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Positive interactions in plant communities and the individualistic-continuum concept

Abstract The individualistic nature of communities is held as a fundamental ecological tenet by many ecologists. The empirical rationale for the individualistic hypothesis is largely based on gradient analyses in which plant species are almost always found to be arranged independently of one another in "continua" along environmental gradients. However, continua are correlative patterns and do not identify the processes that determine them, and so they do not necessarily preclude the possibility of interdependent interactions within plant communities. For example, the common occurrence of positive interactions suggests that plant species may not always be distributed independently of each other. If the distributions and abundances of species are enhanced by the presence of other species, their organization is not merely a coincidence of similar adaptation to the abiotic environment. Interpretations of gradient analyses also appear to assume that interactions among species should be similar at all points along environmental axes, and that groups of species should be associated at all points on a gradient if interdependence is to be accepted. However, virtually all types of ecological interactions have been shown to vary with changes in the abiotic environment, and a number of field experiments indicate that positive effects become stronger as abiotic stress increases. Furthermore, interactions among plants have been shown to shift from competition to facilitation along environmental continua. Thus, significant interdependence may occur even when species do not fully overlap in distribution. Higher-order, indirect interactions between animals and plants, and among plants, also suggest that interdependence within communities occurs. Eliminating a species involved in an indirect interaction may not necessarily mean that its beneficiary will be eliminated from a community, but the prospect that the distribution and abundance of any species in a plant community may be positively affected by the effects that other species have on their competitors suggests that communities are organized by much more than "the fluctuating and fortuitous immigration of plants and an equally fluctuating and variable environment" as stated by Henry Gleason. The ubiquity of direct and indirect positive interactions within plant communities provides a strong argument that communities are more interdependent than current theories allow.

Key words Ecosystems · Facilitation · Gradient analysis · Holistic · Interdependence

Introduction

One of the most familiar disputes in ecology concerns the nature of communities, and is personified by Fredrick Clements and Henry Gleason (Clements 1916; Gleason 1926; Goodall 1963; McIntosh 1967; Austin 1990). Clements and other early ecologists viewed communities as holistic and interdependent whereas Gleason argued that communities were simply an assortment of species with similar adaptations to the abiotic environment. Surveys of the ecology texts on my shelves indicate that Gleason, who stated that a plant community is "scarcely even a vegetational unit, but merely a coincidence," has emerged as the favorite among ecologists. With the exception of habitat typers in the western USA (Cook 1996), and some European schools, most academics and land managers appear to recognize the Gleasonian conceptual model of communities in their classification approaches (Austin 1990; Schrader-Frechette and McCoy 1993).

From other perspectives, however, Gleason's success is not so complete. There appears to be some discrepancy between individualistic views of species assemblages versus the interconnectedness of the functions of those same species. In some texts that promote Glea-

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sonian "*communities*" as having "species that distribute themselves over ecological gradients of conditions independently of the distributions of other species," other chapters describe "*ecological systems*" or "*ecosystems*" as having "total interconnectedness," "consisting of a unified group of components forming a systematized whole," and "united by some form of regular interaction or interdependence." Gleason does not appear to be the favorite of those being trained by Gleasonians. In informal surveys of students in my ecology classes over the last few years, I have asked students to identify with either Gleason's quote above or Clement's (1916) position that "as a organism the formation arises, grows, matures, and dies … repeating with essential fidelity the stages of its development." Despite the extreme nature of the quote, students tend to show solidarity with the "system" perspective, and over 75% consistently choose Clements' holistic vision. Academics seem to be more comfortable with holistic "ecosystems" rather than "communities" (Odum 1969; Jordan 1981; McNaughton and Coughenhour 1981; Knight and Swaney 1981; Patten and Odum 1981; DeAngelis et al. 1986; but see Wilson 1976, 1980; Engleberg and Boyarsky 1979). The Ecological Society of America, in an assessment of the use of science in achieving the goals of the Endangered Species Act (Carroll et al. 1996), recommends consideration of the following as priorities: "does the species play an especially important role in the ecosystem in which it lives? Do other species depend on it for their survival? Will its loss substantially alter the functioning of the ecosystem?" The implication is that some interdependence may be expected in natural systems.

