Revista Chilena de Historia Natural
*63:* 149-156, 1990

COMMENTARY

# Competition between distantly related taxa: three reasons why it is not more often reported

## Competencia entre taxa distantemente relacionadas: tres razones por las cuales no es a menudo reportada

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**ABSTRACT**

The information on food competition between distantly related animal taxa, published between 1970 to 1989 for terrestrial ecosystems, was reviewed. Aside from the many studies reporting competition between congeneric, confamilial or conordinal species within several trophic guilds, there are a few well-documented cases of competition between species belonging to different Classes, Phyla and Kingdoms. Three reasons may account for the little interest received by competition between distantly related taxa: 1) deeply rooted ideas about the proper way to study competition, 2) the way in which resources are defined; and, 3) methodological constraints, that limit the detection of the phenomenon and interpretation of the patterns resulting from it. I concluded that competition between closely related taxa is just one particular case of competitive interaction, not a general one. Recognition of this fact suggest that ecologists may improve their undertanding of competition and its relation to community structure, if and when taxon-oriented research programs are left aside and functional (guild) oriented approaches are emphasized. An approach that focuses explicitly on resources, and in the effects of different consumers on their dynamics.

**Key words:** Competition, terrestrial ecosystems, phylogenetic dissimilarity, resources, guilds.

**RESUMEN**

Se revisó la información sobre competencia por alimento entre taxa animales distantemente relacionadas, publicada entre 1970 y 1989 para ecosistemas terrestres. Además de los casos clásicos que reportan competencia entre especies congenéricas, confamiliares o conordinales, para distintos gremios tróficos existe evidencia de competencia entre especies que pertenecen a distintas Clases, Phyla y Reinos. Se proponen tres razones que dan cuenta del poco interés por estudiar la competencia entre taxa distantes: 1) ideas profundamente arraigadas en los ecólogos, acerca de la manera adecuada de estudiar fenómenos de competencia, 2) la manera en que los recursos por los cuales existe competencia son definidos; y, 3) restricciones metodológicas que limitan la detección e interpretación del fenómeno y de los patrones que de él resultan. Se concluye que la competencia entre taxas cercanamente emparentadas representa un caso particular de interacción competitiva y se recomienda un cambio de foco en los estudios de competencia, desde un énfasis en las taxas que compiten a uno centrado en los recursos por los cuales los distintos consumidores compiten.

**Palabras claves:** Competencia, ecosistemas terrestres, disimilitud filogenética, recursos, gremios.

## INTRODUCTION

Interspecific competition has received a great deal of attention from ecologists for a long time (Jackson 1981). Although generalizations about its importance are not without criticism, recent reviews of the empirical evidence (Connell 1983, Schoener 1983, Branch 1984) point out that competition can, but need not always, generate patterns of community structure. There are many reasons why competition's role (or lack thereof) in structuring communities is not often assessed adequately. These include (see, also Keddy 1989) the fact that negative results are not often published, which hinders statistical inferences about the prevalence of competition in nature. Likewise, the available sample of studies assessing competition is not a random sample of natural situations but instead is biased in favor of groups apt

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(Received 19 March 1990).

to provide positive results. The latter point is apparent in the disproportionate number of studies on competition between closely related organisms. The reason for this latter bias apparently rests on the belief that phylogenetically distant organism do not usually use similar resources, which renders them unlikely candidates for the detection of interspecific competition. Additionally, a taxonomic bias is also introduced by the taxonomic competence of the investigators, who tend to restrict their focus of inquiry to particular groups of species. As a consequence of these two biases one is lead to belief that interspecific competition, when it occurs, usually involves closely related taxa.

Here I argue that the prevalence of competition between distantly related taxa has been underestimated, partially as the result of methodological problems and of narrow and static definitions of consumers' resources. I also point out that there is no theoretical reason to expect that this type of competition is rare in nature, because competition between closely related species is only a particular case of competitive interactions.

