11 Poethig, R.S. (1990) *Science* 250, 923–930
12 Samson, D.A. and Werk, K.S. (1986) *Am. Nat.* 127, 667–680
13 Klinkhammer, P.G.L., Meelis, E., de Jong, T.J. and Weiner, J. (1992) *Funct. Ecol.* 6, 308–316
14 Bernardo, J. (1993) *Trends Ecol. Evol.* 8, 166–173
15 Mooney, H.A. *et al.* (1988) *Oecologia* 72, 502–506
16 Evans, G.C. and Hughes, A.P. (1961) *New Phytol.* 60, 50–180
17 Terry, N. (1968) *J. Exp. Bot.* 61, 795–811
18 Hughes, A.C. and Evans, G.C. (1962) *New Phytol.* 61, 154–174
19 Corre, W.J. (1983) *Acta Bot. Neerl.* 32, 49–62
20 Rice, S.A. and Bazzaz, F.A. (1989) *Oecologia* 78, 502–507
21 Pearsall, W.H. (1927) *Am. J. Bot.* 41, 549–556
22 Troughton, A. (1956) *J. Brit. Grass. Soc.* 11, 56–65
23 Ledig, F.T. and Perry, T.O. (1965) *Proc. Soc. Am. For.* 39–43
24 Ledig, F.T., Bormann, F.H. and Wenger, K.F. (1970) *Bot. Gaz.* 13, 349–359
25 Coleman, J.S., McConnaughay, K.D.M. and Bazzaz, F.A. (1993) *Oecologia* 93, 195–200

26 Poorter, H. and Remkes, C. (1990) *Oecologia* 83, 553–559
27 Poorter, H. and Pothmann, P. (1992) *New Phytol.* 120, 159–166
28 Ackerly, D.D., Coleman, J.S., Morse, S.R. and Bazzaz, F.A. (1992) *Ecology* 74, 1260–1269
29 Hunt, R. (1990) *Basic Growth Analysis*, Unwin Hyman Press
30 Tremmel, D.C. and Bazzaz, F.A. (1993) *Ecology* 74, 2114–2124
31 Mohler, C.L., Marks, P.L. and Sprugel, D.G. (1978) *J. Ecol.* 66, 599–614
32 Joliceur, P. (1989) *J. Theor. Biol.* 140, 41–49
33 Mead, R. and Curnow, R.N. (1983) *Statistical Methods in Agriculture and Experimental Biology*, Chapman & Hall
34 Potvin, C., Lechowicz, M.J. and Tardif, S. (1990) *Ecology* 71, 1389–1400
35 Wong, S.C. (1979) *Oecologia* 44, 68–74
36 Hilbert, D.W. (1990) *Ann. Bot.* 66, 91–99
37 Bazzaz, F.A. (1990) *Annu. Rev. Ecol. Syst.* 21, 167–196
38 Schmid, B. (1992) *Evol. Trends in Plants* 6, 45–60

Positive interactions in communities

Mark D. Bertness
Ragan Callaway

Current concepts of the role of interspecific interactions in communities have been shaped by a profusion of experimental studies of interspecific competition over the past few decades. Evidence for the importance of positive interactions – facilitations – in community organization and dynamics has accrued to the point where it warrants formal inclusion into community ecology theory, as it has been in evolutionary biology.

Mark Bertness is at the Dept of Ecology and Evolutionary Biology, Brown University, Providence, RI 02912, USA; Ragan Callaway is at the Division of Biological Sciences, University of Montana, Missoula, MT 59812, USA.

Early ecological theory included both positive and negative interactions among species as important driving forces in the structure and organization of natural communities[1,2]. More recently, the role of competition in natural communities has received considerable attention (see Refs 3,4), while positive interactions have received little attention and are largely ignored in current models of community organization[5,6]. We broadly define positive interactions as all non-consumer interactions among two or more species that positively affect at least one of the species involved; thus, we include facultative and obligatory facilitations and mutualisms. Whereas the ecology and evolutionary biology of mutualisms has attracted recent attention[7], the role that they play in the structure and organization of natural communities has not.