The widespread acceptance of individualistic species assemblages, but holistic ecosystems, in academic ecological thought suggests a paradox rather than simple semantic differences. The definitions of communities and ecosystems are irrelevant to the fundamental issue of independence versus interdependence (see Begon et al., pp. 613–614 for a lucid discussion of this). The important question is: do assemblages of organisms exhibit any interdependence, and if so, how interdependent are they? Whether or not the traditional domains of ecosystems such as energy, water, or nutrient flux play a part in the interactions does not matter. The importance of the independence-interdependence issue is not just academic: there are far-reaching implications for how we conserve and utilize resources in our natural world. For example, some defenders of environmental stewardship contend that organisms in natural communities are interdependent and the loss of seemingly insignificant species may have important effects on other species (Freedman 1989; Ehrlich 1990; Ehrlich and Wilson 1991; Miller 1993; Noss and Cooperrider 1994). In contrast, the view that species are individualistic and interchangeable has been used to advocate proactively "shaping and synthesizing new ecosystems, even in the 'natural' environment" (Johnson and Mayeux 1992).

One of the strongest empirical rationales for Gleason's individualistic hypothesis developed between the 1950s and 1970s when plant ecologists conducted large numbers of gradient analyses. In virtually all gradient analyses, plant species were found to be arranged independently of one another along environmental gradients (Whittaker 1951, 1953, 1956, 1977; Curtis 1959; McIntosh 1967; Peet 1981; Ter Braak and Prentice 1988; Austin 1990; Collins et al. 1993; but see Wilson et al. 1996). This independent distribution is generally referred to as the continuum, in which "vegetation may be interpreted as a complex and largely continuous population pattern" (Whittaker 1956). Put another way, distributions of plant species rarely overlap completely. Continua of independent distributions have generally been interpreted as evidence for Gleason's concept of individualistic species assemblages and this concept has been organized into the 'individualistic-continuum' (hereafter IC) theory (Goodall 1963). Gradient analyses are the most commonly cited evidence for the IC theory, but other arguments have been based on the effects of species losses and the introduction of exotic species (Johnson and Mayeux 1992).

The IC theory is built on a foundation of the overriding importance of the abiotic environment in community organization. Under the IC, species distributions and abundances are thought to be based on the ranges in their tolerances to various abiotic factors and resource requirements – their "fundamental niches" (sensu Hutchinson 1957). Although this is not always clear in the literature, interspecific competition and the compression of fundamental niches into "realized niches" along natural gradients may also be emphasized in the IC perspective (see Wiens 1989; Austin 1990). Even Gleason believed that the distribution of a species could be affected by its "meeting with such strenuous competition from other plants that only a few individuals have a chance to grow" (Gleason and Cronquist 1964). Continuous species distributions along gradients may be expressed as Gaussian, skewed, or bimodal curves (Mueller-Dombois and Ellenberg 1974; Austin 1990; Collins et al. 1993), but are rarely attributed to any factor other than the physical environment and resource competition.

However, continua are correlative patterns and do not identify the processes that determine them. Some experiments have supported the individualistic interpretation of continua by demonstrating the combined effects of abiotic factors and resource competition on gradients (Grime 1973; Grace 1987; Keddy 1989; Pennings and Callaway 1992); but do continuous distributions necessarily preclude the possibility of some interdependence within plant communities? Other processes, such as mutualisms, herbivory, parasitism, and positive interactions may also affect plant distributions on gradients. Here, I reconcile how plants can be distributed continuously, but interact interdependently via direct and indirect positive interactions.

What are positive interactions?

Positive interactions, or facilitation, occur when one species enhances the survival, growth, or fitness of another. Facilitation has been reviewed and discussed in detail elsewhere (DeAngelis et al. 1986; Hunter and Aarssen 1988; Wilson and Agnew 1992; Bertness and Callaway 1994; Callaway 1995; Callaway and Walker 1997), so I will only include a brief synopsis here. Plants have many different kinds of positive effects on other plants. In a review of plant-plant facilitation, Callaway (1995) described direct positive mechanisms such as favorable alteration of light, temperature, soil moisture, soil nutrients, soil oxygenation, or substrate, and indirect mechanisms such as protection from herbivores, attraction of shared pollinators, root grafts, and beneficial changes in soil mycorrhizal or microbial communities. Of 128 studies of positive interactions among plants, 33 included evidence from field experiments. Consumers can also have strong indirect positive effects on some plant species by disproportionately reducing the competitive advantage of other competitively dominant species.

