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THE INTENSITY OF COMPETITION VERSUS ITS IMPORTANCE: AN OVERLOOKED DISTINCTION AND SOME IMPLICATIONS

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ABSTRACT

The intensity of competition is a physiological concept, related directly to the well-being of individual organisms but only indirectly and conditionally to their fitness, and even more indirectly to the evolution of populations and the structure of communities. The importance of competition is primarily an ecological and evolutionary concept, related directly to the ecology and fitness of individuals but only indirectly to their physiological states. The intensity of competition is not necessarily correlated with the intensities of predation, disturbance, abiotic stress, or other ecological processes. The importance of competition is necessarily relative to the importances of other processes. Intensity refers primarily to the process of present competition, whereas importance refers primarily to the products of past competition.

The distinction between the intensity and the importance of competition clarifies two long-standing ecological debates. Some ecologists have proposed that competition is greater in more stressful habitats, others the opposite, and still others that no such relationship exists. Evidence cited to refute or support these positions often confuses intensity and importance. Distinguishing between them focuses questions more sharply and indicates what sorts of new evidence should be sought. The more widely known debate over the prevalence of competition as an agent of community structure is a debate about the importance of competition, but evidence about the intensity of competition has often been used by both sides. We argue that intensity and importance need not be correlated, and so measurements of the intensity of competition are not directly relevant to this debate.

This distinction also generates testable hypotheses and suggests directions for research. For example, we hypothesize that competition can be unimportant even if it is very intense: no such hypothesis is possible unless importance is distinguished from intensity. We discuss the application of these ideas to methods and theories used to study competition, ecological communities, and the evolution of competitive ability. We advocate a research approach that presumes multiple, interacting causes, including competition, affecting community structure, and we show how the distinction between intensity and importance helps to make this feasible.

INTRODUCTION

WHY DO ECOLOGISTS disagree so vehemently about the role of competition in nature? After all, competition is one of the central concepts in ecology and evolutionary biology (Wiens, 1977, 1984; Schoener, 1983). Surely we should have reached a consensus by now, at least on whether competition is worth further empirical or theoretical study. Lewin (1983a,b) provided a general re-

view of the current debate on the prevalence and importance of competitive interactions. Several of the participants in the debate stated their views and rebutted one another in the following papers: Connell, 1975, 1980; Wiens, 1977, 1984; Connor and Simberloff, 1979, 1984a,b; Strong, Szyska, and Simberloff, 1979; Hendrickson, 1981; Simberloff and Boecklen, 1981; Strong and Simberloff, 1981; Roughgarden, 1983; Strong, 1983; Gilpin and Diamond, 1984a,b). A recent number of *The Amer-*

ican Naturalist (Vol. 122, No. 5, November 1983, reissued as Salt, 1984), devoted to this and related issues, makes it clear that the controversy has not ended. We will use this and other sources to show that ecologists have overlooked an important distinction in the study of competition, which when recognized reduces the disagreement over the role of competition in nature, generates testable hypotheses, helps us to understand important theories and methods, and indicates directions for research.

The overlooked distinction is between the *intensity* of competition among individuals of one or more species, on the one hand, and the *importance* of competition to individual fitness, community structure, and the coevolution of species, on the other. "Intensity" qualifies the *process* of competition, whereas "importance" concerns the *products* of competition. Our remarks are prefigured by the distinction between present competition and the effects of past competition (Schroder and Rosenzweig, 1975; Connell, 1980; Fonteyn and Mahall, 1981; Rathcke, 1984) and by the arguments to define competition by its mechanism rather than by its results (Milne, 1961; Grime, 1977, 1979). We will argue that the importance of competition is not necessarily correlated with its intensity, either in theory or in fact.

Because we developed these ideas during a study of the relationship between competition and abiotic stress in plants (as proposed by Grime, 1977, 1979), we will introduce them in that context, but our arguments apply to other situations and to other organisms, in general.

STRESS AND COMPETITION: INTENSITY AND IMPORTANCE

Stress and Strain

Grime defined stress as "the external constraints which limit the rate of dry-matter production of all or part of the vegetation" (Grime, 1977: 1175). To make this definition more precise and applicable to organisms in general, we propose that it be called abiotic stress and defined thus: *abiotic stress is an external condition, apart from the activities of other organisms, that induces strain in an organism.* We adopt Levitt's (1972) usage of "stress" to refer to an external condition or process and of "strain" to refer to the internal physiochemi-

cal changes in an organism in response to a stress.

Strain may be measured in a variety of ways. In animals, we might estimate strain by measuring and making intergroup comparisons of growth rate, adult size, amount of stored fat, metabolic rate, adrenal gland size, or hormone levels. In plants, appropriate measures might be growth rate, photosynthetic rate, amount of stored photosynthate, tissue water potential, or turgor pressure. Of course, this list is far from complete.

To make our discussion clearer, we offer the following description. We assume that every organism has an optimal physiological state. This state is obviously hard to define or measure, since the physiological status of an individual is constantly changing in response to the abiotic environment, the activities of its neighbors, its own development, and so on. Even though we cannot precisely define an organism's optimal physiological state, the concept still has meaning in that we can usually recognize suboptimal or pathological physiological states. Also we can experimentally determine various aspects of the optimal state, such as optimal growth rate, optimal reproductive output, and optimal adult size.

A complication arises when we consider that all these various demands on the metabolism of an organism cannot be simultaneously optimized, but we can still conceive of some optimal balance or timing of them. By optimal physiological state we ultimately mean the physiological state that would, if permanent, maximize the organism's fitness in the evolutionary sense of reproductive success (however defined). By taking sufficient care, we can usually recognize when some essential aspect of an organism's functioning is impaired by its physiological state, and its fitness would thereby be reduced if the state continued long enough. This proviso of sufficient duration is not trivial, as we will show in our discussion of the intensity and the importance of competition.

We do not mean to imply by this description of an optimal physiological state that organisms somehow strive for this state, nor that natural selection has necessarily produced organisms capable of attaining such a state in their native environments. Indeed, we assume that organisms usually, if not always, find themselves in suboptimal physiological states.

We use “strain” to refer to deleterious, suboptimal physiological states. We presume, further, that strain is sometimes, but not always, translated into measurably reduced growth rate, size, or reproduction, or into increased mortality or emigration and thus into reduced fitness. See Levitt (1972) for a detailed discussion of elastic (reversible) and plastic (injurious) strains. Despite our discussion of optimal physiological states, it is not always necessary to know or to postulate a definite value for the optimum. If we are interested in comparing the states of two organisms, it may be sufficient to know which one is farther from its optimum.

Competition

Among the definitions of competition familiar to us, we prefer that of Grime: competition is “the tendency of neighboring plants to utilize the same quantum of light, ion of a mineral nutrient, molecule of water, or volume of space” (Grime, 1977: 1170). This definition has several advantages, among them its specificity about the things for which plants may compete and its exclusion of other processes, like allelopathy, often included under the name of competition. It suffers two disadvantages, however. First, this definition is specific to plants, whereas we wish to make our argument as general as possible, and so the requirement of proximity and the list of resources are not appropriate. Since a short, complete list of the resources for which animals, fungi, microbes, and plants may compete is impossible, we will use the phrase “resource items.” We prefer “resource items” to “resources” because “resources” is ambiguous between kinds and particulars, whereas we want to emphasize that competition is for particulars. Our first reformulation of Grime’s definition is then: *competition is the tendency of organisms to use the same resource items.*

The second drawback to this definition is the word “tendency,” which betrays the teleological nature of competition. For the organism not gaining the resource item we are tempted to say that it “needed” or “wanted” or in some sense “strove for” the item; similarly, for the organism gaining the item through competition, we mean that it not only “strove for” but in some sense is “better off” for having the item. Further, the use of the word “tendency” portrays competition as a potential rather than an actual process. That is, “ten-

dency” may also be interpreted, as one reviewer suggested, to mean that for any individual there is a high probability that, in the absence of a competitor, it would have used the resource item that it did not acquire in the competitor’s presence. Organisms may have a disposition to compete, but competition, if it exists at all, is an actual process and should be so defined.

