

The spatial consequences of interspecific competition

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Interspecific competition influences the spatial pattern and geographical distribution of plant and animal species.

Spatial effects may be present at the scale of one or two habitats, at a regional scale, or at the scale of the entire geographical ranges of one or more species. If interspecific competition has affected or does affect the spatial distribution of organisms then it should be manifested at all spatial scales in “repulsed” interspecific distribution.

We review the methods used and results obtained thus far in studies of the spatial consequences of interspecific competition at all spatial scales. We find that spatial effects occur more frequently and are logistically easier to detect at the scale of habitats than at larger spatial scales. Those instances where spatial effects have been documented usually involve interference competition. These instances are dominated by vertebrates, social insects, or other organisms that are essentially sessile or at least occupy feeding or breeding territories for part of their life.

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1. Introduction

Interspecific competition has been conjectured to influence the spatial distribution of organisms at scales ranging from a single microhabitat to the entire mapped geographical distribution of a species. The logic implicit in each of these conjectures is that competition between species, acting either via ongoing inhibition of adjacent individuals or through natural selection, leads species to diverge in their occupancy of space. This is because individuals of different species that overlap in their use of the environment and resources are at an immediate and a selective disadvantage. Therefore, the spatial consequence of competition at all scales should be manifested in interspecifically “repulsed” distributions. By repulsed we mean that the spatial distribution of a pair of species overlaps less than would be expected for independently distributed species.

The spatial effects of interspecific competition may be caused by suppression of growth or reproduction. These effects can involve changes in morphology, resource use, behavior, survival or abundance. However, to be spatial consequences in the

sense used here, these effects must result in a pattern discernible in one or more spatial dimension. The kinds of spatial patterns inferred to result from interspecific competition include: repulsed interspecific nearest neighbor distances, repulsed interspecific association, habitat segregation, niche shifts, zonation, ecological release, “checkerboard” geographical distributions, and abutting limits of geographical ranges.

For example, Yeaton & Cody (1976) and Yeaton et al. (1977) illustrate that the interspecific nearest neighbor distances of several species of desert plants tend to be larger for large sized plants than for small plants. They infer that this interdependency between size and distance must arise because of competitive suppression of small plants by adjacent large plants. Turkington and Harper (1979a, b) show that *Trifolium repens*, red clover, tends to occur less often than expected as a neighbor of the grasses, *Agrostis tenuis*, *Cynosurus cristatus*, *Holcus lanatus* and *Dactylis glomerata*. They also implicate competition as the likely cause of these patterns. Grace & Wetzel (1981) demonstrate experimentally that the zonation of the cattails *Typha latifolia* and *T. angustifolia* around freshwater ponds occurs in part because of

competitive interactions. Terborgh (1971) and Terborgh & Weske (1975) suggest that competitive interactions are also partially responsible for the altitudinal zonation of birds on mountains. Diamond (1975) has inferred that the mosaic or "checkerboard" distribution of various bird species among islands arises in part because of interspecific competition. Harman & Berg (1971) reach similar conclusions regarding the distributions of species of snails in ponds in New York. These latter two inferences rest on the contention that such patterns are highly unlikely to arise if species' distributions are in fact independent.

This paper examines the methods used and the evidence obtained in ecological studies of the spatial consequences of interspecific competition at all spatial scales. For convenience of discussion we have divided the spatial continuum into three scales: 1) habitat, 2) regional and 3) biogeographic. These scales obviously overlap and imply different absolute spatial scales for different organisms. We acknowledge that this division of scales is artificial and apologize to those authors whose work we represent at a scale different from their original intention. Our purpose is not to be encyclopedic, nor to provide a quantitative assessment of the occurrence of spatial effects of interspecific competition, but to represent the variety of approaches, results, and inferences drawn thus far. We ask if such effects appear to be more common at particular spatial scales and if they involve particular taxa or mechanisms of competition.

2. The habitat scale

By habitat scale we refer to interactions between species occurring within a single habitat or among two adjacent habitats. Two kinds of studies appear to qualify as within-habitat examinations of the spatial effects of interspecific competition; studies on the neighbor relationships of individual plants and studies of the occurrence of interspecific territoriality in animals. Between-habitat studies include examinations of habitat occupancy and segregation.

