to provide a basis for further progress in competition research and biodiversity management. According to these goals, this book's focus is species coexistence, competitive exclusion and the role of these processes for community diversity. We place less emphasis on those models and experiments which attempt to predict species composition for specific competitive scenarios.

1.1 The Intellectual Debate Until 1990

“Why are there so many or so few kinds of plants and animals?” has been one of the most long-standing debates that have challenged ecologists at least from the publication of Gause’s (1934) classic experiments, which for the first time demonstrated that competing species could drive each other to local extinction. This was later called the “competitive exclusion principle” (CEP, Hardin 1960). Following this line, a most fruitful ecological debate was initiated by G.E. Hutchinson’s seminal article about the “paradox of the plankton” (1961). He pointed at the apparent contradiction between the CEP and the species richness of phytoplankton, a community of primary producers which share a small number of potentially limiting resources (light, CO₂, mineral nutrients), obtain them from a shared resource pool and live in a well-mixed environment without spatial escapes for inferior competitors. Solving Hutchinson’s paradox has become one of the most important issues in theoretical and experimental community ecology, although direct reference to it has been mostly restricted to plankton researchers. The attempts at a solution have encompassed the entire logically possible spectrum:

1. No competition: Competition does not occur at all in nature. According to Simberloff (1983) and others, patterns ascribed to competition during the Hutchinson–MacArthur era (MacArthur and Levins 1967; MacArthur 1968) could as well be explained by random processes. This critique caused considerable unrest in the ecological community of the early 1980s but did not withstand the test of time. However, quite a number of ecologists were left with the impression that the importance of competition as a pattern-forming process in nature had been overestimated previously (e.g. Keddy 1989).
2. Disequilibrium: Competition does occur in nature but competitive exclusion is an artefact resulting from the restrictive conditions of competition models and experiments, particularly spatial homogeneity and temporal constancy. Theoretical concepts invoking spatial or temporal refuges from competitive exclusion have been called (among others) “contemporaneous disequilibrium” (Richerson et al. 1970), “regeneration niche” (Grubb 1977) and the “intermediate disturbance hypothesis” (IDH, Connell 1978). Experimental support for the IDH came from studies with plankton communities and with communities of sessile organisms.
3. Equilibrium: Evolution of competitors leads to a specialisation in optimal resource ratios. Even if the same resources are required (e.g. nutrients and energy for autotrophs) they are required in different ratios, and species with different optimal ratios might coexist in spite of competition. Tilman (1977) demonstrated this with phytoplankton species requiring different rations of mineral nutrients (RRH: “resource ratio hypothesis”). Later, Tilman (1988) extended his approach to terrestrial vegetation, emphasising

trade-offs in competitive abilities for below-ground (water, nutrients) and above-ground (light) resources. The RRH was supported by modelling, experimental and field studies with plankton and with terrestrial plants.

1.2 Progress During the Last Decade

Quite naturally, research proceeded with further experimental and field studies testing and usually supporting the IDH or the RRH. But at the same time, new developments in theory provided the perspective of overcoming the dichotomy between the “equilibrium view” of the RRH and the “disequilibrium view” of the IDH. Among others:

1. Huisman and Weissing (1994) developed a model for phytoplankton competing for light and a mineral nutrient under constant conditions. Because of the different spatial pattern of light supply (vertical gradient) and nutrient supply (well-mixed), several predictions of the RRH do not apply for this resource couple.
2. Tilman (1994) proposed a model in which sessile organisms compete with their neighbours and provide empty space when they die. If there is a trade-off between the ability to colonise empty space and competitive ability, even the dominance of a single dominant competitor will not lead to competitive exclusion.
3. The spatial competition model (Tilman 1994) was extended by Kondoh (2001) by integrating the effects of productivity and disturbance, which according to model simulations have interactive effects on diversity. Interestingly, although this is an equilibrium model, predicted diversity patterns match those from a non-equilibrium model, which also emphasises the interactive effects of productivity and disturbance (Huston 1994).
4. Huisman and Weissing (1999) used simulation studies to test the classic resource ratio model with more than two limiting resources. In this case, population density and resource concentration trajectories did not approach steady state as with one or two limiting resources. Instead, sustained oscillations or chaotic fluctuations were found over a wide range of realistic parameter values. These dynamics generated the necessary degree of temporal variability which precluded competitive exclusion.