We wish to define actual, not potential, competition. We also wish to avoid any difficulties that might arise from a teleological definition of competition. Whether competition is inherently teleological, and whether teleology is appropriate in science are issues of great interest (Short, 1983), but they are beyond the scope of this paper. Therefore, we offer a definition of competition that is neutral with respect to teleological import, but we do not imply that by doing this we eliminate the teleological dimension from competition, nor that it is necessary, desirable, or even possible to do so.

Thus, we refine our definition further: *competition is the induction of strain (Levitt, 1972) in one organism as a direct result of the use of resource items by another organism.* This definition applies to resource competition, or what animal ecologists call exploitation competition. Notice that allelopathy is excluded, for it is an indirect effect arising from the use of resource items metabolically to produce allelochemicals, which are released into the environment and which then may induce strain in other organisms. In contrast, competition-induced strain is a direct result of the failure to acquire a resource item, as such. For similar reasons, predation also is excluded. This definition can be extended to include what animal ecologists call interference competition, in which one organism is prevented from using resource items by some nonlethal behavior (territoriality, aggressive encounters, hoarding) of another. By analogy, this extended definition would admit allelopathy as a form of competition. Some readers may prefer the narrower definition, others the broader. Our arguments primarily concern the narrower concept of competition, but we believe they apply to the broader, as well. The broader definition would be: *competition is the induction of strain in one organism as a result of the use, defense, or sequestering of resource items by another organism.*

According to our definitions, competition and abiotic stress each induce strain in organisms; thus they are commensurable quantities.

Notice, however, that this formulation does not conflict with Grime's (1977, 1979) distinction between competitive and stress-tolerant "strategies." Although competition and abiotic stress both induce strain in organisms, the adaptive responses to different stresses are different. According to Grime, increased rates of growth and resource capture are selectively advantageous responses to the stress of competition, whereas reduced growth rate and the ability to conserve captured resource items are advantageous responses to abiotic stress.

Many definitions of competition include the requirement that a resource be limiting, or be available to the organisms at some level less than their combined demands upon it. This requirement is implicit in both our definitions above, since if a resource is available in excess of the combined demands upon it, organisms will not induce strain in one another by their use (or defense, etc.) of it.

Whether these definitions of competition are entirely acceptable is secondary to our argument. Competition, however defined, includes two aspects: intensity and importance. These definitions make them easier to distinguish, but for our argument distinguishing these aspects, we insist only that competition (however defined) affects organisms by inducing strain in them.

Intensity of Competition

We propose that the *intensity* of competition is the amount of strain competition induces in an organism—i.e., the amount by which the competition-induced component of the sub-optimal physiological state differs from the optimal or approaches the lethal. Let the optimal state of an organism be represented on a scale of well-being by the point O (Fig. 1, Case a). Let competition reduce this organism's physiological state to point C. The intensity of competition is then the difference between the two states: intensity = $O - C$. The units of measurement in Fig. 1 are arbitrary, but in practice the units of intensity would be appropriate to the particular strain measured (see example below).

This representation of the intensity of competition makes no assumption of symmetry of effects in interspecific competition. That is, in competition between two species (say, A and B), the intensity experienced by members of

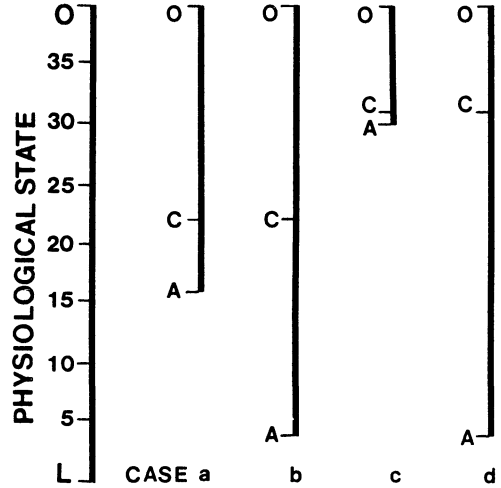


FIG. 1. SCHEMATIC REPRESENTATION OF FOUR PHYSIOLOGICAL STATES OF AN ORGANISM

The ordinate is an arbitrary scale from the lethal state (L) to the optimal state (O). In each case C represents the state resulting from competition, A the actual state resulting from the combined effects of competition and other stresses. See text for discussion.

- Case a: Total strain = $(O - A) = 24$ arbitrary units;
 Intensity of competition = $(O - C) = 18$ units;
 Importance of competition = $(O - C) / (O - A) = 0.75$
- Case b: Total strain = 36 units
 Intensity of competition = 18 units
 Importance of competition = 0.50
- Case c: Total strain = 10 units
 Intensity of competition = 9 units
 Importance of competition = 0.90
- Case d: Total strain = 36 units
 Intensity of competition = 9 units
 Importance of competition = 0.25

species A may be the same as or different from that experienced by members of species B.

The intensity of competition is a function of the degree to which two or more organisms require the same resource items for their optimal functioning. This is different from the amount of overlap between their niches. Niche overlap is a measure of similarity in resource requirements, but it is abstract and potential rather than concrete and actual, because it refers to resources (kinds) rather than resource items (particulars). Thus two organisms may require identical resources (have identical

niches) but not compete at all if they acquire the needed resource items from, say, different places or from an abundant, common pool. Niche overlap specifies a maximum possible intensity of competition, but conditions or behaviors may prevent organisms from competing so intensely, or allow them to avoid doing so.

The intensity of competition is focused on the individual organism and is separable, at least in concept, from the intensities of other processes or conditions. That is, it makes sense to speak of the intensity of competition without reference to the intensity of any other stress. The intensity of competition in a population or community has meaning also; it is in some sense the sum or average of the intensities of competition experienced by all the individuals in the population or community. This is a thoroughly reductionistic or atomistic account.

Importance of Competition

Most organisms in natural circumstances are in a suboptimal condition at least some of the time. The proportion of the overall difference from the optimum attributable to competition is the *importance* of competition. That is, *the importance of competition to an organism is the relative degree to which competition contributes to the overall decrease in growth rate, metabolism, fecundity, survival, or fitness of that organism below its optimal condition.* The importance of competition is necessarily relative to the importances of other processes and conditions (including genetics, chance, predation, parasitism, disturbance, herbivory, and attributes of other organisms) that affect an organism's well-being or fitness. That is, it makes no sense to speak of the importance of competition without at least implicit reference to the importances of other processes.

Although we define the importance of competition at the level of individual organisms, most of the interest in it has been at the levels of populations and communities, and it is thus primarily an ecological and evolutionary concept. Aside from the atomistic meaning at these higher levels, as a simple sum or average of the importance of competition for each individual in the population or community, we do not exclude the possibility of higher-order effects of the importance of competition in evo-

lution or in community composition and structure. As with intensity, the importances of competition to members of two competing species may not be the same.

Suppose other stresses (e.g., cold, nutrient deficiency, disease, parasites) in addition to competition operate on the organism depicted in Case a of Fig. 1 and contribute quantitatively and incrementally to its strain. This further reduction from its optimum can be represented by the point A. The overall strain experienced by this organism can then be represented by the difference $O - A$. The intensity of competition ($O - C$) is unaffected by these additional stresses. The importance of competition is the ratio of the reduction from optimality caused by competition to the overall reduction: $\text{importance} = (O - C)/(O - A)$. Because of the above stipulation that stresses contribute incrementally to the organism's reduction in well-being, this is not a complete account of the difference between intensity and importance, but it captures the kernel. We will try to make this account more complete in our descriptions of the measurement of intensity and importance and their decoupling.

Measuring Intensity and Importance

The intensity of competition may be measured directly by measuring some aspect of the organism's physiological state, as Fonteyn and Mahall (1981) do by comparing xylem pressure potential in plants whose neighbors had been removed to that in plants whose neighbors were undisturbed. In such cases, it is necessary to know or postulate the resource items being competed for. Fonteyn and Mahall (1981) had good reason to suppose that water molecules were the relevant resource items.

