

KEYWORDS IN EVOLUTIONARY BIOLOGY

EDITED BY

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HARVARD UNIVERSITY PRESS
CAMBRIDGE, MASSACHUSETTS
LONDON, ENGLAND

Following Williams, community evolution becomes an artifact of the evolution of individuals (or even smaller units of selection) pursuing their self-interest. In the last decade the idea of higher levels of selection has regained some credibility, David Sloan Wilson and others have shown that individual self-interest is compatible with natural selection of community (or population) characteristics, provided that there exists recurrent periods of dispersal or spread of the communities, for example, by transport on a carrier species. In these periods certain communities are spread differentially by virtue of characteristics of the community, for example, because of the benefits to the carrier species (see GROUP SELECTION). Moreover, in such situations the evolution of characters cannot be understood without reference to the character's indirect effects transmitted through all the linkages in the community (Wilson, 1983a).

The debate on community evolution has not addressed Hutchinson's idea (mentioned earlier) that stable systems could outpersist ones with destabilizing components. Yet, suppose that we define natural selection broadly, as the differential representation of entities over a period of time by virtue of some property or character that differs among those entities. Hutchinson's system evolution is then natural selection of systems according to differences in their stability. Unlike Wilson's scheme, no dispersal stages are assumed in this form of higher-level natural selection.

However, just as characters are not transmitted but must be developed through ontogeny (Oyama, 1985), ecological organization cannot be spread or dispersed without processes of reconstruction of the organization as it spreads or after dispersal. Although an organism has integrity through ontogeny, the organismic or system view of ecological organization is, as we have seen, under question from many sides. The conditions necessary for community evolution to occur along the lines just discussed—in particular, the separation of ecological and evolutionary time scales—are not likely, therefore, to be widespread. The existence and evolution of systems become special outcomes to be explained rather than a starting point or shortcut for theory. Such a perspective does not, however, necessarily validate individualistic positions. Instead, ecologists could work to identify and theorize about the structure of the ecological context in which organisms are mobilizing resources to make their living. They could build theory that allows the structure to have history, that is, to be changing in structure, at the same time as it constrains and facilitates living activity—and its evolution.

COMPETITION: HISTORICAL PERSPECTIVES

Robert McIntosh

ALTHOUGH IDEAS OF competition among organisms antedated Charles Darwin, students of evolution, genetics, and ecology derived their ideas of, and interest in, competition largely from *On the Origin of Species*. In it, Darwin described competition as universal (1859a, p. 60) and as the chief component (pp. 205, 220) of the struggle for existence and of natural selection. "Compete," "competition," and "competitor" are used eighty-one times in the *Origin*, sometimes in conjunction with the familiar phrases "struggle for life," "struggle for existence," and the equally loaded words "battle" and "war." This juxtaposition is blamed by some for subsequent confusion about the meaning of the term "competition." Darwin, however, specifically stated that he used "struggle for life" in a "large and metaphorical sense," including effects on individuals and on their success in leaving progeny. He wrote (p. 116) that the struggle for life occurs: (1) between individuals of the same species, (2) between individuals of different species, and (3) with physical conditions. Although Darwin did not formally define competition, he consistently described it (pp. 69, 78, 140, 175, 205, 320, 400) as a component of the struggle for life involving a relationship between organisms (1 and 2 above), not a relationship between an organism and the physical environment (3) as described by some subsequent writers on evolution and ecology. Darwin also distinguished competition from other interactions between organisms, especially parasitism and predation. He contrasted (p. 69), for example, competition between plants with their destruction by animals. He recognized (p. 175) three types of interaction between organisms: (1) with a species on which an organism depends, (2) with a species by which an organism is destroyed, and (3) with a species with which an organism comes into competition. He clearly distinguished "enemies" from "competitors," and he wrote (p. 77) of the structure of an organism as related to those with which

it comes into "competition for food or residence" or, in contrast, as related to organisms from which it has to escape or on which it preys.