2.1. Within habitats

Plant neighborhood studies have focused on three aspects of the relationship between neighboring plants; simply the neighbor's identity (Pielou 1961, Yarranton 1966, Putwain & Harper 1970, Turkington & Harper 1979a, b, Phillips & MacMahon 1981),

inter-plant distances (Pielou 1962), or size-distance relationships (Pielou 1961, Yeaton & Cody 1976, Yeaton et al. 1977, Phillips & MacMahon 1981, Yeaton et al. 1985). If interspecific competition is influencing the pairwise distribution of species, interspecific pairs of plants will be either rarer as nearest neighbors, will be farther apart or will be farther apart the larger their size. The rub is determining what is expected if interspecific competition is not important, or at least no more important than intraspecific competition.

Pielou (1960, 1961, 1962) pioneered the analysis of interspecific nearest neighbor relations by developing statistical procedures to distinguish between segregated (repulsed) and independently distributed species. She also emphasized that besides competition, the causes of interspecifically segregated distributions include heterogeneity of the environment and clumped patterns of seed dispersal. To this we might add seed predation, herbivory, and higher order and indirect interactions. The variety of possible causes for segregated distributions makes it difficult, based solely on static estimates of spatial pattern, to infer the exact causes of such patterns. Additional evidence pertaining to the growth and reproduction of individuals of each species or to the nature of environmental heterogeneities must be brought to bear in order to choose between these alternative mechanisms.

More recently, Vincent et al. (1976), Meagher & Burdick (1980), Penttinen (1984) and Hutchings & Discombe (1986) have illustrated that statistical inferences based on classical nearest neighbor analyses (Clark & Evans 1954, Pielou 1961) are incorrect. This is because the null distributions of the test statistics currently used are not χ^2 as previously conjectured, but instead depend upon the exact geometry of the populations under study. At present Monte Carlo procedures appear to be necessary to correct for this deficiency. Until studies that have used the classical approaches are reevaluated it is unclear whether the biological inferences they produced are also incorrect.

A more promising approach to the analysis of interspecific spatial relationships rests on the dependency of nearest neighbor distance on the sizes of the "target" plant and its neighbor. If two species are independently distributed then not only should their nearest neighbor distances be no greater than intraspecific distances (corrected for differences in density), but pairs of large individuals should be found as close together as pairs of small individuals, after accounting for the greater physical space occupied by large individuals (Simberloff 1979). These patterns

could still arise because of clumped seed dispersal or reasons other than competition (Skellam 1951, Cole 1960), but probably are less likely to do so. Spatially explicit dynamical simulation models in the vein of Weiner & Conte (1981) and Weiner (1982) would be useful in examining this point.

Pielou (1961) appears to have first illustrated the size-distance relationship for neighboring plants in her study of Douglas fir (*Pseudotsuga menziesii*) and Ponderosa pine (*Pinus ponderosa*). She found that the interspecific size-distance relationship was no different than the intraspecific relationships for either species, illustrating what Goldberg & Werner (1983) have termed size specific "competitive equivalence".

Yeaton & Cody (1976), Yeaton et al. (1977), Phillips & MacMahon (1981) and Yeaton et al. (1985) have examined nearest neighbor size-spacing relationships for desert plants. They performed regressions of the sum of the sizes of pairs of plants on interplant distances, inferring the presence of a competitive relationship if a non-zero slope was detected. So far, the overwhelming result is that most species show inter- and intraspecific size-distance relationships that are consistent with an hypothesis of competition. However, for interspecific competition to give rise to segregated spatial patterns between species, the magnitude of interspecific effects must be greater than intraspecific effects. In other words, if competitors are equivalent then no interspecific spatial patterns should be detectable. Of the 17 interspecific tests performed by the authors cited above, in 10 instances the slope of the size-distance relationship was greater than the intraspecific slope, indicating that interspecific effects were less severe than intraspecific effects.

Within-habitat studies of the spatial relationships of animals have focused predominantly on the phenomenon of interspecific territoriality. Some species of birds (Rice 1978, Garcia 1983, Krebs 1971, Loyn et al 1983), salamanders (Thurow 1976, Jaeger 1981), mammals (Wolff et al. 1983), fish (Ebersole 1977, Low 1971, Thompson & Jones 1983), mollusks (Stimson 1970, 1973), non-social insects (Fitzpatrick & Wellington 1983, McAuliffe 1984, Hart 1985), and social insects (Baroni Urbani 1979, Brian 1983, Savolainen & Vepsäläinen 1987) have been shown to defend breeding or feeding territories against other species. However, even among these taxa (except for social insects) interspecific territoriality appears to be the exception rather than the rule.

Interspecific territoriality results in a mosaic distribution of individuals foraging upon and patrolling

largely non-overlapping territories. Removal experiments are usually performed to demonstrate that territories could be occupied by individuals of the non-resident species, were they vacated. Some studies bolster these experiments with detailed multivariate analyses of the suitability of individual territories for each species. These observations are collected to demonstrate that all species under study perceive each territory to be a unit of the same habitat and therefore display no preference for particular territories.