*Operational definitions*

Before addressing empirical and theoretical questions I will make clear the assumptions and constraints of this study. I have restricted my analysis to competition for food resources in terrestrial and freshwater ecosystems in which at least one consumer was a vertebrate. I focused on food competition because there is empirical evidence that this type of competition is the most frequently reported for different ecosystems and across many taxa (Schoener 1983). I consider as distantly related taxa any pair of organisms belonging to different Classes, Phyla or Kingdoms. This decision makes sense if it is taken into account, that within the framework of competition theory, the study of competitive interactions has been restricted mainly to congeneric or confamilial organisms. Another reason for choosing Classes as the cutoff taxonomic level, lies on the fact that species belonging to different Classes often show large dissimilarities in ecological, morphological and physiological traits (e.g., foraging mode, mobility, body size, metabolic rate), directly related to the search, capture, and processing of food. These differences are not so clear between organisms that belong in different orders, such as owls and diurnal raptors (Jaksić & Carothers 1985).

*The evidence*

I performed a survey of the published research that documented evidence (correlational or experimental) on competition between distantly related organisms covering the period 1970-1989 (20 years). I selected thirteen journals that often publish ecological research in freshwater and terrestrial ecosystems regardless of taxonomy (American Naturalist, American Zoologist, Ecological Monographs, Ecology, Journal of Animal Ecology, Limnology and Oceanograpy, Nature, Oecologia, Oikos, and Science), and also those focused in specific vertebrate taxa (Condor, Journal of Mammalogy, and Copeia). By experimental evidence I mean responses (functional and/or numerical) that result from the controled addition or removal of at least one species of a pair or a group of presumably interacting species, as well as those resulting from food-manipulation experiments. Under correlational evidence I classify those studies that document indirect evidence of food competition, including differential food-niche overlaps, reciprocal changes in density or species abundances along environmental gradients, and also those that report direct evidence involving observations of interference, which although illustrating the potential for competition, fail to uncover its effects on traits related to fitness, such as growth or survival.

The total number of studies that met the requirements was 44. Classified by year of publication, there is a clear mode in 1979 (Fig. 1). The number of studies published from 1970 to 1978 (13 in nine years) is lower than that published between 1980 and 1989 (23 in ten years). This