Early students of evolution and genetics referred to a struggle for life and competition but did not formally define competition, elaborate on Darwin's usage, or pursue detailed studies. Mayr (1988) writes that competition "disappeared from the consciousness of evolutionists when geneticists began to dominate evolutionary thinking" (p. 143). Whatever the cause, extended discussion of competition or citation in the indices of early books on evolution are infrequent.

Early ecologists, however, did recognize competition as an important process in the organization of communities, even though they left its meaning unspecified. The American plant ecologist Frederic E. Clements (1905) published what may be the earliest formal definition of competition for biologists—"the relation between plants occupying the same area and dependent upon the same supply of physical factors" (p. 316). Clements observed that green plants, unlike animals, all use the same components of their environment and that competition between plants is indirect, one plant affecting the physical environment by using light, nutrients, or water which, in turn, affects adjacent plants. Clements' text added elements to the formal definition that were elaborated in the first extended survey of competition (Clements, Weaver, and Hanson, 1929, p. 317): competition occurs "when the immediate supply of a single necessary factor falls below the combined demands" of the competitors. Most subsequent definitions turned on this idea of common demand of two or more organisms for a resource in limiting supply, although consensus on concept and terminology was long delayed (see RESOURCE).

Competition was independently considered in the 1920s in the context of theoretical mathematical models and experimental studies of population growth. Raymond Pearl and L. J. Reed (1920) rediscovered the "logistic" equation of population growth, which is commonly represented by the differential equation:

$$\frac{dN_1}{dt} = rN_1 \left(\frac{K_1 - N_1}{K_1} \right)$$

where N_1 is number of individuals of species 1, t is time, r is the maximum rate of population increase in an unlimited environment, and K_1 is a limiting population. The logistic equation represents the population growth rate of a single species, which approaches 0 as N_1 approaches the limiting value K_1 . A. J. Lotka, working in Pearl's laboratory, and V. Volterra, working independently, developed equations for competition between two spe-

cies and subsequently extended it to many species (Kingsland, 1985). The Lotka-Volterra competition equations are:

$$\frac{dN_1}{dt} = r_1 N_1 \left(\frac{K_1 - N_1 - N_2}{K_1} \right)$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(\frac{K_2 - N_2 - N_1}{K_2} \right)$$

where t , N , r , and K are defined as in the logistic equation. The burden of the logistic and competition equations is that populations of competing organisms are controlled by a common factor such as food or other essential of life.

G. F. Gause (1934), a Russian entomologist influenced by the work in Pearl's laboratory, set out to test the mathematical models of competition in laboratory experiments. He enunciated what became variously known as Gause's law, or the Lotka-Volterra principle, that "one of the species in a mixed culture drives out the other entirely" (Gause, 1934, p. 113). Hardin (1960) reviewed these eponyms and urged substitution of the more descriptive phrase "competitive exclusion principle." Paradoxically, Hardin described the ambiguities of the principle as its chief merit.

With or without formal mathematical exposition, and without complete consensus on their definition or mechanism, competition and competitive exclusion, under a variety of names, have occupied the attention of ecologists from the 1930s to the present. The link of competition with regulation of populations was emphasized by the Australian ecologist A. J. Nicholson (1933, p. 140), who asserted that any factor that produced population balance was "almost necessarily some form of competition" and was correlated with the number of individuals—that is, was "density-dependent." Unfortunately, Nicholson's definition of competition included "the ease with which they are found by enemies," confounding competition with predation.

Ecologists clarified the meaning of competition by focusing attention on the role of limiting resources. Clements and Shelford (1939, p. 139), reiterating earlier definitions by Clements, wrote, "competition may be defined inclusively as a more or less active demand in excess of the immediate supply of material or condition on the part of two or more organisms." A. C. Crombie (1947) defined competition as "the demand, typically at the same time, of more than one organism for the same resources of the environment in excess of immediate supply" (cf. Milne, 1961, p. 44). Crombie used the term "interference" as a type of competition in

which one organism inhibits another "(through direct attacks, conditioning the environment, consuming food, etc.)" (p. 49).