We found no instances where a species defends territories against other species, but not against conspecifics. Yet, many species are intra- while not interspecifically territorial.

It would be useful to compare the behaviors, energy and time investment, and the degree of territory overlap, characterizing intra- versus interspecific territoriality in order to better understand the selective forces that have led to these phenomena (Cody 1969, Murray 1971, 1976). However, that interspecific territoriality is a within-habitat manifestation of the spatial effects of interspecific competition appears to us incontrovertible.

2.2. Between habitats

Understanding the distribution of species among habitats requires an analysis of both intrinsic and extrinsic factors underlying habitat use. These factors include the species' habitat preference, habitat selection in its purest form, its physiological, mechanical and behavioral ability to use a habitat, and the role of other species in constraining habitat occupancy. Comparative autecological data cannot always account for differences in the distribution among habitats of closely related species. For example, Lee (1963) found no physiological basis for the observation that, when sympatric, *Neotoma lepida* and *N. fuscipes*, two closely related species of woodrats, occur in different habitats. In allopatry, it was found that these species preferred habitats with high densities of a choice food plant, *Quercus turbinella*, but in sympatry *N. lepida* switched to habitats that supported lower densities of *Quercus* (Cameron 1971). Detailed behavioral observations suggested that this shift in habitat use by *N. lepida* was due to aggression and resource defense by *N. fuscipes* (Cameron 1971).

It is common practice to use species removal experiments to study the role of competition in determining habitat occupancy. Such experiments involve the comparison of habitat use by a species in the

presence and in the absence of a putative competitor. These kinds of experiments have shown that many species do not occupy as wide a range of habitats as they are physiologically capable of occupying and that interspecific competition appears to be the cause of such habitat restriction (Tansley 1917, Kruckenberg 1954, Connell 1961, Harper et al. 1961, Ivlev 1961, Snaydon 1962, Lie et al. 1967, Sheppe 1967, McKell et al. 1969, Putwain & Harper 1970, Culver 1970, Brown 1971, Heller 1971, Sheppard 1971, Del Moral & Cates 1971, Jaeger 1971, Menge 1972, Menge & Menge 1974, Vance 1972, Morris & Grand 1972, Davis 1973, Holmes 1973, Rosenzweig 1973, Rice 1974, Colwell 1973, Werner & Hall 1976, Fellows & Heed 1972, Pickett & Bazzaz 1978, Chappell 1978, Hairston 1980, Grace & Wetzel 1981, Coen et al. 1981, Silander & Antonovics 1982, Alatalo 1982, McCreary et al. 1983, Bowers 1986, Gurevitch 1986, Southerland 1986, Bowers et al. 1987, and see Colwell & Fuentes 1977, Schoener 1983 and Connell 1983 for reviews). While this is not meant to be a comprehensive list of such studies, we think that it is sufficient to demonstrate that interspecific competition is important in the spatial organization of many communities. However, there are some communities that rarely appear to show such a pattern, such as phytophagous insects (Lawton & Strong 1981). Species removal experiments bolstered by observational and laboratory work can reveal much about the ability of certain species to respond to vacated habitats opened up through manipulation and, hence, the interplay between intrinsic and extrinsic determinants of habitat use.

This is not to suggest that removal experiments always result in habitat shifts. Scott & Dueser (1987) removed *Peromyscus leucopus* from shrubby habitats on barrier islands, but *Mus musculus* failed to abandon sparsely vegetated fore dune habitats for the presumably superior back dune regions. The failure to document habitat shifts in such studies may be attributable to several factors beyond the mere lack of sufficient statistical power, a serious problem in many species removal experiments (see Dueser et al. 1987 for review). First, some species may not actively compete for habitats. Each species' habitat preference may have evolved independently. Second, because of past competitive interactions a species may have evolved characters that now render it incapable of occupying the habitat of another species (Schroder & Rosenzweig 1975, Connell 1980, Rosenzweig 1981). Third, when viewed in the context of the whole community indirect interactions involving other

competitors or predators may dampen or totally suppress habitat shifts (Lawlor 1979, Werner 1986).