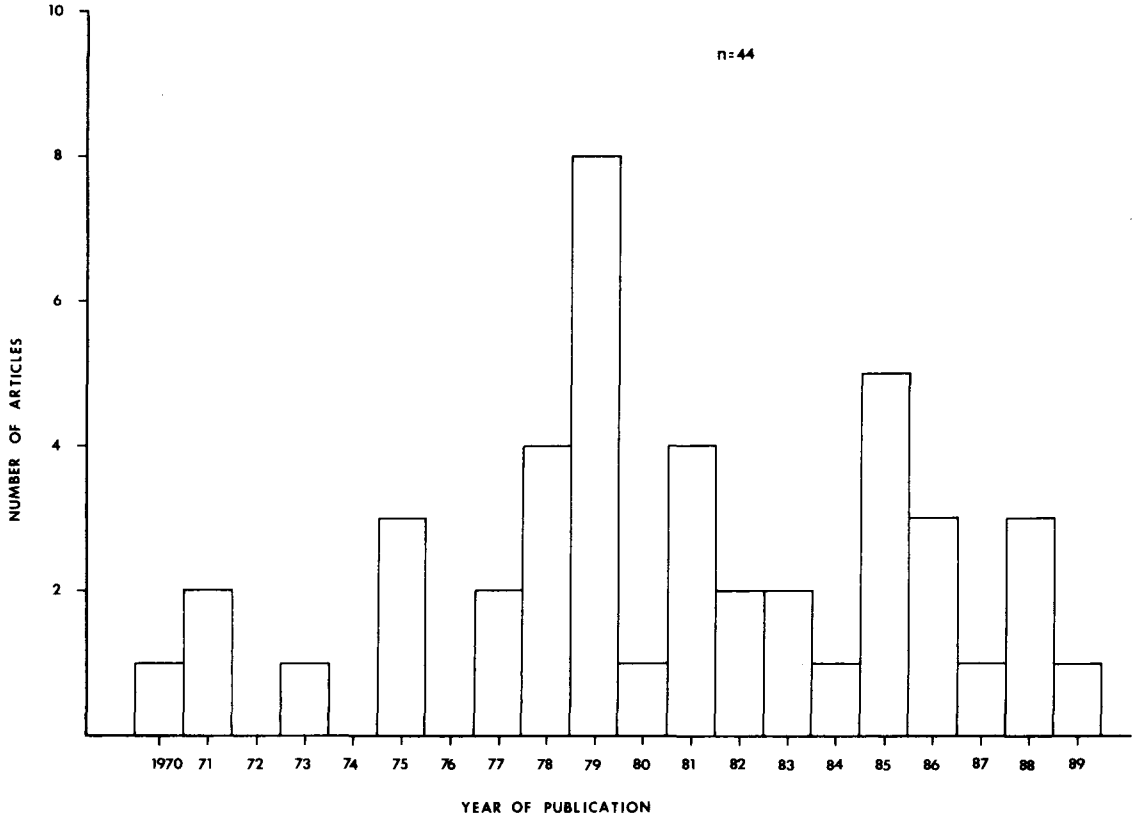


*Fig. 1:* Number of articles reporting evidence on competition between distantly related taxa, classified by year of publication in a survey of thirteen leading journals (see text for details). The articles included in this graph are marked with an asterisk in the Literature Cited section.

Número de artículos que entregan evidencia de competencia entre taxa distantemente relacionadas, clasificados por año de publicación en un escrutinio de trece prestigiosas revistas (véase el texto para detalles). Los artículos incluidos en este gráfico están marcados con un asterisco en la sección Literatura Citada.

pattern may be interpreted as reflecting the influence of the symposium on competition between distantly related taxa, published in 1979 (American Zoologist [1979] 19: 1027-1175). However, Fisher's exact test applied to the data classified as being published before or after, but not including 1979, renders an insignificant result ($P > 0.10$). Overall, the evidence reported is largely correlational (75% of the studies), which imposes a serious constraint for interpreting specific features of the competitive processes invoked. Among the 44 studies, competition between distantly related taxa was reported for several feeding guilds, including granivores (30%), insectivores (30%), nectarivores (16%), frugivores (9%), carnivores (7%), herbivores (4%), planktivores (2%) and periphytivores (2%). Of the total pool of studies, 48% documented interclass competition, 50% interphyletic, and 2% interkingdom competition. This indicates that a continuum of interspecific competition between increasingly dissimilar taxa exists. It ranges from competitive interactions between populations of different species belonging to the same genus, to interactions between species' population belonging to different kingdoms, such as fungi and mammals (Janzen 1977, Inouye 1981), plants and ants (Rissing 1989), and fungi and mites (Karban 1989).

Although food competition between distantly related taxa is known to occur, the study of this process has not pervaded the literature, nor has it attracted much attention from ecologists, despite the impetus received in 1979 by the above mentioned symposium. This situation is

anomalous in ecology where new concepts and methodologies usually stimulate rigorous research into new areas (Abrahamson *et al.* 1989), as is apparent with concepts such as guilds (Jaksić 1981, Hawkins & MacMahon 1989) or with new methods of inquiry such as null models (Harvey *et al.* 1983, Strong *et al.* 1984). In the next section I offer three reasons to account for the meager evidence published and the little impact of the concept of competition between distantly related taxa on the study of this ecological phenomenon.

*Three reasons why competition between distantly related taxa is not more often reported*

1. *The "proper" way to study competition*

Apparently, the first to state explicitly that competition between distantly related taxa should be rare in nature was Darwin (1884: 77-89, quoted by Hurlbert *et al.* 1986): "The struggle will generally be more severe between species of the same genus, if they come into competition, than between the species of distinct genera... competition will be more severe between allied forms, which fill nearly the same place in the economy of nature". The rationale here is the same than Hardin (1960) used to propose the competitive exclusion principle, an idea that can be traced from Darwin through Grinnell and to Gause, which states that species having identical patterns of resource utilization cannot coexist. Coexistence is thought possible only if the limiting resources are different for each species or if some degree of segregation along niche axes is attained through resource partitioning. The conclusion derived from these constructs is that phylogenetic dissimilarity confers ecological dissimilarity, and thus it is logical to expect that competition is most intense between allied forms (e.g., Elton 1946).