E. P. Odum (1953) continued the connection of competition and population growth in the first edition of his influential textbook. Odum adapted from sociology and introduced to ecologists a symbolic classification of interactions between species based on three possible effects on population growth: (0) if neutral, (+) if positive, (-) if negative. One of the possible combinations of these is symmetrically negative (-/-) and is designated as competition. Predator/prey and host/parasite interactions are asymmetrical (+/-). The plus and minus symbols accord with the subjective implications of some earlier definitions and the signs of the theoretical mathematical equations of Lotka and Volterra (Williamson, 1972). Odum (1953) added to the negative effects of the shortage of necessary resources other negative effects such as the secretion of harmful chemicals (antibiosis, allelopathy). In a second edition (1959; cf. Milne, 1961) he extended, but did not clarify, his definition by adding "mutual predation," "susceptibility to carnivores, disease, etc." (p. 231).

Nicholson (1954) returned to the subject and described two categories of competition—"scramble" and "contest." "Scramble" refers to competition for a resource in limiting supply, without direct interaction among the organisms, in which each secures some portion of the resource. "Contest" occurs when an organism interacts directly with another and restricts its access to the resource. Thus some organisms get as much of the resource as they can secure and others get little or none.

Thomas Park (1954a, pp. 178–181) similarly recognized two categories of competition under different names. "Exploitation," like Nicholson's "scramble," is "a more or less active demand" for needed resources that operates only if resources are limited and limiting. "Interference" competition, like Crombie's (1947) similar usage and Nicholson's "contest," occurs when "populations compete for limited resources through mutual interference, which differentially affects multiplication and survival."

In spite of some clarification, ecologists continued to express dissatisfaction concerning use of the term "competition." L. C. Birch (1957) reviewed the meanings of competition in ecology, genetics, and evolution. He lamented that the word had largely lost its usefulness as a scientific term and had resulted in much misunderstanding and confusion. He advanced a meaning in the "strict sense": "competition between animals occurs when a number of animals (of the same or different species) utilize common resources the supply of which is short; or if the resources are not in short supply, competition occurs when the animals seeking that resource nevertheless harm one another in the process" (p. 16).

M. H. Williamson (1957, p. 423) turned to the Oxford English Dictionary and evolved a definition: "two species are in competition when

they have a controlling factor in common and conversely if two species are in competition they have a controlling factor in common." This definition is reminiscent of A. J. Nicholson (1933) in its emphasis on the controlling factor and is described by A. Milne (1961, p. 48) as "the most baffling meaning." The continuing problem of defining competition was evident in a 1960 symposium, "Mechanisms in Biological Competition," at which the participants were unable to agree on a definition, although all agreed on the desirability of *experimental* inquiry into the ill-defined process (Milthorpe, 1961).

Milne (1961, p. 60) offered his own "single strict definition." "Competition is the endeavour of two (or more) animals to gain the same particular thing, or to gain the measure each wants from the supply of a thing when that supply is not sufficient for both (or all)." Even Milne's comprehensive review of prior definitions did not resolve the problem. None of the various definitions offered satisfied all ecologists. H. G. Andrewartha (1961, p. 174) decried competition as a "panchreston" like humors and elan vital and wrote, "I hope that we ecologists may soon be able to add competition to this list of abandoned carcasses." J. L. Harper (1961, p. 1) also advocated abandoning the term competition and replacing it with "interference" to describe "the hardships caused by the proximity of neighbors (usually feeding at the same trophic level)."

Robert MacArthur, the principal figure in the revival of theoretical mathematical ecology in the 1960s, wrote (1972a, p. 256), "I also believe that no precise definition can be related to competition and that the current precise definitions are premature." Nevertheless, he offered (1972b, p. 21) a wide, if tentative, definition: "two species are competing if an increase in either one harms the other." He gave three examples: (1) "species A and B can fight"; (2) "A can reduce B's food supply"; (3) "A can by its own losses increase B's predators."