3. The regional scale

If viewed on a large spatial scale many simple habitats or habitat complexes can be arrayed on an environmental gradient. Most of these larger-scale gradients involve the gradual and continuous change in some physical factor such as soil moisture, pH, elevation, salinity, water level, disturbance, productivity, or soil particle size. The distribution of species along such gradients have long been of interest to ecologists. Initially, gradient analysis was used to resolve the controversy over the individualistic and the community unit view of species distributions (McIntosh 1967, Whittaker 1967). More recently, it has been used to study the relative importance of physical and biotic factors (including competition) in limiting species distributions. For example, by examining the shape of species' abundance curves over a gradient, including the patterns of overlap between ecologically similar species, it has been suggested that one can infer whether competition or physiological limitations are important in setting distributions on localized gradients (Terborgh 1971, Terborgh & Weske 1975).

Hutchinson (1953) argued that when two species, ecologically similar except for their tolerance for one factor, inhabit a gradient where that factor varies, there will be points where competitive dominance shifts from one species to another producing a pattern of zonation. Gause & Witt (1935) examined the competitive dynamics of two species along a temperature gradient and concluded that temperature can change the outcome of competition producing a zonation pattern that would range from mixed species assemblages to single species situations. Because of passive seed dispersal and the lack of active choice in habitat occupancy the distribution of plants may show quite a different pattern. Skellam (1951) has shown that, with a random distribution of seeds, two ecologically similar species can coexist locally and only when seed density becomes high will competition work to the exclusion of one or the other. Seed aggregation can also lead to coexistence because of the high proportion of unoccupied space (Cole 1960, Weiner & Conte 1981). In such cases, two species may reach an equilibrium which is dependent on how many seeds are produced by each species, the competitive ability of the species where they co-occur, their den-

sities, and their overall spatial patterns. That many plants on environmental gradients appear and disappear independent of other plants, forming more a continuum of vegetation than a replacement series (e.g., Whittaker 1967) is consistent with Skellam's (1951), Cole's (1960), and Weiner & Conte's (1981) conclusions.

However, there are gradients where even plants may be expected to competitively exclude each other. For example, as the steepness of the gradient is increased, dispersal into the region of contact (or overlap) will increase because the optimum environment for each species will be spatially more proximate, thus increasing the potential for competition (Beals 1969). As an example, Yeaton (1981) and Yeaton et al. (1981) have studied the distribution of pine trees (*Pinus*) on the steep altitudinal gradients of the Sierra Nevada Mountains in California. They found several instances where particular species ended their distributions abruptly and appeared to be replaced by a species of similar growth form. Several of these species reached their highest densities just before disappearing, suggesting that these represent instances where one species competitively replaces another rather than reflecting mere differences in their physiological tolerances.

There are many other instances where competition appears to play a role in the distribution of ecologically similar species on environmental gradients. Brown (1971), Heller (1971) and Chappell (1978) studied chipmunks (*Eutamias*) on mountains in the western United States and concluded that competition is the primary factor responsible for their discrete and nonoverlapping distributions on elevational gradients, although the outcome of these interactions appears to be habitat dependent. Pyke (1982) showed that species of bumble bees (*Bombus*) with similar proboscis lengths appeared to replace each other along an elevational gradient in Colorado. Terborgh (1971) and Terborgh & Weske (1975) reported data showing that the distribution of many species of birds on Peruvian mountain ranges is consistent with that expected under a model of competition (a similar pattern has been reported by Diamond 1973). Hanski (1983a) found that among carrion-feeding beetles in Sarawak the number of pairs of congeners displaying elevational replacement was substantially greater than expected if distributions were independent. Lubchenco (1980) used experimental species removals to demonstrate that the lower limits to the distribution of algal species on an intertidal gradient are predominantly due to competition, though predation is also

involved. Similar examples for other intertidal organisms are chronicled by Connell (1961, 1975), Menge & Sutherland (1976), Lubchenco & Menge (1978), and Sousa et al. (1981). Silander & Antonovics (1982) showed that the distribution of some plants along a gradient of coastal communities was affected by competition. Anderson et al. (1981) argued that the replacement of coral reef fish along a 50-km gradient running from the outer barrier to a near shore reef was primarily due to interspecific competition. Other similar examples supporting the notion that competition is an important factor at the scale of environmental gradients include the work of Pielou & Routledge (1976), Yeaton et al. (1985), and Southerland (1986). Notable instances where competition did not appear to be important in the distribution of species along environmental gradients includes the studies of Whittaker (1967), Rabinowitz (1978), McCreary et al. (1983), Grime & Lloyd (1973) and Hughes & Thomas (1971).