Fonteyn and Mahall (1981) studied competition between two species of desert shrub, *Ambrosia dumosa* and *Larrea tridentata*. They set up three treatments and a control by removing from around monitored plants either (1) all other shrubs, (2) all conspecific shrubs, (3) all contraspecific shrubs, or (4) no shrubs (control). They report that before dawn on 31 July, 1978, the mean xylem pressure potential in monitored *Larrea* plants in control plots was -54.7 bar; in plots with all other shrubs removed, it was -47.2 bar, in plots with all *Larrea* plants (except the monitored one) removed,

it was -50.1 bar; and in plots with all *Ambrosia* plants removed, it was -51.3 bar.

We calculate the mean intensity of intraspecific competition to be the difference in mean xylem pressure potential between plants free of competition and those competing with other *Larrea* plants: -47.2 bar $- (-51.3$ bar) $= 4.1$ bar. The mean intensity of interspecific competition is the difference in mean xylem pressure potential between *Larrea* plants free of competition and those competing with *Ambrosia* plants: -47.2 bar $- (-50.1$ bar) $= 2.9$ bar.

To calculate the intensity of abiotic water stress and the importances of abiotic water stress and of the water stresses due to intraspecific and interspecific competition, we need a value for the optimum xylem pressure potential, which we do not know, but we can simplify the arithmetic by assuming it to be 0 bar. The mean intensity of abiotic water stress is the difference in mean xylem pressure potential between the optimum and plants in plots with all other vegetation removed:

$$0 \text{ bar} - (-47.2 \text{ bar}) = 47.2 \text{ bar.}$$

We can also calculate the relative, short-term importances of these different agents of water stress. The *Larrea* plants in control plots experienced competition-induced water stress from members of their own species and from *Ambrosia* plants, as well as abiotic water stress. They thus give us a measure of the overall reduction of these plants from their optimal physiological state: $O - A = 0$ bar $- (-54.7$ bar) $= 54.7$ bar. The importance of intraspecific competition is its intensity divided by this overall decrease: $4.1 \text{ bar}/54.7 \text{ bar} = 0.075$ (importances are unitless fractions). Similarly, the importance of interspecific competition is $2.9 \text{ bar}/54.7 \text{ bar} = 0.053$, and the importance of abiotic water stress is $47.2 \text{ bar}/54.7 \text{ bar} = 0.863$. As with the intensities calculated above, these importances are the means of the importances experienced by the individual monitored plants. Although the calculations of the intensity of abiotic water stress and of all these importances are strongly affected by the choice of an optimal value, the relationship between the importance of intraspecific competition and the importance of interspecific competition is not. Thus, as we noted in our discussion of strain, we do not

need to know the true optimal xylem pressure potential to compare the intensities and importances of intraspecific and interspecific competition.

These importances are correlated with their corresponding intensities, but this fact does not constitute an argument against our position that intensity and importance are not necessarily correlated. We are quite prepared to find that they are correlated in some cases, perhaps in many or most cases; we claim only that they *need* not be. Furthermore, this example is constrained exactly as our hypothetical example (see Fig. 1) is constrained. Note that the strain resulting from the combined abiotic, intraspecific, and interspecific water stresses is -54.2 bar, very close to the -54.7 bar pressure potential in control plants (probably not significantly different), an observation indicating that these were the only water stresses with measurable intensities over the time-scale of the experiment. However, these estimates of importance omit processes other than competition for water and abiotic water stress that may influence the fitness of the plants (e.g., competition for mineral nutrients, other abiotic stresses, herbivory, other disturbances). Fonteyn and Mahall (1981) recognized this. They wrote:

[T]he results obtained from the field experiment do indicate that interference between species is more intense than that within species, [but] the importance of these interactions in the formation and maintenance of the patterns exhibited by *Larrea* and *Ambrosia* has not been directly assessed (p. 891).

Intensity may also be measured more indirectly as the amount of decrease in growth rate (population or individual), fecundity, size, or fitness caused by competition, independent of the decrease caused by other factors. With such indirect measurements the distinction between intensity and importance becomes especially difficult to discern, because both intensity and importance can be measured in terms of growth rate, fecundity, and the like. The distinction, however, is nonetheless real: it is the distinction between raw amount and proportional amount, respectively, of the overall difference from optimum that can be attributed to competition.

If competition is occurring in a population,

we expect that its intensity will be different for different members; central tendency measures (e.g., mean, median) detect the average intensity experienced by all members of the population. Some of the overall decrease in growth rate, fecundity, and the like, will be caused by factors other than competition. The combined intensity of all these other stresses is measured by the amount of decrease remaining after the effects of competition have been accounted for. The proportion of the overall decrease accounted for by competition is its importance; this can be measured in terms of the variance in some measure of the well-being of the members of the population. Thus, indirect measures of intensity and importance may take the forms of a central tendency and variance accounted for, respectively.

Indirect measures of intensity have two advantages over direct ones: they are integrated or averaged over the population and over time, and they are meaningful only if competition has some measurable importance in the population. They thus give us some assurance that the effects we measure are long-term and significant. An example of a technique that provides such a variance measure of importance and a central tendency measure of intensity is size-distance regression.

Size-distance regressions take as variates the distance between a pair of neighboring plants and the sum of their sizes, as measured by basal areas, canopy areas, or canopy volumes, for example. A significant regression means that larger plants tend to be farther apart, and this can be interpreted as evidence of competition (or at least interference, *sensu* Harper, 1961) between them (Yeaton and Cody, 1976; Yeaton, Travis, and Gilinsky, 1977; Gutierrez and Fuentes, 1979; Fuentes and Gutierrez, 1981; Phillips and MacMahon, 1981; and Welden, 1984). Size-distance regressions have also been applied to corals (Stimson, 1974), and we suppose they are applicable to other sessile organisms with some plasticity of growth response. Other observations and experiments can eliminate allelopathy and other processes as possible causes of this spatial pattern and help to confirm the causal role of competition (Welden, 1984).

The coefficient of determination (r^2) of a size-distance regression estimates how much variation in the distances between plants is ac-

counted for by variation in their combined sizes (see Kleinbaum and Kupper, 1978: 71–77; Sokal and Rohlf, 1981: 570–571; Waller, 1981). The remaining unaccounted-for variation is assigned to error, which includes such things as effects of other competitors, measurement error, genetic differences, environmental heterogeneity, predation, herbivory, disturbance, and chance. Thus the coefficient of determination measures the importance of competition between the studied species relative to all other factors affecting the spacing of the plants. This estimated importance combines the separate importances to each of the two competing species.

The intensity of competition is measured by the slope of the regression line. Consider two size-distance regressions that differ only in their slopes (Fig. 2). A given increment in sum of sizes corresponds to a larger increment in distance between neighbors for plants described by the steeper line than for those described by the shallower (Fig. 2A). Conversely, a given increment in distance corresponds to a smaller increment in sum of sizes for plants described by the steeper line than for those described by the shallower (Fig. 2B). Both indicate that the inhibition, in growth or size, of one plant by another is greater at a given combination of separation and sum of sizes for plants described by the steeper regression line. The slope of the regression line is thus a central tendency estimate of the intensity of competition. Again, this estimated intensity combines the separate intensities experienced by each of the two competing species.