Although he preferred mathematical definitions, Williamson (1972, pp. 109, 112) offered two verbal descriptions of competition: (1) "competition will be in respect of the factors that control the population because of their variation with density, that is, they are density-dependent" (p. 109); (2) "the criterion for competition will be that of affecting each other's numbers downwards. This indicates that they share controlling factors" (p. 112).

One difficulty in establishing the meaning or terminology of competition is that the term is applied to diverse categories. In some uses it clearly applies to interactions between individuals and the effect on their growth and size or shape. In others it applies to the effects on reproduction and the consequences for population growth. The effects are felt by individuals but are manifest in population growth rate and are related to fitness. Competition may also be attributed to levels beyond populations within a species. Species are commonly said to compete, or to have competed, with

resultant morphological, habitat, or geographic displacement, or even extinction. Higher taxa such as families or phyla are sometimes described as competing, and even floras or faunas are said to compete to replace other like categories. Not uncommonly entire complex aggregations such as communities or ecosystems are described as competing with each other, resulting in successional or geographic displacement. The definition or mechanism of competition at levels beyond the species is not clear. Most studies of competition involve individuals or populations of a species (intraspecific) or pairs or groups of related species (interspecific). In instances where widely divergent taxa use the same resource (e.g., rodents, birds, and insects on seeds) the term "diffuse" or "generalized" competition may be used. However, demonstration of such competition is unusual.

Evolutionary studies, genetics, and ecology remained substantially independent of each other in the early decades of this century. J. B. S. Haldane (1932) recognized competition between adult animals and between intrauterine embryos but referred (p. 126) to "weeding out of individuals in competition with their environment." J. S. Huxley (1942, p. 34), in *Evolution and the Modern Synthesis*, commented that competition in rare species is more likely to be between the individual and its environment. He concurred (p. 484) with Haldane in contrasting intraspecific competition with competition with the environment. Ernst Mayr (1942, p. 271) asserted that knowledge of competition and predation was slight and wrote, "In fact it is surprising how badly ecologists have neglected the questions." It is not clear, however, whether Mayr's remarks reflected the failings of ecologists or the segregation of the disciplines. Ruse (1982, p. 176) wrote that evolutionists acknowledged ecology but did not "incorporate ecological thought in any systematic formal way into evolutionary theorizing." He commented that the geneticists Theodosius Dobzhansky and F. A. Ayala ignored the ecological background of evolutionary theory. I. I. Schmalhausen (1949, p. 61) was unusual among evolutionists in providing an explicit definition of competition: "when members of one species are subjected to the same abiotic or biotic danger there is possible natural selection of some who escape limitation." His elements of competition included struggle—for food, with enemies and parasites, and with severe climatic conditions—equating it to Darwin's struggle for life in its broadest scope and not in accord with concepts of competition then current among ecologists.

The gap between ecologists on the one hand and geneticists and evolutionists on the other narrowed in the 1950s as the importance of competition came to be recognized by other biologists. Mayr (1963, p. 664) provided a definition of competition, "the simultaneous seeking of an essential resource of the environment that is in limited supply" rather than limiting supply, on which some ecologists insist.

H. H. Ross (1962) adapted the definitions of ecologists, defining "direct" competition as occurring when organisms use a commodity in short supply simultaneously, side by side, and in the same way. Animals in "indirect" competition use the same commodity but at different times or use different parts of it. Ayala (1970a) disputed the generality of the competitive exclusion principle, reviewed the meanings of competition, and explicitly differentiated competition from the more inclusive natural selection. He adopted the ideas on competition advanced by Nicholson (1954) and Park (1954a) and approved of the definition given by Birch (1957). T. V. Grant (1971), under a heading "Ecological Interaction," described competition as use of a resource needed by two or more organisms which is present in limiting amounts. Not all writers on evolution, however, were entirely clear about, or accepting of, definitions of competition widely adopted among ecologists (e.g., Simpson, 1949; Stebbins, 1966). Some continued to equate competition with predation or the more inclusive struggle for life (Darlington, 1980; Conrad, 1983).