There are major problems in rigorously demonstrating that species' distributions on gradients are affected by competition. Virtually any large or intermediate-scale natural gradient is likely to contain a multiplicity of variables that change coincidentally and these may act individually or collectively to influence the distribution of plant and animal species. One problem is deciding which of these variables (or which set of variables) actually limits species' distributions. In situations where the environmental gradient is steep and two species' distributions abut and overlap, experimentation or detailed observation can be used to test for competition in that area. But there are major problems in projecting these results over other portions of the gradient to account for the distribution of species on a larger scale (Bowers 1986). For example, even a slight shift in a critical factor can change the balance of competition between species. In such cases is it correct to single out either competition or physiological ability as the most important factor? Another problem is that major environmental gradients usually support from tens to hundreds of species and identifying those cases where one species might limit the distribution of another can be very difficult and is usually arbitrary.

Over parts of their geographic ranges some species' distributions may not be determined by an interplay of species interactions with environmental gradients. For example, in southern Finland or in the Piedmont region of Virginia, USA the suitability of forest patches for breeding by passerine birds may vary haphazardly rather than display monotonic or

simple modal geographical patterns. If this is true and we assume that spring migrants may colonize and persist equally well in all forest patches in these regions, complex mosaic regional patterns of forest patch occupancy could result were interspecific competition occurring. We found no studies that have examined species' distributions at this regional or "landscape" scale to determine if interspecific competition has affected species' distributions. This may be partly because we have considered some studies to represent biogeographic scales rather than regional scales (e.g. Jaeger 1971, Brown 1971). However, we believe this actually represents a lack of study of complex non-gradient patterns of plant and animal distribution at regional scales.

4. The biogeographic scale

By biogeographic scale we refer to patterns that encompass much or all of the geographical range of one or more species. At geographical scales three kinds of distribution patterns have been interpreted to arise because of competitive interactions among pairs or groups of species: parapatric or abutting geographical ranges of closely related species, checkerboard or mosaic distributions of species on islands or in insular habitats, and differences in the range of habitats a species occupies when putative competitors are absent (i.e. ecological release).

While abutting limits to geographical ranges have been inferred to result from competitive exclusion (Lack 1944, MacArthur 1972, Brown & Gibson 1983), in only a few instances have data been brought to bear on this question. On the other hand, many instances of hybridization along parapatric range boundaries have been reported (Remington 1968, Grant 1971), and for these instances it is difficult to imagine that interspecific competition is setting each species' range limit.

Miller (1964) concluded that four species of pocket gophers, competitively exclude each other by aggressive behavioral interactions. This inference was not based on field observations of interspecific interactions, but on extrapolating behavior observed between conspecific individuals. Miller (1964) did marshal field data to give convincing arguments that neither the physical environment nor barriers to dispersal prevented these species from occupying each others range. Experiments by Vaughn & Hansen (1964) show that these species can persist in each other's range, but do not do so for reasons that are

unclear. Brown (1971), Sheppard (1971), and Heller (1971) provide similar arguments to explain the parapatric ranges of several species of chipmunks (*Eutamias*), and also provide direct field evidence of aggressive interference competition. Chappell (1978) performed the crucial removal experiments that support this conclusion.

Jaeger's (1970, 1971, 1974) studies are exemplary in setting out the kinds of experiments and observations necessary to reach firm conclusions concerning the current role of competitive interactions in setting range limits. He performed reciprocal transplant experiments to determine if interspecific competition set the distributional limits of two parapatric salamanders of the genus *Plethodon*. He looked at the survival of *P. nettingi shenandoah* and *P. cinereus* in single and two species enclosures within the range of each species. He found that *P. cinereus* does not persist in the range of *shenandoah*, even in *shenandoah's* absence, but that *shenandoah* persists in the range of *cinereus* only when *cinereus* is absent. Because he observed natural dispersal of *shenandoah* into *cinereus'* range and because he found no evidence of other biological interactions preventing *shenandoah* from persisting in *cinereus'* range, Jaeger (1971) concluded that *cinereus* excludes *shenandoah* from its range, but is prevented from persisting in *shenandoah's* range because of physiological limitation. Subsequent experiments by Wrobel et al (1980) indicate that the mechanism underlying this interaction is aggressive interference competition.

Related to the issue of what role competition plays in setting range limits is the question of overlap in geographical distributions. Allopatry and parapatry are merely the most extreme forms of reduced sympatry. For non-insular species, only Jackson (1974), Pielou (1978, 1979) and Bowers & Brown (1982) have attempted to determine if putative competing species overlap in geographical distribution less than expected under an hypothesis of independent distributions. Jackson (1974) provides no statistical test, but concludes that competition does not appear to limit the geographical distributions of marine bivalve mollusks. His conclusion is based on observing considerable overlap in distribution among congeneric species. Pielou (1978, 1979) found that among species of littoral algae, the ranges of congeneric species overlap more frequently than for non-congeners. She interpreted this as inconsistent with an hypothesis of competition setting range overlap. Bowers and Brown (1982) examined the guild of granivorous rodents in the Great Basin, Mojave, and

Sonoran deserts of North America to determine if similarly sized guild members tend to co-occur as often as dissimilar species. They proposed that competition would be most intense between species of the same body size because these species would be most closely matched in resource use. Their findings indicate that similar sized guild members co-occur less often than expected if they were independently distributed.

