Ecosystem processes and the regeneration niche

Removal experiments, in which certain organisms are eliminated from established natural communities, have received renewed attention as tools for assessing the effects of functional biodiversity on ecosystem processes. The approach has several advantages (e.g. realism), but also some drawbacks. One of the drawbacks is that, when an established species is removed from a community and an ecosystem effect is detected, it is difficult to distinguish between the effect of the absence of the removed organism and the effect of the act of removal. This is particularly true for terrestrial plant communities in which removing whole plants inevitably causes major soil disturbance. Amy Symstad and David Tilman have just presented a fine example of another aspect to consider in the interpretation of removal experiments[1]: recruitment limitation, that is, the effect of the species that gets into the space – and takes up the resources – left behind by the removed species.

They performed a plant-removal experiment in which they manipulated functional group diversity (forbs, cool-season C_3 graminoids and warm-season C_4 graminoids) and composition of a sand prairie–grassland in Minnesota, USA. They monitored the effects of these manipulations on ecosystem properties, such as plant biomass production, nitrogen dynamics in the soil and community resistance to a simulated drought, and found that the removal of different functional types affected ecosystem function. However, rather than attributing these responses to the absence of the functional groups that had been eliminated, the authors attributed them to differential recruitment abilities of the remaining functional groups. In plots where forbs and C_3 graminoids were removed, there was a larger proportion of open ground, and higher nitrogen leaching from the soil, than in plots from which forbs and C_4 graminoids were removed. That was because C_4 graminoids (remaining in the first case) have stronger recruitment limitations, that is, occupy free space and thus take up available resources more slowly than do C_3 graminoids (remaining in the second case), which are able to fill in the gaps much more quickly.

Does this mean that removal experiments are basically flawed? I believe not. On the contrary, this study adds a new dimension to the search for causal links between biodiversity and the way ecosystems work. Traditionally, biodiversity–ecosystem function studies have focused on the niche of established plants. The fact that recruitment limitation can influence ecosystem processes calls attention to the regeneration niche (*sensu* Grubb 1977)[2]. Differences among organisms in their local recruitment ability, hardly taken on board in experimental studies in this area, might be important in determining at least the transient effects of diversity loss on ecosystem function. If the fast-growing research field of biodiversity and ecosystem function is to contribute to the understanding and management of natural ecosystems, it needs a diversity of approaches. The study by Symstad and Tilman adds to that diversity by stressing that not only what is lost, and how many different species are involved, but also what gets in and how fast, are functionally important.

1 Symstad, A.J. and Tilman, D. (2001) Diversity loss, recruitment limitation, and ecosystem functioning: lessons learned from a removal experiment. *Oikos* 82, 424–435

2 Grubb, P.J. (1977) The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biol. Rev.* 52, 107–145

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Overt versus covert competition in Soay sheep

Sexual selection theory encompasses both overt precopulatory mate securing tactics and covert postcopulatory gametic competition. As a consequence, copulation success need not translate into fertilization success. In mammals, one of the key adaptations to sperm competition is the insemination of large numbers of sperm, which is associated with an evolutionary increase in testicular size. Based on the lottery principle, males that inseminate most sperm tend to fertilize most ova. However, the production of sperm and seminal fluid is costly, because frequently copulating males have to replenish depleted supplies. Thus, there might be a tradeoff between pre- and postcopulatory success, with frequently successful maters losing out in sperm competition. This appears to be the case in feral Soay sheep (*Ovis aries*) on the island group of St Kilda, UK, detailed in a new study by B.T. Preston *et al.*[1]

During the five-week rut, rams compete fiercely for access to females in oestrus and females engage in promiscuous matings with up to seven different males. Large males copulate more frequently than do their smaller rivals and, during the first three weeks of the rut, they sire more offspring than do small males. Although large males maintain their precopulatory advantage during the last two weeks of the rut, they do experience a waning success in sperm competition and, by the end of the rut, paternity is shared equally between large and small males. To test whether this mismatch between copulation rate and fertilization success is explained by dominant rams becoming progressively more sperm depleted, Preston *et al.*[1] collected semen towards the end of the rut from natural matings, using an 'intra-vaginal device' (*viz.* condom). They found that large, frequently copulating males transferred fewer sperm per ejaculate, and produced a greater proportion of morphologically abnormal sperm, than did small males. Both measurements indicate sperm depletion in large males.

This study is of value because it provides good evidence that costs associated with ejaculate production might constrain male reproductive success, especially in species in which females mate promiscuously. In addition, it raises some interesting questions about mechanisms. If dominant males do inseminate less sperm towards the end of the rut (this was not directly measured), does this result from frequent copulation *per se*, or is it a