Some of these new models have been tested and confirmed by experiments, others are not yet tested but deserve interest because of the potential for a new synthesis in competition theory.

1.3 Consequences for the Structure of the Book

The new models of the 1990s point at the importance of how competitors and their resources are distributed in space. Therefore, the spatial distribution and utilisation of space will be the central organising principles of our book.

In two theoretical chapters, models for competition in well-mixed environments (Chap. 2) and space-explicit models (Chap. 3) are presented and discussed. Four empirical chapters summarise experimental and observational evidence that supports or refutes theory presented in the first chapters. We focus on four types of communities, which represent very different forms of spatial organisation:

- More or less passively mixed plankton communities (Chap. 4) provide the best possible natural approximation to mixed reactor models. Competitive interactions occur between entire populations. There are no permanent neighbourhood relationships between individuals.
- Mobile animals (Chap. 5) differ from plankton in that they can actively choose the site of resource acquisition and have action ranges exceeding the scale of spatial patchiness of their resources.
- Sessile plants and animals depend on local resource availability without a chance to search for better sites and interact competitively with permanent neighbours. In our book, we provide separate chapters for benthic communities on rocky shores (Chap. 6) and for terrestrial vegetation (Chap. 7). An important distinction between the two is that the former cannot exploit the third dimension below ground, while the latter can.

In a final synthesis chapter (Chap. 8) we attempt to summarise the progress of the last decade, highlighting both advances made and remaining questions that may provide fruitful avenues for future research.

References

- Connell JH (1978) Diversity in tropical rain forests and coral reefs. *Science* 199: 1302–1310
- Connell JH (1983) On the prevalence and relative importance of interspecific competition: evidence from field experiments. *Am Nat* 122:661–696
- Gause GJ (1934) *The struggle for existence*. Williams and Wilkins, Baltimore
- Grace JP, Tilman D (1989) *Perspectives on plant competition*. Academic Press, New York
- Grubb PJ (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biol Rev* 52:107–145
- Hardin G (1960) The competitive exclusion principle. *Science* 113:1292–1298
- Huisman J, Weissing F (1994) Light-limited growth and competition for light in well-mixed aquatic environments. *Ecology* 75:507–520

- Huisman J, Weissing F (1999) Biodiversity of plankton by species oscillations and chaos. *Nature* 402:407–410
- Hutchinson GE (1961) The paradox of the plankton. *Am Nat* 95:137–145
- Huston MA (1994) Biological diversity. Cambridge University Press, Cambridge
- Keddy P (1989) Competition. Chapman and Hall, London
- Kondoh M (2001) Unifying the relationships of species richness to productivity and disturbance. *Proc R Soc Ser B* 268:269–271
- MacArthur RH (1968) The theory of the niche. In: Lewontin RC (ed) Population biology and evolution. Syracuse University Press, Syracuse
- MacArthur RH, Levins R (1967) The limiting similarity, convergence and divergence of coexisting species. *Am Nat* 101:377–385
- Richerson P, Armstrong R, Goldman CR (1970) Contemporaneous disequilibrium, a new hypothesis to explain the “paradox of the plankton”. *Proc Natl Acad Sci USA* 67:1710–1714
- Schoener TW (1983) Field experiments on interspecific competition. *Am Nat* 122:240–285
- Simberloff D (1983) Competition theory, hypothesis testing and other community ecology buzzwords. *Am Nat* 122:626–635
- Tilman D (1977) Resource competition between planktonic algae: an experimental test and theoretical approach. *Ecology* 58:338–348
- Tilman D (1982) Resource competition and community structure. Princeton University Press, Princeton
- Tilman D (1988) Plant strategies and the structure and dynamics of plant communities. Princeton University Press, Princeton
- Tilman D (1994) Competition and biodiversity in spatially structured habitats. *Ecology* 75:2–16



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