Bowers & Brown's (1982) conclusion that similar sized guild members have repulsed geographical distributions is consistent with hypotheses other than interspecific competition. Chief among these is evolution by descent. Many of the similar sized guild members that Bowers & Brown (1982) examined are likely to be what Mayr (1963) terms "geographical species". They are related by descent with their parapatric or allopatric sister taxa and may display such distributions exactly because of the geographical component to speciation (Mayr 1963). Without evidence that these species have and do attempt to disperse and occupy sites in each other's geographic range, and that they fail to persist because of the congeners presence, geographical speciation remains a plausible alternative explanation for these distribution patterns. Bowers & Brown (1982) illustrate (their fig. 3) that many of the negatively associated species that have similar body sizes are congeneric, but a substantial number are unrelated. The role of geographical speciation in generating parapatric and allopatric ranges could be examined by a cladistic analysis of the phylogenetic relationships among these taxa. If a guild member's sister species tends to be a dissimilarly sized sympatric species rather than a similarly sized allopatric species then geographical speciation is unlikely to have produced the kind of pattern observed by Bowers & Brown (1982).

Interspecific competition has been invoked often to explain the mosaic distributions of various taxa on islands or other insular habitats (Grant 1970, Nevo et al. 1972, Diamond 1975, Abbott et al. 1977, Abbott 1977, King & Moors 1979). While these kinds of distributions are also consistent with the hypothesis that they were caused and are maintained by interspecific competition, they are also consistent with other hypotheses including: geographical speciation, lack of dispersal, differences in suitabilities of islands between species, predation, disease, and parasitism. Just as for parapatric continental distributions, evidence of active dispersal and subsequent resistance by resident species would be necessary to confirm an hypothesis of competition.

To find that a few pairs of species tend to overlap in distribution very little, if at all, should not be viewed as unusual when one considers the massive number of pairs of species searched to find these instances. Connor & Simberloff (1979, 1983, 1984, 1986) and Simberloff & Connor (1980, 1981) have suggested that the hypothesis of interest is whether for a particular fauna or flora the pattern of species co-occurrences follows that expected under an hypothesis of independent distributions or suggests aggregation or a tendency for exclusive geographical ranges. Much debate has focused on the exact form and protocol for generating an expected pattern of species' co-occurrences given independent distributions (Diamond & Gilpin 1982, Gilpin & Diamond 1982, 1984, Harvey et al. 1983). However, there appears to be general agreement with the hypothesis suggested by Connor & Simberloff (1979) (see analysis in Gilpin and Diamond 1982).

The results thus far suggest that some faunas show aggregated distributions, co-occur more often than expected (birds of the Bismarck Islands, Gilpin & Diamond 1982), some do not differ from expected (birds of the New Hebrides and Galapagos, Connor & Simberloff 1979, Simberloff & Connor 1980), and some show too many pairs of species with exclusive geographical distributions (birds and bats in the West Indies, Connor & Simberloff 1979). As discussed above, without evidence other than that on geographical distribution it is impossible to confidently attribute any of these patterns to a particular causal mechanism.

Data on dynamical changes in the geographical distributions of species are also pertinent in determining the spatial consequences of interspecific competition. Most of these data arise because of the introduction of species to regions they previously did not occupy. Simberloff (1981) reviews this literature and concludes that in very few instances do introduced species compete with indigenous ones. Furthermore, only for introduced ants have competitive effects on geographical distribution been observed (Haskins & Haskins 1965, Crowell 1968). Other instances where a change in the geographic range of a resident species occurred after another putative competitor was introduced appear to involve simultaneous habitat changes, predation, or disease (Birch 1979, Simberloff 1981). These observations suggest that contrary to earlier ideas, communities are not saturated with species and that they appear not to resist invasion (Simberloff 1981). However, the data available to chronicle the effects of introduced species on

native species, is largely anecdotal. These data are usually poorer in quality than experimental evidence or controlled field observations. It is also possible that many introductions failed because of interspecific competition.