For example, Welden (1984) calculated a size-distance regression measuring competition between two shrubs, *Artemisia tridentata* and *Amelanchier utahensis* at one site to be:

$$Y = 0.53m + (0.09m/m^2)X, \\ r^2 = 0.6702, n = 30, p < 0.0001,$$

where Y is the distance separating the paired shrubs and X is the sum of their canopy areas. This equation indicates that about 67 per cent of the variance in distance between these shrubs was accounted for by the sum of their sizes. Because allelopathy and other possible explanations of this spatial arrangement were eliminated, this is the importance of competition in the spacing of the plants. The intensity of competition is $0.09m/m^2$ (i.e., $0.09m$ of

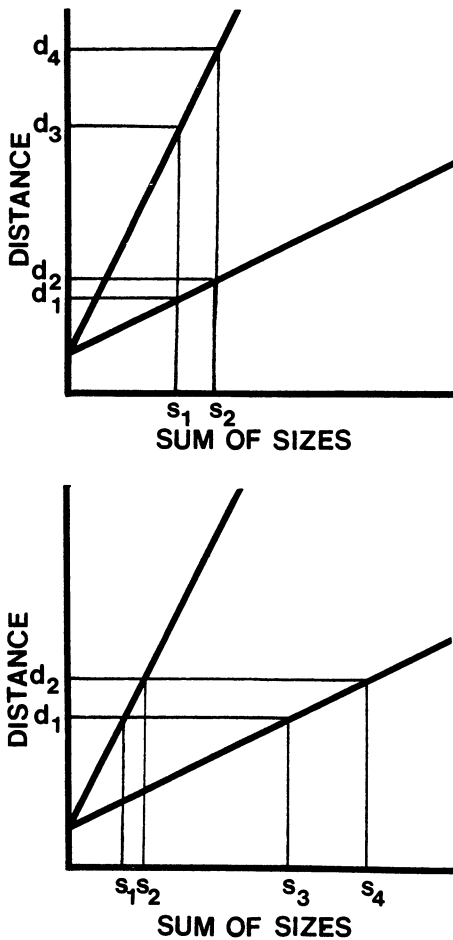


FIG. 2. TWO HYPOTHETICAL SIZE-DISTANCE REGRESSIONS, DIFFERING ONLY IN SLOPE

(A) The dependent variable is the distance separating a pair of plants, the independent variable is the sum of their sizes (e.g., canopy areas or basal areas). The steeper slope indicates more intense competition, because it associates a given increment in sum of sizes ($s_2 - s_1$) with a larger increase in distance ($d_4 - d_3 > d_2 - d_1$).

(B) The same hypothetical regressions. Again the steeper slope indicates more intense competition, because it associates a given increment in distance ($d_2 - d_1$) with a smaller increase in sum of sizes ($s_4 - s_3 > s_2 - s_1$).

separation/m² of canopy area), the slope of the regression. These estimates of intensity and importance take into account all processes influencing the spatial arrangement of the plants (presumably by means of differential growth and mortality rates) over a time span ap-

proaching the age of the oldest shrubs on the site, and are thus more inclusive than Fonteyn and Mahall's (1981) short-term physiological measurements (which may have reflected only elastic strain, *sensu* Levitt, 1972).

INTENSITY AND IMPORTANCE DECOUPLED

Ecologists have widely assumed, perhaps unconsciously, that more intense competition is more important (in some sense). We contend that intensity and importance of competition are not necessarily correlated by virtue of their meanings or any logical consequence thereof.

Fig. 1 represents four possible states of an organism, in which its well-being is entirely determined by various stresses that contribute quantitatively and incrementally to its strain or reduction from the optimal state. The effect of competition is to reduce the physiological state of the organism from the optimum (point O) to point C. Other stresses (e.g., cold, nutrient deficiency, disease, parasites) together reduce its physiological state further to point A. The intensity of competition (O - C) in Case a is the same as in Case b, but the importance of competition $[(O - C)/(O - A)]$ is less in Case b, because the overall reduction in well-being (O - A) is greater. Cases c and d differ from each other in the same way. The intensity of competition in Case c is less than that in Cases a and b, but the importance of competition is greater, because it accounts for a larger proportion of the overall reduction in well-being. Thus, intensity and importance of competition need not be correlated, in part because intensity is an absolute measure whereas importance is a proportional one.

Even so, this picture of intensity and importance is biased in favor of a correlation between the two. We have described it as showing four possible states of an organism, but it might also depict the states of four different organisms or the average states of four different populations or communities. If that is the case, then we have equated the range of states from optimal to lethal for organisms that might have very different tolerance ranges. Also, we have assumed for purposes of illustration that stresses produce strains that are simply additive, but they may well interact synergistically. Removing these simplifying assumptions would only strengthen our argument that in-

tensity and importance are not necessarily correlated.

Further, this depiction omits other factors that influence an organism's chances of survival and reproduction (see quotation from Fonteyn and Mahall, 1981, above). For example, if a predator eats an individual, the contributions of competition, abiotic stress, and the like, to its previous physiological state are unimportant. It may be true in some cases that the individual was in a place or condition that made it more vulnerable to predation because of competition (or other stress agents), but the predator killed it, not by adding incrementally to its strain, but by creating a new independently lethal trauma. Thus, the effect of the predator on this individual is not commensurable with the effects of the various agents of stress depicted above; predation was very important to this individual, but competition was not, even if it was very intense (as in Case a of Fig. 1). To put it another way, competition acted in a quantitative way, adding to the organism's strain, whereas predation acted qualitatively, killing it outright. Predation may not always act in this way—i.e., predators do not always succeed in killing the intended victim, but may injure it, or prevent it from foraging for a while, thereby adding to its strain. However, predation and many other factors (e.g., fire, landslides, lava flows, wind throws) often act independently of an organism's physiological state.

A second argument for decoupling intensity and importance of competition is suggested by the phrase "if. . . continued long enough" in our description of stress. That is, even a very weak stress may decrease an organism's fitness if it continues long enough. However, a brief, intense, but sublethal stress or strain may increase an organism's fitness by stimulating acclimation, or it may have no lasting effect at all. Perhaps we should use cumulative measures of stress and strain, similar to the cumulative measure of heat expressed as degree-days, which combine instantaneous intensity with duration (Idso, Jackson, and Reginato, 1978). See Levitt (1972) for a more complete discussion of the effects of persistent strain.

Thus competition may have a low intensity but be very important if it is virtually the only factor affecting the fitness of the organisms in-

involved. On the other hand, competition may be very intense but unimportant if the fitness of the organisms is largely determined by other factors. In the second case, the influence of other factors does not make the competition less intense, only harder to detect. The distinction between intensity and importance applies to other processes than competition. Predation, disturbance, and abiotic stress may also be intense but unimportant, for similar reasons.

That these circumstances (important weak competition or unimportant strong competition) may not actually arise does not weaken our argument. We claim only that importance and intensity have different meanings and ought to be kept separate. Even if it is shown that they are always strongly correlated (and this would be a notable empirical discovery), that would not negate our distinction. Intuitively, it seems unlikely that weak competition could ever be very important in a natural community because other processes always operate, but it does seem likely that the other extreme is common. Members of two species living together in a very stressful habitat may require many of the same resource items, and thus compete intensely. At the same time, their growth rates, survival, or reproductive success may be determined almost entirely by their abilities to cope with or escape predation, abiotic stress, defoliation by herbivores, other forms of disturbance, or the action of allelopathic agents released by their neighbors, thus rendering competition unimportant.

PROCESS AND PRODUCT

Although we have explicitly defined competition in terms of the process of organism-induced strain, we and others have often used the word "competition" equivocally, referring sometimes to the process of competition and sometimes to its product. Many words refer ambiguously to both a process and its product—e.g., "harvest." In the case of ordinary words like "harvest," this ambiguity is usually removed by context, but in the case of "competition" the ambiguity seems more vexing. We discern two reasons for this. First, competition is often conceived to be a self-extinguishing process. Niche divergence, competitive exclusion, and habitat shift are all products of competition which reduce or elim-

inate present competition. Thus the process of competition is often inferred from its absence, in contrast to the more usual situation of "harvest" in which one has a harvest (product) in hand at the end of the harvest (process). Second, in most cases the process of competition is not observed at all, but is inferred from its products (Rathcke, 1984). This is akin to observing hay stacks in a field and inferring the process of harvesting them. Whereas hay stacks are very unlikely to result from any process other than harvesting (and so the inference is good), nonoverlapping niches or habitat shifts may result from processes other than competition (and so the inference requires further evidence).

The process-product ambiguity of competition can be avoided by carefully distinguishing between the intensity and the importance of competition, for importance can be attributed to the products of a process long after it has ceased, whereas intensity can only be attributed to an existent process. This dichotomy is somewhat obscured when we (quite legitimately) measure the intensity of past competition by its present products, but we need only remind ourselves that we are attributing intensity to a process existent in the past (history leaves its mark—see the quotation from Schroder and Rosenzweig, 1975, below).