The lack of recent attention paid to the role of positive interactions in communities is at least partly due to their uncritical acceptance by early ecologists and the preoccupation of contemporary community ecologists with competition (but see Ref. 8). In addition, much of the early development of ecology which highlighted positive interactions pre-dated the common use of field experiments in ecology and thus received little critical testing[9]. Moreover, fascination with competition has focused attention on communities where competition is conspicuous, potentially distracting ecologists from even recognizing positive interactions. Consequently, while facilitative and/or positive interactions are part of most working ecologists' conventional wisdom, and while anecdotal examples can be shown in most communities, the general importance of positive interactions to community diversity, structure and productivity is rarely acknowledged.

Modern ecology's view of positive interactions is particularly puzzling given the prominent role that they play in many communities and their importance as evolutionary forces. Few ecologists would deny the potential importance of mycorrhizal associations in forests and coral-zooxanthellae associations in coral reefs, even though our understanding of the community impact of these associations is almost entirely speculative. Moreover, while the evolutionary role of positive interactions has become clear over the past decade (e.g. the evolution of eukaryotic cells, and flowering plants and their pollinators), positive interactions remain absent from general models of community dynamics and organization. How can an evolutionary play featuring strong positive interactions take place on an ecological stage where positive interactions are insignificant? Textbooks, however, strongly support our contention that positive interactions are currently largely overlooked by community ecologists. Whereas ecology textbooks earlier this century devoted as much attention to positive interactions as they did to competitive ones, modern textbooks hardly mention positive interactions in a community context[10].

Recent theoretical (e.g. Refs 11,12) and empirical (e.g. Refs 13,14) work has suggested that positive indirect interactions and feedback mechanisms in food-webs may be common important forces in natural communities. In this article, however, we focus on the direct, non-trophic positive interactions that early ecologists suggested were critical aspects of community dynamics and organization[1,2]. Direct positive interactions occur when neighbors modify physical and/or biotic conditions and lead to positive effects. Although these positive interactions have been largely ignored by theoretical ecologists, evidence from a wide range of communities has begun to emerge during the past five to ten years indicating that direct positive interactions may be common, predictable and pervasive forces in natural communities and in physically harsh environments in particular. Here, we examine a small subsample of this evidence and re-evaluate the role of direct positive interactions in ecological communities.

Do positive interactions affect recruitment?

Positive interactions during recruitment in desert plants were hypothesized thirty years ago, based on spatial patterns suggesting that neighbors buffer one another from potentially limiting physical stresses[15,16]. But ecologists have tended to view these interactions as idiosyncratic features of deserts rather than examples of general principle and, until recently, have not experimentally tested these ideas. Nurse-plant effects and positive density-dependent recruit survivorship, however, have recently been found in other harsh physical environments.

suggesting that habitat-amelioration by neighbors, not deserts, is the common denominator of positive recruitment events. Positive recruitment interactions are common in salt-marsh plant communities, driven by neighbor-buffering of harsh edaphic conditions[17]. Similarly, positive recruitment interactions driven by neighbor habitat-amelioration have been shown for intertidal barnacles[18], mussels[19] and algae[20] and terrestrial plants[21].

Do positive species interactions influence species distributions?

While positive species interactions during recruitment may be pervasive and important forces under harsh environmental conditions, if positive interactions do not influence adult species distribution and abundance patterns, their poor treatment by contemporary ecologists may be somewhat justified. Despite lack of attention, however, numerous compelling examples with both plants and sessile animals suggest that positive associations may commonly influence distribution patterns. The upper intertidal limits of algae[20] and sessile invertebrates[18] have been shown to be positively affected by group benefits of thermal and desiccation buffering. For vascular plants, positive interactions driven by habitat amelioration have been experimentally shown to influence distributions by dictating recruitment success[21], or through interactions among established adults[22]. The impact of positive interactions on species distributions has simply not received enough attention for us objectively to assess its general importance.

Do positive interactions affect succession?

