Testing the relative importance of positive and negative effects on community structure

In spite of the early emphasis of plant ecologists on positive species interactions (or facilitation) as a major determinant of community structure, experimental evaluation of this issue languished until recently[1]. However, during the past two decades community ecologists have devoted increasing attention to this issue[2]. Studies in terrestrial plant assemblages, salt marsh communities and marine benthic communities have shown convincingly that positive interactions can be important, particularly where environmental stress or consumer pressure is strong. Collectively, this evidence leaves little doubt that positive effects [e.g. commensalism (+/0 interactions) and mutualism (+/+ interactions)] must be considered in studies of community dynamics.

However, what remains unclear is the relative importance of positive interactions compared with other interactions and processes in determining community patterns. Studies aimed at detecting positive effects have been quite successful[1,3]. However, as with earlier attempts to evaluate the importance of negative effects (such as competition and predation[4–6]), until the proportional contribution of all major processes to community structure is determined in a broader context, we will still not know if positive effects (or the conditions under which they occur) contribute substantially to community patterns. In other words, if we could partition total community variance into the components explained by each process, would positive effects contribute a large (e.g. >25%) or small proportion (e.g. <10%)? Would such proportions change with alterations in environmental stress or productivity? Such knowledge is crucial if we are to understand how communities and ecosystems work or to predict their response to perturbations, such as global climate change.

Research on salt marshes and on rocky shores, led Mark Bertness *et al.*[3] to document and to quantify the effects of positive interactions on community structure. In a new paper[7], Bertness *et al.* attempt to explicitly address the relative importance of positive effects versus neutral and negative effects under varying conditions of environmental stress. They used a rocky intertidal community in a Maine estuary (USA) to test how habitat modification by an algal canopy affects survival, growth, recruitment, predation and grazing of major community components. In this ecosystem, previous research has documented positive canopy effects (e.g. on predation rate of whelks on mussels[8]) and negative canopy effects (e.g. on barnacle recruitment[9]); thus, there is reason to believe that properly designed experiments could discover how such effects might vary in relation to environmental stress.

Species interactions on the Maine coast

Rocky shores in New England are characterized by a wide range of environmental conditions and species abundances. Summer temperatures can exceed 40°C, but winter temperatures can be less than −18°C. Given such extremes, it is a marvel that the biota of rocky shores in this region is so abundant and so lush. However, in this habitat the dominant macrophyte on relatively wave-sheltered shores is the long-lived (5–25 yr) fucoid alga, *Ascophyllum nodosum*. This plant reaches >2 m in length and at low tide forms a thick, moist layer of vegetation commonly covering 100% of the underlying rock substratum[7,9]. Sessile invertebrates (e.g. mussels and barnacles) are generally scarce beneath the canopy, but are somewhat more abundant at the upper edge than at the lower edge of the *Ascophyllum* zone[9]. Green crabs (*Carcinus maenas*) and littorine snails (*Littorina littorea*) are also abundant.

As quantified by Bertness *et al.*[7], the algal canopy keeps understory temperatures up to 5–10°C cooler than in areas without a canopy. Their work took advantage of a feature of rocky intertidal habitats that makes them particularly amenable to such investigations – the existence, over a short distance (a few meters), of a steep gradient of environmental stress. Because of the alternation of exposure to air and to water during regular tidal changes, the proportion of time that intertidal organisms are emersed increases with increasing tidal height. Thus, by establishing identical experiments at the upper and the lower edges of the *Ascophyllum* zone, they tested the responses of organisms and species interactions to conditions of relatively high and low stress (high shore and low shore, respectively).

The experiments combined algal removal, unaltered stands and artificial shade to generate three treatments: +canopy +shade (plots with normal *Ascophyllum* cover left intact), −canopy +shade (plots with *Ascophyllum* cleared but shaded with plastic mesh arches) and −canopy −shade (plots with *Ascophyllum* cleared). They tested canopy effects on the colonization of filter-feeding mussels and barnacles, grazing gastropods and predatory crabs by placing recruit collectors in all three plots. The effect of the canopy on the survival and growth of mussels and grazing gastropods was tested using caged, marked individuals that were translocated to higher and to lower plots. Barnacle survival and growth was estimated from photographs taken in autumn, six months after the individuals had settled. Rates of crab predation on mussels were quantified using short-term tethering experiments. Canopy effects on herbivory and algal recruitment were tested using herbivore exclosures with appropriate controls.