The importance of competition is not only relative to that of other processes, it is also relative to various ends, each with its own time scale. That is, competition may be important to the growth, survival, reproduction, or fitness of an individual, or to spatial patterning of members of a population, the coevolution of coexisting species, or the distribution of species along environmental gradients. No doubt the reader can supply other ends.

Schroder and Rosenzweig (1975) and Connell (1980) made the distinction between present and past competition, and presaged our proposed distinction between intensity and importance of competition. Schroder and Rosenzweig (1975) wrote:

. . . the conclusion that the interspecific competitive alpha [a measure of intensity of competition] is zero does not lead to the conclusion that interspecific competition is unimportant in the system. Instead . . . such competition has molded the system (p. 9).

The difference between past and present competition is more complex than this. Fonteyn and Mahall (1981) implied an intermediate product: spatial patterning of vegetation (see also Sherwood and Risser, 1979, quoted below). Spatial segregation of competitors can also reduce competition between them, and thus might be expected as a result of competition in the recent past.

We can speak of three broadly conceived time scales relevant to this discussion (Table 1). The shortest, from nearly instantaneous to about the lifetime of an individual, we can call the immediate time scale. The products (effects) of competition on this time scale are found in physiological, behavioral, and developmental responses of individual organisms. The intermediate time scale, of somewhat less than one lifetime to a few generations, is associated with ecological products like spatial patterning (in sessile organisms), adjustment of territory sizes, reduced fitness of individuals and resulting selection pressures, species composition of communities, immigration and emigration, and distribution of species along environmental gradients. The longest time scale, from several to very many generations, is associated with the evolutionary products of competition, such as the coevolution of competitors, niche divergence, habitat shift, competitive exclusion, and the evolution of competitive ability and territorial behavior. Of course the time scales and their results overlap considerably.

This discussion of different ends of importance and their associated time scales suggests another argument for separating intensity and importance. As we move from the immediate physiological effects of competition to its long-term ecological or evolutionary effects, the chain of causes and effects becomes longer and more tenuous. It is more tenuous because, at every step, our inferences are qualified by such phrases as "all other things being equal," "may result in," "usually results in," "if other factors do not intervene," and similar bet-hedging. For example, competition always results in strain in an individual (by our definition). If it continues long enough and other factors do not intervene ("all other things being equal"), it will reduce that individual's fitness. If enough individuals in the population are thus affected, a measurable selection pressure will begin to

TABLE 1
Time scales and products of competition

	Time Scales		
	Immediate	Intermediate	Long-Term
Duration (in generations)	Less than one	One to several	Several to very many
Products	Physiological	Ecological	Evolutionary
Importance to ends	Physiological state	Individual fitness	Coevolution of competitors
	Growth rate	Spatial patterning	Evolution of competitive ability
	Adult size	Community composition	Niche divergence
	Fecundity	Distribution of species along environmental gradients	Resource use
	Well-being	Adjustment of territory sizes	Competitive exclusion
			Evolution of territorial behavior

operate. But this selection pressure will produce evolutionary effects (e.g., niche divergence) only if a variety of conditions are met, among them that the population is large enough that genetic drift is unimportant, that mating is random, that the population has the genetic capacity to respond in an adaptive way, that other exclusive selection pressures are not more important, and so forth.

By the time the chain of inference stretches from physiological to evolutionary effects so many conditional statements have been included that it becomes likely that some are not met. Often it is assumed that the conditions are met, or that the violations are not important enough to negate the conclusion, but the longer the chain of inference the less likely these assumptions are to be true or are to be taken into account in a finite research program. We must also be aware of the possibility that observed patterns at any link in the chain may be caused by processes other than competition, either acting alone or in combination with competition (Hilborn and Stearns, 1982). Intensity and importance are thus most strongly linked at the immediate physiological level, but we have shown that even at this level the two are not necessarily correlated.

Different importances are probably connected. As competition becomes more important in determining the well-being or ill-being of individuals, it presumably becomes more important in determining their fitness, in the evolution of the populations to which they belong, and in the composition of their communities (e.g., through competitive exclusion). We

should not take these connections for granted, however, but regard them as objects of study.

Before exploring some applications of the distinction between intensity and importance of competition, we pause to summarize some of the main points of the distinction. The intensity of competition for an individual is the amount of strain which that individual experiences as a result of the use (or defense, or sequestering) of resource items by another. Thus, intensity is most closely connected with immediate physiological effects on the well-being of individuals. It is separable, at least in concept, from the intensities of other ecological processes. The intensity of competition at the population or community level is in some sense a sum or average of the intensities experienced by individuals.

The importance of competition to an individual, by our definition, is the relative contribution of competition to that organism's overall reduction from its optimal physiological condition. Since ecologists are often more interested in explaining population-level and community-level phenomena, however, our analysis connects the importance of competition more closely with long-term ecological and evolutionary effects, through the fitness of individuals, on the structure of communities and the gene pools of populations. The importance of competition is necessarily relative to the importances of other processes.

We have shown that the importance of competition (at any level of integration) is not necessarily correlated with its intensity (at the same or any other level of integration). In brief,

this is because competition is one cause among many in a complex network of interacting causes (Hilborn and Stearns, 1982) that in combination give rise to ecological effects, such as fitness, community structure, and niche packing.

APPLICATIONS

Understanding Grime

The distinction between intensity and importance helps us to understand one of the more important recent developments in plant ecology, which may have applications to animal ecology as well (see Southwood, 1977). In a paper that has provided the stimulus for many others, including this one, Grime (1977) wrote:

When the four permutations of high and low stress with high and low disturbance are examined . . . it is apparent that only three are viable as plant habitats. This is because, in highly disturbed habitats, severe stress prevents recovery or reestablishment of the vegetation. It is suggested that each of the three remaining contingencies has been associated with the evolution of a distinct type of strategy, i.e., low stress with low disturbance (competitive plants), high stress with low disturbance (stress-tolerant plants), and low stress with high disturbance (ruderal plants). These three strategies are, of course, extremes. The genotypes of the majority of plants appear to represent compromises between the conflicting selection pressures resulting from particular combinations of competition, stress, and disturbance (p. 1169).

Elsewhere, Grime (1984) asserted that

. . . the primary mechanism controlling the nature and distribution of plant populations, species and communities arises from three selection processes which operate in the present and have also exerted a dominant influence in the evolution of plants. Two of these selection processes may be defined as *stress* . . . and *disturbance*. . . At high intensities both stress and disturbance select for particular types of life-history and physiology. . . Where the intensities of stress and disturbance are low, rapid rates of resource capture and growth are possible and a third selection process (competition . . .) becomes of overriding importance and selects for a quite different set of plant characteristics (p. 29–30, emphasis original).

We interpret Grime to make three claims,

one theoretical and two empirical. The first empirical claim is that these three selection pressures (stress, disturbance, and competition) have been and are the most important ones in the evolution of (vascular land) plants. The theoretical claim is that if there are only three basic kinds of selection pressures operating on plants, the relative importance assumed by any one of them in the evolution of a given species is necessarily inversely related to the combined importance of the other two. The second empirical claim is that the importance of a given selection pressure is correlated with its intensity in the habitat.

Generating Hypotheses

The distinction between intensity and importance leads to testable hypotheses. If we consider Grime's theory in this light, we derive three hypotheses:

- (1) As abiotic stress becomes more intense, competition becomes less *important*;
- (2) as abiotic stress becomes more intense, competition becomes less *intense*; and
- (3) as competition becomes less *intense* it becomes less *important*.

If intensity and importance are assumed to be equivalent or correlated, as is usually done, then any of these statements can be deduced from the other two (indeed the third is a tautology). If, however, our distinction between intensity and importance is accepted, then none of them can be deduced from the others, and the third is not tautological. We do not claim that Grime has made these predictions, nor that they are true (indeed our own evidence is contrary to them). We present these hypotheses only to demonstrate that our distinction between intensity and importance of competition leads to testable hypotheses, and thus has empirical content.

Parallel hypotheses can also be formulated for the relationship of competition to disturbance (or to predation, parasitism, or disease), but we have concentrated on abiotic stress because it is commensurable with competition, and comparisons are therefore easier. These hypotheses can be tested by measuring the intensity and importance of competition in habitats with varying intensities of abiotic stress. To do this, methods are needed that in-

dependently measure the intensity and importance of abiotic stress and competition.