Primary and secondary succession were originally thought to be driven by facilitative and positive interactions[1,2]. In 1977, however, Connell and Slayter[9] pointed out that convincing experimental demonstrations of facilitated succession

were lacking. Whereas the intent of their paper was to focus experimental attention on successional mechanisms, its effect was to sour ecologists on invoking positive processes in explaining successional patterns.

Recent work with marine vascular plant communities, however, has illustrated the importance of positive interactions during succession even in communities that are conspicuously structured by competition. Whereas the striking zonation of salt-marsh plant communities is often driven by competitive dominance, secondary succession is also commonly driven by facilitative processes[23,24]. Disturbance-generated bare patches in marshes often become hypersaline due to direct exposure of soil to radiation, increasing evaporation and elevating salinities. As a consequence, initial patch invaders are salt-tolerant fugitives that shade the soil, ameliorating high patch salinities, and thus facilitating the colonization of other marsh plants. As a result of this simple relationship, facilitative interactions are a predictable feature of physically harsh but not physically benign bare patches where competitive processes prevail.

Facilitated succession has also recently been demonstrated in seagrass beds. Seagrass colonization of sandy substrate is limited by low substrate nutrient levels, which can be ameliorated by algal neighbors[25]. Consequently seagrass colonization is facilitated by algae in low-nutrient substrates, but interactions between seagrasses and algae would be expected to be entirely competitive in high nutrient content substrates.

Are these atypical results? Probably not. Marshes and seagrass beds are simply good systems to work with to address these questions because of the strong, direct, quantifiable affects marsh plants and seagrasses have on their physical environment and the relatively small spatial scale at which these plant/

edaphic factor feedbacks operate. Positive habitat modification by primary space holders is a common, general phenomenon (Table 1), but the spatial scale at which these feedbacks operate is often too large and diffuse to easily work with. For example, trees clearly have a major effect on forest physical conditions, but the spatial scale at which these effects operate is larger than most study sites. Most studies of forest secondary succession focus on relatively small spatial scales such as tree-fall gaps and find that competitive interactions prevail. At larger spatial scales, such as the slopes of Mt St Helens[30], the mesquite grassland–woodland complex in the southwest United States[33] and in Mediterranean climate oak savannah[34], succession patterns are decidedly facilitative.

Amelioration of physical stress

The early work of Gause[35] and Park[36] emphasized the importance of environmental conditions in dictating species interactions, but contemporary ecologists have focused their attention on biotic interactions largely decoupled from physical variation[37]. Work in intertidal communities, where physical gradients occur on small spatial scales that are simply too conspicuous to be overlooked, are an exception. Even intertidal marine ecologists, however, have focused most of their attention on physically mild, low intertidal habitats and have rarely tested the role of physical factors in setting upper intertidal species distributions. Upper intertidal species distributions appear to be frequently set by positive interactions[18,20]. Decoupling of abiotic and biotic effects occurs as ecologists design field experiments to minimize or control for environmental variation, and utilize greenhouse and laboratory studies to limit the effects of environmental variation on interactions. Much has been learned about the nature of species interactions using controlled environments, but discussions of these studies all too frequently forget that environmental variation was removed.

We suggest that positive interactions during succession and recruitment, as well as among established adults, are unusually common characteristic forces in harsh physical environments for the simple reason that primary space-holders frequently buffer neighbors from potentially limiting stresses. As such, accurate assessment of the importance of positive interactions in communities may require recoupling of abiotic and biotic effects and the study of interactions within the framework of the physical environment. The extensive list of potentially limiting physical factors that neighbors can

Table 1. Some examples of the variety of harsh physical conditions ameliorated by sessile organisms

Physical stress	Organisms
Heat/desiccation	Barnacles[18], mussels[19], intertidal algae[20], desert shrubs[26]
Low nutrient levels	Terrestrial plants[21,30], seagrasses[25], marsh grasses[27]
Osmotic stress	Marsh grasses[23,24]
Soil oxygen	Marsh grasses[28]
Soil moisture	Terrestrial plants[29]
Disturbance	Mussels[19], marsh grasses[27], algae[31], trees[32]

ameliorate (Table 1) suggests that neighbor buffering of physical stresses is not an idiosyncratic feature of certain communities, but a general phenomenon. Examination of species interactions in their physical context ought to persuade ecologists to emphasize positive interactions in community paradigms.