Positive mechanisms may act simultaneously with competitive mechanisms, and the overall effect of one plant species on another depends on which mechanisms are the most important in a given environment (Callaway and King 1996; Callaway and Walker 1997; Holmgren et al. 1997). For example, the positive effects of canopy shade or nutrient augmentation may not be manifest until roots of the plant providing the shade are excluded (Callaway et al. 1991; Aguiar et al. 1992; Callaway 1994; Chapin et al. 1994).

The common occurrence of positive interactions suggests that plant species may not always be distributed independently of each other. Clearly, if the distributions and abundances of species are enhanced by the presence of others, their organization is not merely a "coincidence" of similar adaptation to the abiotic environment. The conceptual problems that positive interactions pose for the IC theory get worse when we consider that plants can interact with each other very differently along environmental continua.

Shifts in the importance of positive interactions along environmental gradients

IC interpretations of gradient analyses appear to assume that interactions among species should be similar at all points along environmental axes – consider the significance placed upon completely overlapping species distributions as evidence of interdependence. In other words, if the positive effects of one species on another are important, should those species not be associated at all points on the gradient? However, a number of field experiments indicate that positive effects become stronger as abiotic stress increases (Walker and Chapin 1987; Bertness and Shumway 1993; Bertness and Hacker

1994; Bertness and Yeh 1994; Chapin et al. 1994; Greenlee and Callaway 1996; R.M. Callaway, submitted). These studies have demonstrated that under conditions of drought, low nitrogen availability, high soil salinity, or at the extremes of the timberline, the cumulative effects of one species on another can be positive, whereas the relationship between the same species in more benign conditions can be negative. Wilson and Nisbet (1997) presented a two-species model in which shifts in competition and facilitation led to sharp discontinuities in population densities along an environmental gradient.

The potential for a species to have a negative effect on a neighbor at one point on an environmental gradient and a positive effect at another point creates problems for traditional interpretations of the continuum as evidence for individualistic distributions of plant species. Species may have some degree of interdependence at some points on gradients, but may interact individualistically at others. For example, Pinus albicaulis (whitebark pine) and Abies lasiocarpa (subalpine fir) dominate the upper elevational end of most elevational gradients in the northern Rockies (Daubenmire 1952, 1956; Pfister et al. 1977). In many xeric microhabitats, P. albicaulis is the dominant of the two species at or near the timberline, but it also overlaps with A. lasiocarpa at lower elevations where the latter is more abundant. Thus these two species exhibit the classic continuum that is the cornerstone of the IC theory. However, a more detailed examination of interactions between these species creates a more complex picture (Fig. 1). P. albicaulis appears to have a cumulative competitive effect on A. lasiocarpa at lower elevations, where there are no significant spatial associations and the death of P. albicaulis corresponds with higher A. lasiocarpa growth rates. But at timberlines in xeric areas, A. lasiocarpa is highly clumped around P. albicaulis and the death of the latter is associated with decreased A. lasoicarpa growth rates (R.M. Callaway, submitted). Similar processes are also apparent in alpine communities of the central Caucasus
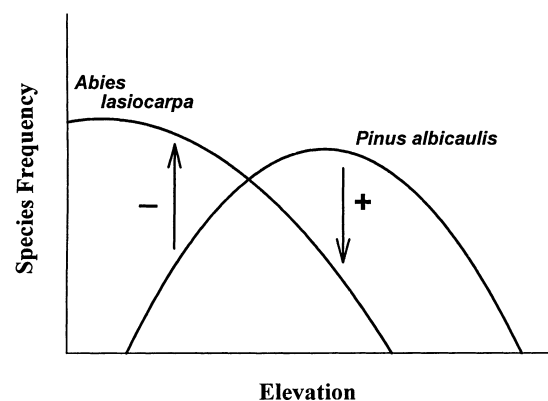

Fig. 1 Schematic continuum of *Pinus albicaulis* and *Abies lasiocarpa* on elevational gradients in the northern Rocky Mountains. Differences in the effects of *P. albicaulis* on *A. lasiocarpa* are denoted with *arrows* data from R.M. Callaway (submitted)

Mountains of the Republic of Georgia. There, Kikvidze (1993, 1996) measured numerous significant positive spatial associations and found evidence for facilitation via amelioration of abiotic stress. At high elevations, significant positive spatial associations were four times more common than negative associations (Z. Kikvidze, unpublished data). However, at low elevations, positive spatial associations were four times *less* common than negative associations.