Stress amelioration models[10] predict that positive interactions should increase in importance as indicators of community structure, with increasing stress. Thus, the expectation was that high-zone experiments would reveal a stronger positive influence of the canopy than in the low-zone experiments. For example, if organisms recruited less densely, grew slowly, survived poorly or fed slowly in the hotter, drier conditions in plots lacking *Ascophyllum*, relative to organisms in the cooler, moister conditions in plots under the *Ascophyllum* canopy, then the canopy was beneficial to these organisms. By contrast, higher recruit density, faster growth, higher survival or more rapid consumption in cleared plots would indicate a negative effect of the canopy. Importantly, a shift from more negative to more positive canopy effects between lower and higher tidal height experiments (as indicated by height × canopy statistical interactions in analyses of variance) would signal that species interactions were modified as expected when experiencing increased stress.

What were the positive effects documented in this study[7] and what were their overall contibutions to community structure? Recruitment of mussels (1996 only) was differentially enhanced by the canopy at higher tidal heights. Crab (1995 only) recruitment was also enhanced but the effect did not vary with tidal height. Recruitment of barnacles and littorine snails was reduced, not increased, by the canopy. For all these species, recruitment tended to be higher at lower tidal heights. Survival of mussels and barnacles, and growth of mussels were enhanced by the canopy at higher tidal heights, but other responses to the canopy at higher levels were neutral (littorine survival and barnacle growth) or negative (littorine growth).

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The results suggested that the predicted changes did indeed occur. At the community level, the percentages of direct interactions that were positive, neutral (i.e. not different between +canopy and −canopy plots) and negative, respectively, were 44, 33 and 22 in the high zone and 0, 56 and 44 in the low zone. Therefore, as expected, positive interactions were relatively frequent under conditions of high stress but absent under conditions of low stress.

Do these results demonstrate that positive effects are relatively more important determinants of community structure in the high zone than in the low zone? Although the results are suggestive, frequencies of effects categorized by the sign of the effect (+, 0 or −) do not necessarily reveal their relative importance. Moreover, these short-term results do not necessarily reveal how patterns requiring longer periods of time will arise. These[7], and previous, experiments[11,12] suggest that, in spite of increased mussel recruitment, growth and survival under the canopy at high levels, crab predation and low recruitment might be largely responsible for the long-term sparseness of mussels and barnacles under the canopy. Crab predation was stronger at lower levels but did not vary with canopy cover, at least on the scale of the 1.5 × 1.5 m plots used in these experiments.

What processes underlie the high abundance of *Ascophyllum*? Fucoid recruitment was dense in the absence of littorines, but grazing virtually eliminated fucoid recruitment in the Maine experiments[7], both at high levels and at low levels in the presence and the absence of the canopy. At least in +grazer treatments no canopy effect on fucoid recruitment was detected. *Ascophyllum* canopy enhanced recruitment of *Ascophyllum* juveniles, but only in −grazer treatments (exclosure cages). Evidently, the dominant *Ascophyllum* canopy arises from infrequent escapes in size (i.e. growth to grazer-invulnerable size) by a few algal recruits from grazers, which persist once they have passed through a grazer-vulnerable size[13].

Conclusions

Thus, at wave-sheltered areas of low flow, positive interactions with the dominant canopy-forming species, *Ascophyllum*, seem at least partly responsible for elevated abundances of mussels and barnacles at the upper edge of the *Ascophyllum* zone. Compared with lower levels, where negative interactions are the dominant structuring forces, positive interactions are relatively more important in the high zone. At the same time, these positive effects appear subtle, and are tightly interwoven with a complex matrix of positive, neutral and negative effects.