R. D. Holt (1977) identified "apparent" competition, which occurs when two prey species are limited by a common predator. If one prey increases in density the density of the predator increases, leading in turn to an increase in the mortality rate of the other prey. The two species are in competition, according to J. M. Emlen (1984), via an intermediary organism, namely, the predator.

It can be said that definitions of competition in evolutionary and ecological literature are converging. Most definitions are adaptations of the early uses of Clements as summarized by Birch (1957). Competition is predicated upon collective demand for a common resource when the available supply is inadequate for all of the organisms. The ideas and terminology suggested by Nicholson (1954) are widely used: "scramble" competition, also called exploitation, passive, or consumptive competition, is the use of a common resource when the supply is inadequate for all and is limiting to the competitors. "Contest" competition, also called by some interference or active competition, is the use of a common resource where fighting or other direct harmful behavior, or a chemical inhibition, limits access to the resource. Although considerable agreement on the definition of competition has been achieved, dispute about its mechanism and significance for ecological and evolutionary dynamics of populations continues.

COMPETITION: CURRENT USAGES

Evelyn Fox Keller

A PARTICULAR problem arises for anyone inquiring into the systematic neglect of cooperative (or mutualist) interactions and the corresponding privileging of competitive interactions, evident throughout almost the entire history of mathematical ecology. When we ask practitioners in the field for an explanation of this historical disinterest in mutualist interactions, their response is usually one of puzzlement—not so much over the phenomenon as over the question. How else could it, realistically, be? Yes, of course, mutualist interactions do occur in nature, but not only are they rare, they are necessarily secondary—indeed, it is often assumed that they are in the service of competition: such phenomena have at times actually been called “cooperative competition.” The expectation of most workers in the field that competition is both phenomenologically primary and logically prior is so deeply embedded that the very question has difficulty getting airspace: there is no place, as it were, to put it. My question thus becomes: what are the factors responsible for the closing off of that space?

Part of the difficulty in answering this question undoubtedly stems from the massive linguistic confusion in conventional use of the term “competition.” One central factor can be readily identified, however, and this is the recognition that, in the real world, resources *are* finite and hence ultimately scarce. Scarcity, in the minds of most of us, automatically implies competition—both in the sense of “causing” competitive behavior and in the sense of constituting, in itself, a kind of *de facto* competition, independent of any actual interactions between organisms. So automatic is the association between scarcity and competition that, in modern ecological usage, competition has come to be defined as the simultaneous reliance of two individuals, or two species, on an essential resource that is in limited supply (see, e.g., Mayr, 1963, p. 43). Because the scarcity of resources can itself hardly be questioned, such a definition lends to competition the same *a priori* status.

This technical definition of competition was probably first employed by V. Volterra (1926), A. J. Lotka (1932), and G. F. Gause (1932) in their early attempts to provide a mathematical representation of the effects of scarcity on the population growth of “interacting” species, but it soon came to be embraced by a wider community of evolutionary biologists and ecologists—partly, at least, in an attempt to bypass the charge of ideologically laden expectations about (usually animal) behavior, and in fact freeing the discourse of any dependence on how organisms actually do behave in the face of scarcity. The term “competition” now covered apparently pacific behavior just as well as aggressive behavior—an absurdity in ordinary usage, but protected by the stipulation of a technical meaning. As Ernst Mayr explains,

To certain authors ever since [Darwin], competition has meant physical combat, and, conversely, the absence of physical combat has been taken as an indication of the absence of competition. Such a view is erroneous . . . [T]he relative rarity of overt manifestations of competition is proof not of the insignificance of competition, as asserted by some authors, but, on the contrary, of the high premium natural selection pays for the development of habits or preferences that reduce the severity of competition. (1963, pp. 42–43)

Paul Colinvaux goes one step further, suggesting that “peaceful coexistence” provides a better description than any “talk of struggles for survival”: “Natural selection designs different kinds of animals and plants so that they *avoid* competition. A fit animal is not one that fights well, but one that avoids fighting altogether” (1978, p. 144).