Amelioration of consumer pressure

Whereas positive interactions are likely to be predictable features of communities under harsh physical conditions, positive interactions among potential competitors are also probably more common under intense consumer pressure than generally acknowledged. Palatable vascular plants[38] and algae[39] have both been shown to derive associational benefits from living with less palatable neighbors. In an analogous way to the role of physical stress in dictating the nature of interactions among neighbors, consumer-driven associational benefits are clearly dependent on intense consumer pressure. Without consumer pressure, these associations are entirely competitive. Consumer-mediated associational benefits, however, also have not been given the empirical and theoretical attention they deserve, and are not widely appreciated.

Are positive interactions predictable features of natural communities?

Positive interactions may be predictably important forces in certain environments, even though they are currently ignored in most models of the organization of natural communities. As a starting point, future community paradigms might include the following hypotheses (summarized in Fig. 1). First, positive interactions should be particularly common in communities developing under high physical stress and in communities with high consumer pressure. Second, in intermediate habitats, where the physical environment is relatively benign and consumer pressure is less severe, positive interactions should be rare; as a result, competitive interactions should be dominant structuring forces. However, increased physical stress and consumer pressure may predictably lead to positive interactions driven by neighbor amelioration of potentially limiting physical and consumer stresses, respectively. Contemporary ecologists have underestimated the community role of positive interactions by focusing attention on communities exempt from extreme stress, failing to appreciate the relationship between positive and negative interactions, and particularly by largely ignoring the community consequences of potential
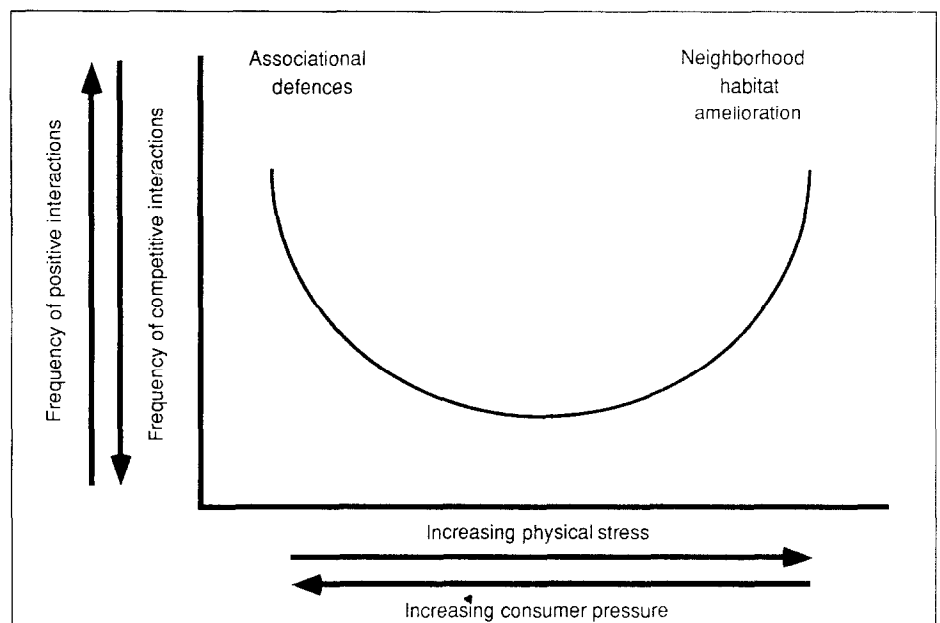

Fig. 1. Conceptual model of the occurrence of positive interactions in natural communities. Positive interactions are predicted to be rare under mild physical conditions and low consumer pressure. Neighbor amelioration of physical stress and association defenses, however, are hypothesized to lead predictably to positive interactions under harsh physical conditions and intense consumer pressure, respectively.

positive feedback mechanisms between organisms and their environment.