Because of the tacit acceptance of this logic, the study of competition has focused on closely related taxa, thus representing the "proper" way of doing research on competition. Indeed, this is the way that is exemplified and encouraged in textbooks (e.g., Pianka 1983, Ricklefs 1976, Krebs 1978, Begon *et al.* 1988). However, the emergence of the guild concept (Root 1967) gave way to an alternative view, recognizing that phylogenetically dissimilar species may use the same resources in the same manner within communities (Brown & Davidson 1977, Jaksić 1981). If shared resources are in limiting supply, then competition between distantly related taxa may not be rare in nature. Consequently, the potential for detecting this type of interaction depends on the way investigators define the resources being competed for. As I will show in the next section, the definition made by researchers of resources for which organisms presumably compete, is biased in making apparent only direct competition between closely related species.

2. *The narrowness of investigator-defined resources*

A resource is an investigator-defined category that may determine the way to address the study of competition as well as the possibility of its detection. This is particularly apparent when the resource defined by the investigator undergoes ontogenetic changes or originates different structures at different life-history stages that are strongly dependent on each other. For example, it is known that during the life cycle of a plant, seeds are produced for reproduction and dispersal, and that the fate of the plant and that of the seeds are intimately related to the extent that an adverse effect upon one or another life-history stage results in an adverse effect on both. In this case (if one is interested in the detection of competition) it would be misleading to distinguish a guild of grazers (that exploits the adult plant) from another of granivores (that exploits the propagules of the plant), because the resource is essentially the same, and the species in the two guilds are indirectly interacting. In this respect, the work of Inouye (1981) is particularly important, because it demostrates experimentally that a parasitic fungus

that infects the vegetative parts of a plant indirectly competes with a rodent that feeds on the seeds of this plant, despite the fundamental demographic differences between exploitation of foliage (herbivory) and exploitation of offsprings (granivory). Consequently, a broader and dynamic definition of resources that takes into account the history of transformations of the resources themselves, should contribute to make apparent indirect interactions between phylogenetically distant consumers specialized on different stages of the resource, commonly perceived by ecologists as different resources. The above does not imply that competition between distantly related taxa may not be apparent when the limiting resource is static (i.e., one which does not undergo a history of transformations or a complex ontogeny). Actually, in intertidal systems where the limiting resource is rocky substrate, a type of resource without a history of transformations, competition between distantly related taxa is the rule rather than the exception (Woodin & Jackson 1979, Fairweather 1989).

### 3. *The elusiveness of pattern recognition and the limitation of methods*

On working with closely related species, it has been usual to apply a comparative approach to the study of competition (Davidson *et al.* 1980). Because similarities are predominant between phylogenetically close organisms, the comparative approach to competition emphasizes dissimilarities and interprets them as the outcome of segregation in resource use to reduce overlap and thus interspecific competition. Frequently these studies focus on differences of coexisting species in body size, microhabitat use, foraging mode, size of feeding structures, and activity times, among others. This approach has given raise to key ecological concepts, such as Hutchinsonian ratios, limiting similarity, and character displacement, that have stimulated not only theoretical research, but a great deal of empirical work, because it gives operational prescriptions for interpreting field data. Unfortunately, this approach cannot be applied meaningfully to distantly related organisms (but see Schluter 1986), where differences in morphology or behavior, a product of phylogenetic distinctiveness, predominate over similarities. This fact hinders interpretation of differences as the result of competitive interactions, because each taxon may perceive and interact with its environment in a different way, and also because each one faces different tradeoffs and constraints that influence the evolution of morphological, physiological, and behavioral traits. This in turn may lead to asymmetrical responses (Diamond 1987) or to undetectable ones. Further, differences in body size, life-history characteristics, and modes of exploitation of resources may enable distantly related taxa to compete strongly but still coexist (Brown *et al.* 1979, 1981, 1986). The failure of the comparative approach to cope with the complexities posed by competition between distantly related taxa, works against the detection of patterns, which is the starting point for most ecological inquiries. These methodological difficulties in recognizing patterns demonstrated by phylogenetically distant organisms has seriously limited the ability of researchers to investigate the underlying competitive process, which is reflected in the meager evidence currently available.