The reciprocal circumstance to species introductions are instances where a species is found in the absence of putative competitors. These examples usually involve comparisons between insular and continental populations of the same species, or at least comparisons between populations embedded in communities with differing numbers of putative competitors. If when competitors are absent, or the diversity of competitors is reduced, a species expands its occupancy of habitats, then the species is said to display "ecological release". Even though such shifts occur at the scale of the habitats, we consider them as geographical phenomena since they only became apparent when widely separated habitats are examined. For example, the ant *Paratrechina bourbonica* is found in the Florida Keys where it is embedded in a community of 65 species of ants. *P. bourbonica* nests in low dead tree stumps and occasionally in holes in large low rotting trees, never anywhere else. *P. bourbonica* also occurs in the Dry Tortugas embedded in a community of fewer than ten species of ants. In the Dry Tortugas, *P. bourbonica* occupies its normal nest sites, but also nests on the ground, under stones, and within the walls of a building (Simberloff, pers. comm.). This habitat expansion is probably due to the absence of the competitors that occupied these habitats on the Florida Keys. On the other hand, *Pseudomyrmex elongatus* is also found in the Florida Keys and the Dry Tortugas. However, in both regions it nests only in hollow twigs high in trees such as the red mangrove, *Rhizophora mangle* (Simberloff, pers. comm.). It is not clear why *Paratrechina* shows release and *Pseudomyrmex* does not, but it is clear from these examples that ecological release does not always occur and that it is difficult to predict in advance which species will show it. Crowell (1962), Roughgarden (1974), Schoener (1975), Lister (1976a, b) and Larsen (1986) chronicle other instances of apparent ecological release or its absence. Even in those instances where habitat expansion is observed, although competition might seem the most compelling cause, differences in the physical environment, habitat availability, predators, parasites and diseases could also be responsible. Without evidence concerning the cause of habitat restrictions on the mainland or in the more species rich community, it is

premature to attribute all instances of apparent ecological release to reduced interspecific competition.

5. Discussion

Competition is a dynamical process working between individuals within populations. Projecting it to account for phenomena on a regional or geographic scale changes the focus from the rates of growth and survival of competing individuals or populations in relative isolation to that of a network of competing populations occurring over a range of conditions whose dynamics are determined not only by local demographic and environmental conditions, but also by biogeographic events impinging on immigration and emigration and by the spatial structure of the environment. Although there have been some attempts to model the dynamics of competition at the regional level (for review see Hanski 1983b) we note that the theoretical basis for understanding the effects of competition on geographical distribution is not well-founded. While this has not discouraged ecologists/biogeographers from invoking competition as a process to explain geographic patterns, we believe that it has contributed to the general lack of scientific rigor and the absence of experimentation in the study of such phenomena.

One problem is that changing the scale of focus from the habitat to the regional or geographic level also involves a change in the timescale over which processes become expressed. Local population phenomena are usually measured on an ecological time scale set by the dynamics of population increase. The geographic timescale, however, is linked with evolutionary processes that are bounded on one end by the rate at which local populations adapt to their environment, and on the other by process of speciation, and biogeographical events controlling primary and secondary range contact. While in some cases, local and regional time scales can be similar (Hanski 1983b) most evidence suggests they are quite different (Levins 1968).

The material we have presented is intended to characterize the wide variety of approaches and results that have been employed to study the spatial consequences of interspecific competition. We have omitted many studies in this process. However, we have illustrated that interspecific competition may or may not have spatial consequences, over a continuum of spatial scales, and that particular kinds of evidence

are crucial to support inferences regarding the presence or absence of such effects.

Based on this distillation of literature we make three observations. First, it appears that demonstrating that interspecific competition has spatial consequences is more difficult at regional and biogeographic scales than it is at habitat scales. Second, it appears that most often spatial effects of competition involve interference rather than exploitation competition. Third, and as a consequence of the prior observations, spatial effects are most often detected among sedentary organisms, vertebrates, and ants. We will treat these observations *seriatim*.

The detectability of competitive effects on the spatial distribution of plants and animals has two major facets: the biological, logistic, statistical, and experimental design aspects of showing such effects, and the question of whether they are actually less common at particular spatial scales.

At the habitat scale, nearest neighbor studies suffer statistical problems and for the most part consist only of data on static patterns. More information on the dynamics of plant populations, including knowledge of the spatial pattern of seed dispersal and herbivory will be necessary to permit firm conclusions regarding the causes of interspecific spatial patterns. Unfortunately, neighborhood based manipulative experimental designs (Goldberg & Werner 1983) cannot detect spatial effects beyond the neighborhood analyzed, so it will be difficult to extrapolate from these studies to explain the general interspecific spatial pattern of plant communities. However, these experimental designs can estimate the magnitudes of inter- and intraspecific competition in effecting growth, survival, and reproduction. If they are found to be equal then ongoing interspecific competition could be eliminated as a cause of the observed spatial pattern.