Bertness *et al.* have provided an important step in the direction of evaluating the relative influences of positive and of negative species interactions in relation to environmental stress. Their work makes a strong case for the need for similar efforts in other systems, and provides a valuable template upon which to build creative short- and long-term studies that can tease out the relative and the interactive effects of positive, neutral and negative species interactions on community structure.

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References

1 Callaway, R.M. (1995) Positive interactions among plants. *Bot. Rev.* 61, 306–349
2 Kareiva, P.M. and Bertness, M.D. (1997) Re–examining the role of positive interactions in communities. *Ecology* 78, 1945
3 Bertness, M.D. and Leonard, G.H. (1997) The role of positive interactions in communities: lessons from intertidal habitats. *Ecology* 78, 1976–1989
4 Connell, J.H. (1983) On the prevalence and relative importance of interspecific competition: evidence from field experiments. *Am. Nat.* 122, 661–696
5 Schoener, T.W. (1983) Field experiments on interspecific competition. *Am. Nat.* 122, 240–285
6 Sih, A.P. *et al.* (1985) Predation, competition and prey communities: a review of field experiments. *Ann. Rev. Ecol. Syst.* 16, 269–311
7 Bertness, M.D. *et al.* (1999) Testing the relative contribution of positive and negative interactions in rocky intertidal communities. *Ecology* 80, 2711–2726
8 Menge, B.A. (1978) Predation intensity in a rocky intertidal community. Effect of an algal canopy, wave action and desiccation on predator feeding rates. *Oecologia* 34, 17–35
9 Menge, B.A. (1976) Organization of the New England rocky intertidal community: role of predation, competition and environmental heterogeneity. *Ecol. Monogr.* 46, 355–393
10 Bertness, M.D. and Callaway, R. (1994) Positive interactions in communities. *Trends Ecol. Evol.* 9, 191–193
11 Leonard, G.H. *et al.* (1998) Flow-driven variation in intertidal community structure in a Maine estuary. *Ecology* 79, 1395–1411
12 Leonard, G.H. *et al.* (1999) How recruitment, intra-specific interactions and predation control species borders in a tidal estuary. *Oecologia* 118, 492–502
13 Lubchenco, J. (1983) *Littorina* and *Fucus*: effects of herbivores, substratum heterogeneity, and plant escapes during succession. *Ecology* 64, 1116–1123

Why egg yolk is yellow

Egg yolk in birds, reptiles and many fish is coloured yellowish-red by carotenoids. Much of what we know about carotenoids in eggs comes from studies on poultry, where the colour of the egg yolk affects our perception of its palatability. However, until recently, apart from questions of consumer taste, there has been no adaptive explanation of why many oviparous animals provision their eggs so richly with carotenoids (Fig. 1). It now appears that, in developing birds carotenoids protect vulnerable tissues against damage caused by free radicals, thus suggesting new perspectives on reproductive trade-offs in females and on the evolution of carotenoid-based visual signals.

Carotenoids are biologically active pigments, which animals must obtain from their diet; they can only be synthesized *de novo* by plants, certain bacteria and fungi. These pigments are most conspicuous in the sexual signals of many animals, and there is support for the idea that such coloration has evolved to reveal the animal's health status, because of increasing evidence that carotenoids are powerful antioxidants and immunostimulants[1,2]. New work by biochemists Peter Surai, Brian Speake and colleagues on the composition of birds' eggs[3,4] has shown that egg yolk carotenoids and related antioxidants reduce lipid peroxidation in the vulnerable, lipid-rich tissues of developing embryos and chicks (caused by free radicals generated during normal oxidative processes), thus protecting the cell membranes and/or cell functions of important organs[3], and the passively acquired antibodies[5], against damage. Oxidative stress is probably most prominent in rapidly growing organisms, such as avian embryos[6], because of the high rates of oxidative metabolism during growth.

The discovery of such a fundamental role for antioxidants in young birds paves the way for new lines of study in ecology. Hypotheses that could be tested include the possibility that carotenoid-based visual traits in female birds advertise their ability

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