Understanding Methodology

The distinction between the intensity and importance of competition also helps us to understand several methods used to study competition. We will point out some of the advantages and disadvantages of these methods, as illuminated by our proposed distinction.

One approach to the study of competition between a given pair of species is to grow them at various densities and mixtures under controlled conditions (as in a greenhouse or growth-chamber) and observe the differences in growth that result from the presence of the competitor. Such experiments are often of considerable interest in their own right, but rarely extrapolate usefully to natural situations (Harper, 1977; Goldberg and Werner, 1983). The reason usually cited for this failure to extrapolate is that conditions in the laboratory do not reflect those in nature, which include other competing species not included in the laboratory study, asynchronous emergence, herbivores, predators, unpredictable climate, chance, and other factors.

In the context of our discussion above, this explanation can be restated. Laboratory experiments (usually) measure the maximal possible intensity of competition between the organisms studied, which is determined by niche overlap. In field situations, however, ecologists are interested in the intensity of competition actually occurring, which is a result of the combined influences of niche overlap, spacing (of sessile organisms), or frequency of contact (of motile organisms), and perhaps the abiotic environment. Even more often, however, ecologists are interested not in intensity, but in the importance of competition, which is not measured in most greenhouse or laboratory experiments because other influences on fitness are deliberately excluded by the experimental design. Some experiments are designed to address importance, as for instance when clipping, repeated reductions in population, various forms of abiotic stress or disturbance, or predators or parasites are deliberately introduced. The interpretation of such experiments is often difficult, and the accuracy of their extrapolation to the field is probably related to the choice of noncompetitive factors

introduced, how these are simulated, and other aspects of the accuracy with which they mimic natural systems. In other words, the experimental design determines the importance of competition in the experiment, which may not match the importance of competition in the natural community of interest.

A more direct approach is to measure intensity or importance of competition in natural populations or communities. Connell (1980, 1983) and others (e.g., Schoener, 1983) have advocated field experiments as perhaps the most effective means of doing this. However, care must be taken in interpreting the results of such experiments. Some experiments measure the importance of competition, if the responses monitored are population-level effects—such as changes in natality or mortality; or higher-level effects—like changes in community composition or niche packing. In contrast, some field experiments (e.g., Fonteyn and Mahall, 1981) measure transient physiological states of the organisms, and thus address intensity of competition, not its importance. These two kinds of experiment are not equivalent, and are not easily compared.

Even among experiments that measure importance of competition, comparisons are not always straightforward because the importances measured are frequently directed toward different ends. Connell's (1983) brief descriptions of the studies he reviewed reveal the variety of ends that ecologists have investigated.

Removal experiments and reciprocal transplant experiments are perhaps the most commonly used methods in experimental field studies of competition. Our distinction between intensity and importance can also be applied to the interpretation of such experiments.

A typical experimental design is to establish a number of plots in an area where the two species (A and B, say) co-occur naturally. Some plots are left undisturbed as controls, in others one species is removed, and in the remaining plots the other species is removed. The sizes of the populations are monitored in the various plots and compared, often by means of an analysis of variance, to detect any responses to the removal of the putative competitor. In such an analysis, we would interpret the difference between the population sizes of species A in plots where species B had

been removed compared to control plots as an estimate of the intensity of competition with species B experienced by species A. The importance to species A of competition with species B would be estimated by the proportion of total variance accounted for by the removal. This is the ratio of the sum of squares due to treatment in this contrast (B present vs. B absent) divided by the total sum of squares, i.e., between groups sum of squares/total sum of squares (Kleinbaum and Kupper, 1978: 71–77; Sokal and Rohlf, 1981: 570–571). The importance of other (uncontrolled) factors would be estimated by the ratio of the sum of squares due to error divided by the total sum of squares (i.e., within groups sum of squares/total sum of squares). Similar computations would yield the intensity and importance of competition with species A experienced by species B.

For example, Hairston (1980) studied competition between two salamander species in North Carolina by using a similar experimental design. We reproduce one of his analysis of variance tables (his Table 2) in our Table 2. This table reflects the effects of removal of *Plethodon jordani* on the abundance of *P. glutinosus* over the years 1974–1978. The treatment effect is the removal, the years effect reflects variation from year to year during the experiment. We calculate (and add to his table) the importance to *P. glutinosus* of competition with *P. jordani* as the sum of squares due to treatment divided by the total sum of squares: $1.09/25.70 = 0.04$. Hairston calculated the intensity of competition experienced by *P. glutinosus* as the difference in population size of *P. glutinosus* between treatment group means and control group means, weighted by the numbers of *P. jordani* removed. He used the conceptual framework of the Lotka-Volterra competition equations (Lotka, 1932) to calculate an $\alpha_{g,j}$ (per capita effect of *P. jordani* on *P. glutinosus*) of 0.194. Adjusted for the difference in biomass of the two species, $\alpha_{g,j}$ is 0.298.

The Lotka-Volterra competition equations have been the basis of many competition studies and models. Although it is beyond our scope here to analyze the extensive literature on this subject, we point out that, at least in their simpler forms, models based on these equations express the effects of competition on a species with only one parameter: α . We

TABLE 2

Variance analysis of the effect of removal of the salamander Plethodon jordani on the abundance of P. glutinosus in the Great Smoky Mountains, over the years 1974–1978

Based on Hairston, 1980: 820. The treatment effect is the removal of *P. jordani*, and the years effect reflects population variation across the years of the experiment. We calculate the estimated importance of each effect by the ratio of the sum of squares due to that effect divided by the total sum of squares, and add this as the rightmost column.

Source of variance	df	Sum of squares	F	Importance
Treatment	1	1.09	7.71**	0.04
Years	4	3.36	5.94***	0.13
Interaction	4	1.31	2.23 NS	0.05
Residual	141	19.94		0.78
Total	150	25.70		1.00

** $p < 0.01$

*** $p < 0.001$.

df, degrees of freedom.

interpret this α (as do many others — e.g., Schoener, 1983) as a measure of the intensity of competition, but many workers have also interpreted it as a measure of the importance of competition. Perhaps these models ought to be revised to include separate terms for the intensity and importance of competition.

Another useful protocol for field experiments has been proposed by Goldberg and Werner (1983). A chosen plant is designated a target individual, and neighboring plants are cleared from an area around it. Either all neighboring plants are removed, or a number of neighbors of a selected species are left in place. The number of remaining neighbors varies in different experimental plots. With enough replications at a variety of neighbor densities, a regression can be calculated between the density of neighbors and the biomass (or number of seeds produced, or some other measure of well-being or fitness) of the target individuals. Competition between different species can be studied by repeating the experiment with targets and neighbors in all possible pairwise combinations of the species in the community.

Goldberg and Werner (1983) also have argued that the intensity of competition is measured by the slope of the regression line. Al-

though they did not mention it, these regressions also have a coefficient of determination (r^2), which measures the importance of competition to the target individual. Such experiments could be replicated along a known gradient of abiotic stress, and so serve as a partial test of the hypotheses enumerated above. The end toward which importance is directed here is either the adult size of the plants or their fecundity, depending on whether the target response measured is biomass or seed production.

Another technique that separately measures intensity and importance (toward a specified end) of competition is that described by Pielou (1960, 1961) and further developed by Yeaton and Cody (1976), Yeaton, Travis, and Gilinsky (1977), Gutierrez and Fuentes (1979), Fuentes and Gutierrez (1981), Phillips and MacMahon (1981), and Welden (1984). Here a regression is calculated involving the distance separating a pair of neighboring plants and the sum of their sizes. We discussed such size-distance regressions earlier as examples of how intensity and importance of competition can be estimated. We now examine this technique in more detail to show how our distinction between intensity and importance helps us to understand the method and (we hope) to standardize its application and the interpretation of results.

Yeaton and Cody (1976) compared intensities of competition between different pairs of species by comparing the correlation coefficients of these regressions. In the same paper, they used the Median test to compare ratios of the size of the smaller neighbor to distance. This they also called a comparison of intensities of competition.