But how neutral in practice is the ostensibly technical use of competition that is employed both by Mayr and by Colinvaux? I want to suggest two ways in which, rather than bypassing ideological expectations, it actually preserves them, albeit in a less visible form—a form in which they enjoy effective immunity from criticism. In order not to be caught in the very trap I want to expose, let me henceforth denote competition in the technical sense as “Competition” and in the colloquial sense (of actual contest) as “competition.”

The first way is relatively straightforward. The use of a term with established colloquial meaning in a technical context permits the simultaneous transfer and denial of its colloquial connotations. Let me offer just one example: Colinvaux’ own description of Gause’s original experiments that were designed to study the effect of scarcity on interspecific dynamics—historically, the experimental underpinning of the “competitive exclusion principle.” He writes: “No matter how many times Gause tested [the paramecia] against each other, the outcome was always the same, complete extermination of one species . . . Gause could see this deadly struggle going on before his eyes day after day and always with the same outcome . . .

What we [might have] expected to be a permanent struggling balance in fact became a pogrom" (p. 142). Just to set the record straight, these are not "killer" paramecia, but perfectly ordinary paramecia—minding their own business, eating and dividing, or not—perhaps even starving. The terms "extermination," "deadly struggle," and "pogrom" refer merely to the simultaneous dependence of two species on a common resource. If, by chance, you were to misinterpret and take these terms literally to refer to overt combat, you would be told that you had missed the point: the Lotka-Volterra equations make no such claims; strictly speaking, they are incompatible with an assumption of overt combat; the competitive exclusion principle merely implies an avoidance of conflict. And yet the description of such a situation, only competitive in the technical sense, slips smoothly from "Competition" to genocide.

The point of this example is not to single out Colinviaux, which would surely be unfair, but to provide an illustration of what is a rather widespread investment of an ostensibly neutral technical term with a quite different set of connotations associated with its colloquial meaning. The colloquial connotations lead plausibly to one set of inferences and close off others—while the technical meaning stands ready to disclaim responsibility if challenged. (See Keller [1987] for a discussion of Hardin's [1960] use of the same slippage in arguing for the universality of the "competitive exclusion principle.")

The second and more serious route by which the apparently a priori status of competition is secured can be explored through an inquiry into the implicit assumptions about resource consumption that are here presupposed and the aspects of resource consumption that are excluded. The first presupposition is that a resource can be defined and quantitatively assessed independent of the organism itself; and the second, that each organism's utilization of this resource is independent of the presence or activity of other organisms. In short, resource consumption is here represented as a zero-sum game. Such a representation might be said to correspond to the absolutely minimal constraint possible on the autonomy of each individual, but it is a constraint that has precisely the effect we are focusing on—namely, establishing a necessary link between self-interest and competition. With these assumptions, apparently autonomous individuals are in fact bound by a zero-sum dynamic that guarantees not quite an absence of interaction but the inevitability of purely competitive interaction. In a world in which one organism's dinner necessarily means another's starvation, the mere consumption of resources has a kind of de facto equivalence to murder. Individual organisms are locked into a life and death struggle not by virtue of their direct interactions but merely by virtue of their existence in the same place and time.

It is worth noting that the very same (Lotka-Volterra) equations readily accommodate the replacement of competitive interactions by cooperative ones, and even yield a stable solution. This fact was actually noted by Gause himself as early as 1935 (Gause and Witt, 1935), and has been occasionally rediscovered since then, only to be, each time, reforgotten by the community of mathematical ecologists. The full reasons for such amnesia are unclear, but it does suggest a strong prior commitment to the representation of resource consumption as a zero-sum dynamic—a representation that would be fatally undermined by the substitution (or even addition) of cooperative interactions.

Left out of this representation are not only cooperative interactions but *any* interactions between organisms that affect the individual's need for and utilization of resources. Also omitted are all those interactions between organism and environment that interfere with the identification and measurement of a resource independent of the properties of the organism. Richard Lewontin (1982) for example, has argued that organisms "determine what is relevant" in their environment—that is, what *is* a resource—and actually "construct" their environment. But such interactions—either between organisms or between organism and environment—lead to payoff matrices that are necessarily more complex than those prescribed by a zero-sum dynamic—payoff matrices that, in turn, considerably complicate the presumed relation between self-interest and competition, if they do not altogether undermine the very meaning of self-interest.