The assumption that interactions between individuals of the same species do not vary with the abiotic environment has been challenged for virtually all important types of interspecific interactions [predation (Martin, 1997), herbivory (Maschinski and Whitham 1989), parasitism (Gibson and Watkinson 1992; Yan 1996), mutualism (Bronstein 1994), competition (Connell 1983; Kadmon 1995), facilitation (Bertness and Callaway 1994), and allelopathy (Tang et al. 1995)], as well as for other processes that occur in ecosystems (Brinson 1993). Shifting positive and negative effects on environmental gradients indicate that "nodes," or fully overlapping discrete groups of species, are not required to demonstrate interdependence among plants in a community. Because plants can have neutral or negative effects on neighbors at one point on an environmental gradient and positive effects at another (Fig. 1), a continuum does not necessarily infer fully individualistic relationships among plant species.

Shifts in the importance of positive interactions over time

Temporal variation in the strength of interspecific interactions has been shown to be relatively common. Connell (1983), Schoener (1983), Fowler (1986), and Goldberg and Barton (1992) discussed interseasonal asymmetry in competitive interactions among plants. To my knowledge, only one experimental study has shown that interactions between species can be negative in one year and positive in another. Greenlee and Callaway (1996) found that the effects of bunchgrass species on the rare mustard *Lesquerella carinata* were competitive in the wet, cool summer of 1993, but highly facilitative during the hot, dry summer of 1994. Their data also support the hypothesis that positive interactions increase in importance when abiotic stress is high. Spatially, *Lesquerella* was associated with bunchgrasses at a xeric site and not associated with bunchgrasses at a mesic site, indicating that cumulative, long-term effects depended on the physical environment. As for shifts between positive and negative interactions on gradients, temporal shifts indicate that the processes that determine species distributions are complex, and continuous distributions of species do not preclude interdependent interactions.

The importance of indirect interactions

Many positive interactions are simple and direct, and pose straightforward problems for a fully individualistic concept of plant communities. However, plant community structure is also highly affected by indirect interactions that modify direct resource competition among species (Kareiva 1994; Wootton, 1994). Positive indirect interactions may occur among plants as strong competitors may relieve weak ones by suppressing intermediate species that more directly harm weaker competitors (Miller 1994). Herbivores may shift the balance of competition by preferentially consuming dominant competitors, altering the competitive hierarchy, and promoting the abundance of species that are otherwise rare or excluded (Tansley and Adamson 1925; Lubchenco 1978; McNaughton 1985; Huntly 1991; Clay et al. 1993). Parasites may alter competitive outcome and indirectly affect plant distributions (Burdon and Chilvers 1977). Parasitic plants provide a striking example of how consumer interactions *within* the plant community can result in high degrees of species interdependence. By preferentially consuming dominant competitors, parasitic plants can have herbivore-like effects and indirectly facilitate the distribution and abundance of other species (Gibson and Watkinson 1991, 1992; Pennings and Callaway 1996). Mycorrhizal mutualists can alter and even reverse the outcome of competition between two species by favoring an otherwise inferior competitor or possibly by directly transferring resources between competitors (Grime et al. 1987; Clay 1990; Hartnett et al. 1993; Marler et al. 1996). Much like direct interactions, indirect interactions may also vary in space and time and can vary in importance along a continuum.

Higher-order interactions suggest interdependence in communities. Eliminating a species involved in an indirect interaction may not necessarily mean that its beneficiary will be eliminated from a community, and higher-order interactions are certainly no reason to "liken the plant-animal formation to an ameboid organism, a unit of parts, growing, moving, and manifesting internal processes which may be likened to metabolism, locomotion, etc. in an organism" (Shelford 1931). But the prospect that the distribution and abundance of any species in a plant community may be positively affected by the effects that other species have on their competitors suggests that communities are organized by much more than "the fluctuating and fortuitous immigration of plants and an equally fluctuating and variable environment" (Gleason 1926).