Fuentes and Gutierrez (1981) employed the same method, but proposed another measure of the intensity of competition:

[T]he strength of the competition process is not the same in all cases. The slope of the regression lines might be considered as a direct measure of the importance of competitive interactions: the greater the slope the stronger the resource-release associated with a unitary distance increment between plants. . . . [T]he quotient of an interspecific slope over its corresponding intraspecific slope is an estimate of the strength of the inter- versus intraspecific effect on both species, that is, of α in the tradi-

tional Lotka-Volterra competition equations (p. 286).

Not only did they disagree with Yeaton and Cody about which regression coefficient measures the intensity of competition, but they provided a particularly clear example of equating intensity and importance of competition.

The distinction between intensity and importance clarifies the interpretation of these regressions. We showed earlier that the coefficient of determination (r^2) estimates the importance of competition, and that the slope estimates its intensity. The end toward which this importance is directed is the spatial arrangement of the plants in the community.

The coefficient of determination of a regression is a function of the slope of the regression and the variances of the two variables. That is,

$$r^2 = b^2 (s_x^2/s_y^2),$$

where b is the slope, and s_x^2 and s_y^2 are the variances of the independent and dependent variables, respectively (Kleinbaum and Kupper, 1978: 158). The presence of the variances in this formula ensures that r^2 and slope are independent in general (that is, a regression may have any combination of high or low r^2 and high or low slope, depending on the ratio of the variances). Although r^2 and slope are independent in general, they may be correlated in a particular set of data by nonstatistical (e.g., biological) causes. This possibility is the subject of the third hypothesis, above.

All previous users of size-distance regressions (except Stimson, 1974) have chosen the sum of sizes of the paired plants as the dependent variable and the distance between them as the independent variable. It is clear to us that the slopes of such regressions are inverse measures of the intensity of competition, rather than direct measures (cf. Fig. 2). Welden (1984) presented a discussion of the choice of the dependent variable. We will deal with this and other difficulties presented by this method in more detail in another paper.

One of us (Welden, 1984) has conducted a study using the method of size-distance regressions. These regressions were calculated for selected neighbors in shrub-dominated and tree-dominated sites along a moisture-stress gradient in the semiarid Piceance Basin of northwest Colorado. Other observations showed no important differences in soil nutrient sta-

tus among sites, and that allelopathy was unimportant in spatial patterning. Significant regressions were found, indicating that competition was occurring among these plants. None of the moisture-stress indexes correlated with any regression coefficient, nor did slopes (intensities) correlate with coefficients of determination (importances). Thus the data confirm none of the hypotheses listed above, but do provide some empirical evidence that the intensity and importance of competition are not correlated.

As we pointed out earlier, these size-distance regressions combine the intensities and importances of competition experienced by the two competing species, which may not be the same. However, the effects of species A on species B can be separated from the effects of species B on species A by calculating slightly different size-distance regressions. These modified regressions could take several forms. One might regress the size of plants of one species on the ratio of the size of plants of a competing species divided by the square of the distances between them. This regression model is represented as

$$\text{Size}_1 = a + b(\text{Size}_2/\text{Distance}^2) + e,$$

where Size_1 and Size_2 are the sizes of plants of the two competing species, a is the intercept and b the slope of the regression, and e represents residual error. Here the coefficient of determination estimates the importance to species 1 of competition with species 2, and the slope estimates the intensity of competitive effects of species 2 on species 1, weighted by size and distance. Other measures of well-being or fitness (e.g., seed production) could be substituted for size. Weiner (1982) used a similar approach. Other regression models would allow us to separate the effects of neighbors' sizes from the effects of their distances, e.g.,

$$\text{Size}_1 = a + b_1\text{Size}_2 + b_2\text{Distance}^2 + e.$$

Like the method of Goldberg and Werner (1983), these modified size-distance regressions allow us to test the three hypotheses given above. They have the advantage over Goldberg and Werner's method of including simultaneous competition with all the other species in the community (in the error term), and thus

the importances of different competitors can be compared.

THE DEBATES

Our proposed distinction between the intensity of competition and its importance contributes to clarifying two debates among ecologists. We quote from various ecologists below, not as criticism of their work or thought, but solely as evidence for our contention that the failure to distinguish clearly between intensity and importance has clouded these debates. Because the authors we quote have not made this distinction, we will sometimes speak loosely (in commenting on their positions) of competition as being greater or less, without specifying whether it is greater or less in intensity, importance, or both, in order to emphasize their apparent disagreement.

Stress and Competition

Ecologists have long been interested in the relationship between competition and abiotic stress in structuring communities, but at least three contrary positions have been presented. Some claim that competition is greater in severe environments, others hold that competition is greater in benign environments, and others take competition to be constant in stressful and benign conditions. Interest in this relationship goes back at least to Darwin, who wrote in *The Origin of Species* (1st ed., 1859) that the action of climate in determining the numbers of a species

... seems at first sight to be quite independent of the struggle for existence; but in so far as climate chiefly acts in reducing food, it brings on the most severe struggle between the individuals, whether of the same or of distinct species, which subsist on the same kind of food. ... [I]n going northward, or in ascending a mountain, we far oftener meet with stunted forms, due to the *directly* injurious action of climate, than we do in proceeding southwards or in descending a mountain. When we reach the Arctic regions, or snow-capped summits, or absolute deserts, the struggle for life is almost exclusively with the elements (p. 121-122, *emphasis original*).

Darwin recognized two kinds of abiotic stress: one the result of a reduction in food supply (by climate); the other a result of "the *directly* injurious action of climate." The first kind of

abiotic stress increases competition, the second reduces it.

C. H. Muller (1952) wrote that in Scandinavian heath and tundra vegetation, coactions characteristic of temperate vegetation are absent:

The great distance of the plants from one another [because of the severity of abiotic stress] makes the dependence of one upon another impossible. Each is a pioneer completely independent of all others. Similarly, the distance between the individuals reduces to nothing the pressure of competition except where two plants are fortuitously established so close to each other that their rhizomatous spread brings them in contact either above or below soil level (p. 305–306).

Muller, like Darwin, claimed that intense abiotic stress reduces competition. Here he is plainly talking about a directly injurious environment.

A century after Darwin, C. M. Donald (1961) wrote:

[I]t might at first be supposed that plant competition for light will be less where the light supply is greater, just as competition for water is less acute in wet regions than in dry regions. But this is not necessarily so. A reasonable criterion of the intensity of competition is the difference in the physiological status of a plant in isolation and a plant of like genotype among competitors. Adopting this index, competition for light is likely to be of comparable intensity whether illumination is weak or strong. . . . [T]he difference will lie in the depth of the canopy rather than the degree of competition (p. 284–285).

Donald makes two claims here: that competition for water is less where water is abundant; but that competition for light is probably the same whether light is plentiful or in short supply. Thus, with some resources the relation of competition to abiotic stress is opposite to that expressed by Muller, and for other resources the level of competition is constant.

Wiens (1977) argued yet another view:

Selection [resulting from competition] may be intense in periods of severe environmental stress or resource limitation (p. 592–593).

As environmental conditions become more benign and resources abundant relative to de-

mands, selection may be relaxed, and phenotypic overlap between the populations increases (p. 594).

At these times, departure from the optima predicted by theory may be commonplace, and competition may be relaxed or absent (p. 595).

Previously I have suggested that . . . loose community structure should be expected in highly variable or harsh environments. . . . Under such conditions, resource levels and environmental conditions may at times be severely constraining, imposing strong selection pressure on populations of coexisting species and prompting intense competition. Such “ecological crunches” may act in a major way to determine the ecological adaptations of species and the biogeographic patterns of community composition. Much of the time, however, the environment may be more benign, and resource levels essentially non-limiting. Under these conditions, populations and communities may be freed of close, direct biotic or even abiotic control, and vary in manners that erode the clean patterns expected from competition theory (Wiens, 1984:448).