Perhaps the simplest example is provided by the "prisoner's dilemma." But even here, where the original meaning of self-interest is most closely preserved, Robert Axelrod (1984) has shown that under conditions of indefinite reiterations, a "tit-for-tat" strategy is generally better suited to self-interest than more primitive competitive strategies.

Interactions that effectively generate new resources—or either increase the efficiency of resource utilization or reduce absolute requirements—are more directly damaging to the principle of self-interest itself. These, of course, are the kinds of interactions that are generally categorized as special cases: "mutualist," "cooperative," or "symbiotic" interactions. The view of these as special cases tends to persist even in the most recent literature, where a new wave of interest in mutualism can be detected among not only dissident but even a few mainstream biologists. Indeed, numerous authors are hard at work redressing the neglect of previous years (see, e.g., Boucher, 1985c, for discussion and references).

Finally, interactions that affect the birth rate in ways that are not mediated by scarcity of resources are also excluded by this representation. Perhaps the most important of these omissions for interspecific dynamics

are those of mutualist interactions, and for intraspecific dynamics, I would point to sexual reproduction—a fact of life, as I have argued elsewhere (Keller, 1987) that potentially undermines the core assumptions of radical individualism.

A second problem with the language of competition arises in evolutionary theory quite generally. I refer to the widespread tendency to extend the sense of “competition” to include not only the two situations distinguished earlier (conflict and reliance on a common resource) but also a third situation in which there is no interaction at all. Here “competition” denotes an operation of *comparison* between organisms (or species) that requires juxtaposition not in nature, but only in the biologist’s own mind. This extension, where “competition” can cover all possible circumstances of relative viability and reproductivity, brings with it, then, the tendency to equate competition with natural selection itself.

Charles Darwin’s own rhetorical equation between natural selection and the Malthusian struggle for existence surely bears some responsibility for this tendency. But today’s readers of Darwin like to point out that he did try to correct the misreading his rhetoric invited by explaining that he meant the term “struggle” in a “large and metaphoric sense”—including, for example, that of the plant on the edge of the desert: competition was only one of the many meanings of struggle for Darwin. Some authors have been even more explicit on this issue, repeatedly noting the importance of distinguishing natural selection from a “Malthusian dynamic.” Lewontin has written: “Thus, although Darwin came to the idea of natural selection from consideration of Malthus’ essay on overpopulation, the element of competition between organisms for a resource in short supply is not integral to the argument. Natural selection occurs even when two bacterial strains are growing logarithmically in an excess of nutrient broth if they have different division times” (1970, p. 1).

Such attempts—by Lewontin and, earlier and more comprehensively, by L. C. Birch—to clarify the distinction between natural selection and competition (what Engels called “Darwin’s mistake”) have done little to stem the underlying conviction that the two are somehow the same, however. Thus, in an attempt to define the logical essence of “the Darwinian dynamic,” Bernstein et al. (1983) freely translate Darwin’s “struggle for survival” to “competition through resource limitation” (p. 192), thereby claiming for competition the status of a “basic component” of natural selection. G. C. Williams (1986) describes a classic example of natural selection in the laboratory as a “competition experiment,” a “contest” between a mutant and a normal allele, in which he cites differential fecundity as an example of the “competitive interactions among individual organisms” that cause the relative increase in one population (pp. 114–115).

The question at hand is not whether overtly competitive behavior or more basic ecological scarcity is the rule in the natural world; rather, it is whether or not such a question can even be asked. To the extent that distinctions between competition and scarcity, on the one hand, and between scarcity and natural selection, on the other, are obliterated from our language and thought, the question itself becomes foreclosed. As long as the theory of natural selection is understood as a theory of competition, confirmation of one is taken to be confirmation of the other, despite their logical (and biological) difference.