Why do positive interactions vary on abiotic gradients?

Competition, by definition, involves a struggle to preempt limiting resources, such as light, water, and nutrients, which ultimately determine rates of carbon acquisition. Under benign abiotic conditions that permit rapid resource acquisition, competition is often more intense than in abiotically stressful conditions (Bertness 1991; Pennings and Callaway 1992; Bertness and Shumway 1993; Bertness and Hacker 1994; Bertness and

Yeh 1994). However, if severe physical conditions restrict resource acquisition, amelioration of the most limiting factor by a tougher neighbor may be more likely to favor growth than competition with that tough neighbor is likely to reduce growth. Holmgren et al. (1997) modeled shifts in competition and facilitation on gradients of shade and drought and argued that facilitation would occur when the improvement of plant water relations exceeded the cost caused by lower light levels.

Are positive interactions species specific?

What if the positive effects of one species on another are not the product of any special characteristic of another species, and the effect can be reproduced by other species, or even a rock or other inanimate object? This is certainly common, since artificial objects have often been used to identify particular positive mechanisms (Callaway 1995). Very few studies have directly considered the species specificity of positive interactions among plants (R.M. Callaway, submitted). Callaway and D'Antonio (1991) found that survival of *Quercus agrifolia* seedlings was much higher under some shrub species than others; however, this was not the case for similar species (Callaway 1992). For other facilitative mechanisms, the interaction may be much more species specific. For example, for one species to protect another from herbivores, the benefactor must have the requisite defense chemicals or morphology. A high degree of species specificity may also be important in positive interactions involving nutrient addition, hydraulic lift, soil oxygenation, pollination, and mycorrhizae (Callaway 1995). There have also been numerous studies of spatial associations that show beneficiaries to be associated with some benefactors much more than other similar species in the community (R.M. Callaway, submitted). In any case, what effects other species or inanimate objects *might* have are not important. What is important is that in nature we find that the distributions and abundance of many plant species are favorably altered by the presence of others.

Is the *plant* community a green herring?

Discussion of the nature of communities is often confused by not specifying the taxa allowed in the clique, or the scale being considered. Even at the beginning, definitions were not clear – Clements (1916) referred to the "formation" and Gleason (1926) to the "plant community." Arguments for the IC theory from gradient analyses focus almost entirely on plant assemblages, and so I have restricted my discussion here to direct positive effects among plants and indirect interactions that alter interactions among plants. However, when we consider the overwhelming importance of trophic mutualisms, the obvious dependence of predators on their prey, inter-

actions between plants and soil microbes, modification of the physical environment by organisms, and indirect interactions involving all of the other kingdoms of life, why should we care whether or not *plant* communities are holistic or individualistic? The fundamental issue is whether or not, and to what degree, organisms in an area are interdependent. But because plant communities have been central to the IC theory, the ubiquity of direct and indirect positive interactions *within* plant communities provides an especially strong argument that communities are more interconnected than current theories allow.

Conclusion

It is not clear why many ecologists tend to perceive *communities* as independent assemblages and *ecological systems* as tightly interwoven, but the paradox illustrates the complexity inherent to understanding species assemblages. However, numerous studies indicate that the abundance, fitness, zonation, and perhaps even local existence of species are not simply due to abiotic conditions and competition, but are highly affected by direct positive interactions within the plant community and complex indirect positive interactions with consumers and mutualists. Perhaps our conceptual models of community organization should incorporate the idea of the abiotic environment as a template on which the effects of competitors, consumers, mutualists, and facilitators on community structure and diversity vary in intensity and importance. The ubiquity of positive interactions indicates that some plant communities may be "real entities" (Van der Maarel 1996), albeit not necessarily with tidy, discrete boundaries. Thus problems with classification will not go away (see McIntosh 1967). "Real" communities do not require that species participate in obligate mutualisms, although the latter play significant roles in some communities (Boucher et al. 1982; Bronstein 1994), nor do they suggest that positive interactions must be species specific. However, in light of our increasing understanding of the importance of direct and indirect positive interactions, plant communities may be more interdependent than currently thought.

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