Additionally, it must be noted that the experimental approach to the study of competition is also constrained when it is applied to competition between distantly related taxa. Often the information that can be retrieved it is less and the difficulties greater than in the case of performing experiments with closely related species, specially because of the different temporal and spatial scales needed to measure the response of each taxon. Following the lead of Schoener (1983), one may distinguish extrinsic and intrinsic factors in experimental studies. The former are related to the biotic and abiotic environment, whereas the latter are associated with the organisms themselves (their characteristic life histories). In an experiment, some major natural factor extrinsic to the target taxon is manipulat-

ed, supposedly the factor of interest whose effect is to be assessed. Usually, no atention is placed on intrinsic factors; it is assumed that they are controlled. One way to control for these intrinsic effects is to carry out the experiment using closely related species with similar physiology and life history, which perceive the same environmental grain. Otherwise one would be measuring the effects of extrinsic factors compounded by variations in the intrinsic factors. Because distantly related taxa interact with their environment on quite different spatial and temporal scales, we cannot arbitrarily impose a particular scale of observation that is valid to compare their responses to experimental manipulation. If this intrinsic effect is not taken into account it is probable to arrive at conclusions that will be artifacts of scale (Wiens 1989). Competition between distantly related taxa is specially difficult to establish rigorously.

In the case of competition between distantly related taxa, where intrinsic factors may play a major role, it is difficult to interpret the result of a reciprocal removal or addition experiment in terms of the direction and strength of the interaction. This problem is especially acute if one applies a density-based phenomenological definition of pairwise competition (Tilman 1987). Perhaps a way to circumvent some of the above-mentioned difficulties is by expressing the effect of a distantly related taxon in relation to the effect of a closely related one, as was elegantly done by Morin *et al.* (1988). However, the problem of scale still persist.

In the light of the complexities, both theoretical and methodological, faced by ecologists interested in assessing competition between phylogenetically distant taxa, the emphasis on competition between closely related organims appears as a dictum of Occam's razor. However, it should be stressed that the under representation of research focused on competition between distantly related taxa does not imply that this phenomenon is infrequent or irrelevant, nor that competition between closely related species is the usual case. Instead, it may reflect limitations in our ability to deal with the complexity of ecological systems, which requires us to cope with indirect, higher order, and apparent interactions.

## CONCLUSIONS

The study of competition has been of great importance in the development of ecology, not only because of its explanatory power, but also because of the discussion that it has generated and the improvement of methodologies and approaches that has resulted. However, much of the evidence about competition comes from the study of pairwise interactions between closely related species. This bias is not justified on either theoretical or empirical grounds. From a theoretical perspective, the concept of guild implicitly indicates that distantly related species may use the same resources and compete. Further, the empirical evidence does demonstrate competition not only between congeneric, confamilial or conordinal species, but also between species in different classes, phyla and kingdoms. Three reasons may account for the little interest received by competition between distantly related taxa: 1) deeply rooted ideas about the proper way to study competition, 2) narrowness in the definition of resources, which in turn causes the exclusion of some consumers; and, 3) methodological constraints, that limit the detection of the phenomenon and the interpretation of patterns resulting from it.

It is worth emphasizing that competition between closely related taxa is just one particular case of competitive interaction, not a general one. Recognition of this fact suggest that ecologists may improve their undertanding of competition and its relation to community structure, if and when taxon-oriented research programs are left aside and functional (guild) oriented approaches are emphasized. An approach that focuses explicitly on resources, and in the effects of different consumers on their dynamics.

ACKNOWLEDGMENTS

I thank to Patricio Camus, Fabian Jaksić, Rodrigo Medel and Peter Feinsinger for critically reading different versions of this manuscript. John Wiens and an anonymous reviewer greatly improved the final version. Juan Carlos Castilla and Sergio Navarrete shared with me their expertise in intertidal systems and provided stimulating discussion. Enrique Martínez and Jacqueline Fernández kindly and promptly sent to me the bibliography that I needed. This research was funded through grant FONDECYT 0585/89 and a fellowship from the Universidad Católica de Chile.

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