At large spatial scales the problem consists mainly of the near impossibility of performing experiments. However, as evidenced by Vaughn & Hansen (1964), Jaeger (1970, 1971, 1974), Wrobel et al. (1980), and Chappell (1978), experiments performed on local scales can be useful in determining the causes of pattern at larger scales. Of course, since the causes of the limits to geographical distribution are multifactorial, and may change from place to place, and time to time, a single experiment at one site at one time will only provide a partial answer. However, evidence on dispersal, behavioral interactions, parasites, predators, and the suitability of habitats in a competitor's range, combined with removal and transplant experi-

ments at several sites and times could paint a fairly complete picture of the causes of distributional limits.

Beyond the difficulties of collecting the evidence necessary to build a strong case for competitive effects on distribution, we also believe that ongoing competition will occur less frequently at large spatial scales. This is largely due to the heterogeneity of the environment which provides opportunities for sympatry even for competing species, and because of the complex spatial dynamics of the component populations of a species at geographical scales (Levin 1976, Levins & Culver 1971, Hanski 1981, 1982, 1983b). The temporal variability of the environment, along with the other species in the community into which each population is embedded, renders it even less likely that pairwise competitive interactions will result in reduced geographic overlap or parapatry. Simberloff's (1981) review of the community level effects of introduced species also argues that diffuse competition may be equally impotent in setting spatial patterns at geographic scales.

The linkage we noted earlier between geographical scales and evolutionary processes, and between small scales and ecological processes, also raises the issue of the "ghost of competition past" and the historical dependency expected between the geographical ranges of closely related species because of geographical speciation. Each of these will tend to make it more difficult to detect competition at large scales. However, studies that combine a detailed knowledge of the evolutionary relationships of populations and species with data on their ecology, may permit the effects of these processes to be detected in modern day geographical distributions.

That competition appears to be more easily and frequently detected at habitat scales may result from characteristics of processes occurring at such scales. One obvious advantage is that those scales we have defined as habitat appear to coincide with the scale most easily studied by field experimentation. Perhaps also the time course of population responses to experiments at this spatial scale occur within the funding period or attention span of most researchers. Whatever the exact cause, our suggestion that spatial effects are more difficult to detect at regional and biogeographic spatial scales is ripe for study and scrutiny.

Our second observation, that interference competition seems to underlie those spatial effects that have been documented is in agreement with earlier conclusions reached by Miller (1964, 1967) and Schoener

(1983). Aggressive behavioral interactions and interference between adjacent individuals via alleopathy, shading, root competition, smothering, and dislodging (note that some of these processes may be viewed as exploitative), have an inherently strong spatial component. The defence of space and its associated resources by occupancy and aggression can easily be envisioned to give rise to repulsed spatial distributions.

Most studies of interspecific competition focus on groups of closely related species. Among such groups interference competition may occur more often than exploitation competition because of the similarity in resource requirements and means of gathering resources displayed by closely related species. Interspecific aggression is also more likely to arise as a result of misdirected intraspecific behaviors between closely related species (Murray 1971, 1976). We note that in instances of interspecific competition between unrelated taxa, ants and rodents or hummingbirds and insects, the mechanism of interaction is exploitation (Brown et al. 1979, Brown et al. 1981).

On the other hand, exploitation or resource depletion competition is probably more difficult to detect under field conditions. This is because the time course of response by a species, no longer confronted with a competitor cropping some part of their shared resource base, is probably longer than that for a species released from the interference of a competitor. Of course, this depends on rates of resource renewal and consumption, but may explain why we could find

no examples of spatial distributions arising because of exploitation competition.

Our last suggestion, that a taxonomic bias toward finding spatial effects of competitive interactions among sedentary organisms, vertebrates and ants exists, may partly explain or result from our second observation. These taxa certainly have the opportunity or the behavioral abilities to engage in interference and aggression. Alternatively, there may be a bias among ecologists in how they choose which organisms to study. Convenience, charm, funding, and economic importance rank along with a taxon's scientific appeal.

We conclude by affirming that spatial effects of interspecific competition have been observed at all spatial scales. These effects are most convincingly documented by transplantation or removal experiments, coupled with autecological and behavioral observations. Employing static data on spatial distributions should always be accompanied by close scrutiny of the evidence, including statistical null models and an awareness of alternative causes of the observed patterns. Information on dynamical changes in spatial distributions will be crucial to a clear understanding of the spatial consequences of interspecific competition.

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