Positive interactions deserve increased empirical attention and should be incorporated into models of community organization. Renewed interest in community repercussions of positive interactions would improve our understanding of natural community structure and dynamics, and could lead to a clearer understanding of community stability issues, as well as reconcile a major disparity in the way ecologists and evolutionary biologists view the world.

References

1 Clements, F.E., Weaver, J. and Hanson, H. (1926) *Plant Competition: An Analysis of the Development of Vegetation*, Carnegie Institute
2 Allee, W.C., Emerson, A.E., Park, O. and Schmidt, K.P. (1949) *Principles of Animal Ecology*, W.B. Saunders
3 Connell, J.H. (1983) *Am. Nat.* 122, 661–696
4 Schoener, T.W. (1983) *Am. Nat.* 122, 240–285
5 Tilman, D. (1982) *Resource Competition and Community Structure*, Princeton University Press
6 Menge, B.A. and Sutherland, J. (1987) *Am. Nat.* 130, 730–757
7 Boucher, D.H., James, S. and Keeler, K.H. (1982) *Annu. Rev. Ecol. Syst.* 13, 315–347
8 Hunter, A.F. and Aarssen, L.W. (1988) *BioScience* 38, 34–40
9 Connell, J.H. and Slatyer, R.O. (1977) *Am. Nat.* 111, 1119–1144
10 Keddy, P.A. (1990) *Bull. Ecol. Soc. Am.* 71, 101–102
11 DeAngelis, D.L., Post, W.M. and Sugihara, G. (1983) *Current Trends in Foodweb Theory*, Oak Ridge National Laboratory
12 Abrams, P.A. (1993) *Am. Nat.* 141, 351–371

13 Paine, R.T. (1980) *J. Anim. Ecol.* 49, 667–685
14 Dethier, M.N. and Duggins, D. (1984) *Am. Nat.* 124, 205–219
15 Muller, C.H. (1953) *Am. J. Bot.* 40, 53–60
16 Niering, W.A., Whittaker, R.H. and Lowe, C.W. (1963) *Science* 142, 15–23
17 Callaway, R.M. *Ecology* (in press)
18 Bertness, M.D. (1989) *Ecology* 70, 257–268
19 Bertness, M.D. and Grosholz, T. (1985) *Oecologia* 67, 192–204
20 Hay, M. (1981) *Ecology* 62, 739–750
21 Callaway, R.M. (1992) *Ecology* 73, 2118–2128
22 Bertness, M.D. and Hacker, S.D. *Am. Nat.* (in press)
23 Bertness, M.D. (1992) *Am. Sci.* 80, 260–268
24 Bertness, M.D. and Shumway, S.W. (1993) *Am. Nat.* 142, 718–724
25 Williams, S.L. (1990) *Ecol. Monogr.* 60, 449–469
26 Franco, A.C. and Nobel, P.S. (1989) *J. Ecol.* 77, 870–886
27 Bertness, M.D. (1984) *Ecology* 65, 1794–1807
28 Shat, H. (1984) *Oecologia* 62, 279–286
29 Joffre, R. and Rambal, S. (1988) *Acta Oecol.* 9, 405–422
30 Wood, D.M. and Del Moral, R. (1987) *Ecology* 68. 780–790
31 Holbrook, N.M., Denny, M.W. and Koehl, M.A.R. (1991) *J. Exp. Mar. Biol. Ecol.* 146, 39–67
32 Holbrook, N.M. and Putz, F.E. (1989) *Am. J. Bot.* 76, 40–49
33 Archer, S., Scifres, C., Bassham, C.R. and Maggio, R. (1988) *Ecol. Monogr.* 58, 111–127
34 Callaway, R.M. and Davis, F.W. (1993) *Ecology* 74, 1567–1578
35 Gause, G.F. (1934) *The Struggle for Existence*, Williams and Wilkins
36 Park, T. (1954) *Physiol. Zool.* 27, 177–238
37 Dunson, W.A. and Travis, J. (1991) *Am. Nat.* 138, 1067–1097
38 Atsatt, P.R. and O'Dowd, D.J. (1976) *Science* 193, 24–29
39 Hay, M.E. (1986) *Am. Nat.* 128. 617–641