Wiens says here that intense abiotic stress increases competition, or at least the selection pressure resulting from competition, whereas benign abiotic conditions reduce competition. He also claims here that competition structures communities only during these times of intense abiotic stress, or “ecological crunches.” Wiens’s views are not quite parallel to the other hypothesized relationships of abiotic stress and competition cited here, because he is interested in the effects of temporal variability and unpredictability of the abiotic environment on communities, rather than the effects of continued, more or less constant abiotic stress.

Sherwood and Risser (1979) also claimed that abiotic stress increases competition:

If both inter- and intra-specific competition is high, as is expected in the Oklahoma Panhandle [because water is scarce], a regular spacing of all individuals could arise as a result of competition. . . . If both inter- and intra-specific competition were low, a random association should occur. This is the expected result in southeast Oklahoma [because water is plentiful] . . . (p. 200).

The apparent disagreement among these authors is reduced if we recognize the distinction between intensity and importance of competition. Darwin, Donald, Wiens, and Sher-

wood and Risser are in agreement that at least some abiotic stresses intensify competition. Wiens, however, differs from the others in supposing that, although intense abiotic stress intensifies competition, competition is less important in harsh environments (because it is not sufficiently intense often or long enough). Darwin, Muller, and Grime are in agreement that sufficiently intense abiotic stress reduces the importance of competition in the structure of communities. In our view, these positions are not necessarily contradictory. Adopting our distinction will also aid in deciding what sorts of evidence are relevant to supporting or contradicting any of these positions.

The Role of Competition in Community Structure

A more widely known debate among ecologists concerns the prevalence of competition as an important agent of community structure. We cite some representative papers in our Introduction, and we quote from several below. We chose these quotations because they are recent, represent the poles of the debate, and are easily accessible to readers, most of them having appeared in one number of *The American Naturalist* (Vol. 122, No. 5, November 1983), which has also been issued separately (Salt, 1984).

We shall not join the debate along the lines taken by most of the contenders. Rather than argue about the appropriateness or logical priority of null hypotheses, or the choice of particular null hypotheses and methods of testing them, we wish to examine how one may (or may not) move from agreed-upon observations of competition to inferences about community structure. We will show that distinguishing between intensity and importance of competition provides a largely unexplored means of approaching this debate.

Roughgarden (1983) wrote:

For example, on the island of St. Maarten there is strong present-day competition between two species of lizards. . . . I hypothesize that the absence of [one species] from sea-level habitat on St. Maarten represents competitive exclusion by [the other]. . . . [W]hat we are testing is . . . whether there really is present-day competition strong enough to cause competitive exclusion . . . (p. 596).

Thus, Roughgarden claims here that competition has been *important* in determining the

distribution of these lizards, and in support of this presents evidence that the competition between them is *intense*. He may also have evidence that the competition is important, but our point is that he cites evidence that competition is intense in support of a claim that competition is important, and thus he assumes a correlation between importance and intensity. Strong (1983) wrote:

I will emphasize . . . weak and inconsequential competition. . . . Strong and persistent competition, however, does not necessarily square a set of species with orthodox competition and niche theory (p. 636).

Selection [by competition] for character displacement would have to be quite intense to be felt through the strong but stochastic forces of selection upon morphology imposed by climatic fluctuation (p. 645).

Interspecific competition is probably not commonly important for herbivorous insects because autecology, vertical food-web factors (from the host plant or from natural enemies), and the weather normally serve to maintain populations below densities that would deplete resources. . . . Given the large literature on herbivorous insects, the paucity of studies showing strong interspecific competition is striking . . . (p. 647–648).

Some cases of interspecific competition among herbivorous insects show how inconsequential this factor can be. One good example is given by . . . experiments with collard-feeding insects, which [were thrown] together into a cockpit of a host garden that maximized chances of intense species interactions (p. 648).

Of all the possible pairwise interactions [of five insect species living] on . . . two plant species, 13 were not statistically significant, five were mutualistic (the opposite of competitive), and only four were competitive. On *H[eliconia] wagneriana* the mutualistic interaction had greater intensity than either of the two competitive interactions. On *H. imbricata* three of the four mutualistic interactions were more intense than either of the competitive interactions. [A] second study . . . found a similar lack of interspecific competitive organization for the community (p. 649).

Discussing another study, Strong commented:

. . . these parasitoids [of an insect] would compete intensely in the laboratory, resulting in patterns of relative abundance very different from those found in nature (p. 650).

These quotations imply that, in Strong's view, competition theory predicts intense competition to be important in controlling populations and in structuring communities. He cites above examples of strong competition that does not exert any such control, as counterexamples to competition theory. If competition theory makes the assumption of equivalence or correlation between intensity and importance necessary, then Strong is correct in considering these to be counterexamples. If, on the other hand, our distinction between intensity and importance can be reconciled with competition theory, then these need not be examples of failures of competition theory, but may be cases in which intensity and importance are not correlated. Connell (1983), in a paper titled "On the prevalence and relative importance of interspecific competition," wrote:

A comparison of relative strengths of intraspecific and interspecific competition is interesting in several contexts. The first concerns the coexistence and abundance of competitors (p. 661).

Some theoretical models also use the relative strengths to predict the possibility of stable coexistence of two competitors at equilibrium (p. 662).

Grazing and mowing act in the same fashion as predation in reducing competition. . . . [A]lso, on recently abandoned fields the abundance may not have reached levels high enough to result in strong interference between the plants (p. 672).

Thus, for Connell, strong interspecific competition implies competitive exclusion, and weak competition is unimportant.

An especially clear statement of the assumption that intensity and importance are connected comes from Hayward and McGowan (1979):

We infer that competition is strong. . . . If competition is strong, though, it is surprising that it has not resulted in niche separation . . . (p. 1054).

To summarize, Roughgarden claims that competition is intense for some organisms and is therefore important in the structure of their communities. Strong, Connell, and Hayward and McGowan claim that competition is unimportant in some communities despite its in-

tensity. One use of the distinction between intensity and importance in this dispute is to indicate what sorts of evidence should be sought to resolve it. That is, if these authors are interested in the prevalence of important competition, then in our view, evidence of intensity is somewhat beside the point.

We suggest further that it may be more profitable to ask not "Is competition important in this community?" but rather, "How important is competition in this community, relative to other processes?" The latter approach has three advantages over the former.

First, it is sometimes implied that the importance of competition in a community can be assessed only by gathering exhaustive knowledge of the autecology and natural history of its constituent organisms. Such knowledge is always valuable, and neglecting it always dangerous, but gathering it is often impractical if not impossible. However, it is possible to gain some knowledge of the role of competition in a community without much autecological knowledge. If the intensity of competition can be assigned to the slope of a size-distance regression line, or to a treatment effect of an analysis of variance for a removal or reciprocal transplant experiment, then the importance of competition is estimated by the variance accounted for, and the combined importance of all other processes is reflected in the residual error. Thus, our distinction allows us to assess the relative importance of competition without knowing in detail what other processes may be operating.

Second, the distinction between the intensity and the importance of competition does not require us to assume an equilibrium model of community structure (cf. Wiens, 1977, 1984). Contrary to many mathematical models of the processes structuring communities, the distinctions between intensity and importance, and between process and product, emphasize that communities are probably still changing, and that the change and the forces that drive it are important objects of study. This approach is what Pielou (1981) called investigating, as opposed to modeling.

Finally, this distinction assumes no preeminence of competition as an explanation for community structure, but emphasizes that it is the investigator's decision to study competition; the same questions of intensity and rela-

tive importance could be asked with reference to predation, abiotic stress, disturbance, or other processes (Connell, 1975; Grime, 1977, 1979, 1984; Strong, 1983). Some students of community structure have at times seemed to assign a potency to competition approaching that assigned to natural selection in the "Panglossian paradigm" (Gould and Lewontin, 1979). Others have seemed to assign abiotic factors or even chance a similar power. In contrast, Grime (1977, 1979, 1984) and Southwood (1977) discussed the interactive effects of abiotic stress, disturbance, and competition on populations and communities. Hilborn and Stearns (1982) provided analytical insight into methods for dealing with multifactor hypoth-

eses of causation with rigor and precision. Like these authors, we prefer an approach to the study of community structure that presumes multiple, interacting causes, and emphasizes the relativity of the importance of competition to the importances of other processes.

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