Frugivory, seed dispersal and plant community ecology

Seed dispersal is a multi-step process that links successive generations of plants. Its most immediate outcome is a heterogeneous distribution of seeds in the ground, which then influences the spatial pattern and overall magnitude of seed predation, seedling establishment and juvenile growth and mortality. Ultimately, seed dispersal exerts a sort of remote control over the density and distribution of adult plants at a variety of spatial scales. Animals play a major role in seed dispersal. They move seeds away from parent plants, and subsequently (and often repeatedly) rearrange the seed shadows on and below the soil surface. A recent meeting in Brazil addressed the manifold facets of seed dispersal and plant-frugivore interactions*. Compared with the previous meetings of 1985 and 1991 (Ref. 1), this one signalled a growing emphasis on demographic and conservation aspects and a decline in the number of evolutionary studies. At a roundtable that closed the meeting, several speakers welcomed the first trend, but lamented the second, calling attention to the promise of modern phylogenetic and molecular methods for studying the evolution of plant–frugivore interactions.

An increasing number of studies document some effect of seed-dispersing animals on seed fate in addition to removing seeds from parent plants, and some are coming close to the ultimate goal of completing the circle from the seed-producing plant to a new seed-producing adult. Héctor Godínez-Alvarez and Alfonso Valiente-Banuet (Universidad Nacional Autónoma de México, Coyoacán, Mexico) studied a columnar cactus (*Neobuxbaumia tetetzo*) that can establish successfully only beneath the canopies of shrubs and trees. By quantifying the number of seeds transported, the effect of gut passage on seed germination, and the frequency of seed deposition under nurse plants, they could estimate, with the aid of a Lefkovitch matrix model, the effect of each frugivorous bat and bird species on the finite rate of increase of the cactus population. They found that the quantity component of seed dispersal (the number of seeds removed by each frugivorous species) is less important for dispersal effectiveness than the quality component (what happens to each seed removed by a consumer). Pedro Jordano (Estación Biológica de Doñana, Seville, Spain) presented work done by him and his collaborators showing that most bird species feeding on the cherries of *Prunus mahaleb* deposit seeds in patches of dense woody vegetation, whereas open microhabitats, which are visited only by redstarts and mistle thrushes, receive very few seeds. Their seed addition experiments indicate that juvenile recruitment in open microhabitats is severely limited by the availability of seeds.

The issue of seed dispersal limitation has far-reaching implications, not only for the spatial distribution of recruits among microhabitats, but also for the dynamics of whole plant populations and communities. If plant species fail to have juveniles present wherever there is an opportunity for recruitment, then less competitive species can win available microsites by forfeit. It has been argued that this effectively delays competitive exclusion, and allows the coexistence of an enormous number of plant species for very long periods, even in the face of strong competitive differences at the local scale[2]. Several authors explored this idea during the meeting. Gene Schupp and Tarek Milleron (Utah State University, Logan, USA) reviewed evidence that certain behaviors of fruit-eating animals do indeed lead to idiosyncratic patterns of seedfall and highly clumped seed distributions, and they argued that cases of dispersal limitation, such as the one reported by Jordano, are likely to be widespread. Helene Muller-Landau *et al.* (Smithsonian Tropical Research Institute, Balboa, Panama) provided further evidence of the latter point. From 13 years of seed trap data and seven years of seedling recruitment data, they estimated that the seeds of most tree species in Barro Colorado Island reach fewer than 10% of available sites in any given year. Many populations do not produce enough seeds to colonize a sizable number of sites, and some deliver a large number of seeds to just a few sites. Further, seedlings fail to establish at many of the sites where seeds fall. They found that recruitment was more strongly limited by the failure of seeds to arrive than by the failure to establish after arrival.

By contrast, John Terborgh (Duke University, Durham, USA) downplayed the role of seed dispersal limitation, ecological drift and non-equilibrium dynamics in the maintenance of tree diversity in tropical forests, and instead emphasized density-dependent processes affecting seed and seedling survival. He observed that the distribution of saplings is largely independent of the distribution of adult trees, and argued that this is because the very few seeds that move far away from parent plants are demographically very important because they suffer disproportionately low rates of pathogen and herbivore attack[3,4].

These, and other contributions, anticipate that seed dispersal studies will have much to say about plant community dynamics. Gene Schupp and others stressed that for this to be true it is essential that we move towards a larger scale approach where plant populations, and not only individual plants or subplots within populations, are sampling units. Carlos Martínez del Rio and Juliann Aukema (University of Arizona, Tucson, USA) offered an example of this approach by documenting patterns of contagious seed dispersal and adult distribution at two spatial scales in parasitic mistletoes (*Tristerix aphyllus* and *Phoradendron californicum*) dispersed by frugivorous birds. Within populations, birds tend to deposit ingested mistletoe seeds on already infected host plants, which they visit to forage for mistletoe fruits. At the landscape level, areas of higher prevalence of mistletoe infection have higher population densities of birds (presumably as a response to the higher supply of mistletoe fruits), and higher rates of mistletoe seed deposition at suitable hosts. Thus, birds seem to create a positive feedback of mistletoe infection and reinfection at two distinct spatial scales.

The role of animal seed dispersers and seed predators in plant population and community dynamics stresses the problems of so-called ‘empty forests,’ where long-lived adult trees witness the disruption of essential species interactions as a result of hunting, forest fragmentation and fruit harvesting by humans[5]. Carlos Peres (University of East Anglia, Norwich, UK) and Mark van Roosmalen (Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil) showed that, at least in Amazonia, large-seeded trees depend almost exclusively on large vertebrates such as primates and ungulates for seed dispersal, whereas small-seeded plants can be effectively dispersed by a wide variety of animals, including many birds. Large vertebrates, however, are being overhunted in all but the most inaccessible of Amazonian forests. The decline

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and extinction of populations of large-bodied vertebrates might bring about the decline of large-seeded trees, and concomitant community-wide changes, over much of the forests. Another possible example of the loss of seed dispersal services comes from Pacific islands, where flying foxes are also suffering dramatic population declines as a result of habitat reduction and hunting. Kim McConkey and Don Drake (Victoria University of Wellington, Wellington, New Zealand) found that in islands with reduced densities of these frugivorous bats a larger proportion of seeds fall undispersed beneath the crowns of mother plants.

The study of seed dispersal is undergoing a profound transformation[6]. The growing knowledge of the demographic consequences of seed dispersal is making the field increasingly relevant to plant population ecology at large. Furthermore, some of the studies that I have chosen to comment on highlight the potential contribution of seed dispersal research to community ecology. The time is ripe for studying the role of seed dispersal in the assembly of plant communities in space and time, and in their potential disassembly following the loss of seed-dispersing animals and the arrival of new ones.

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JOURNAL CLUB

Global warming and the spread of disease: the debate heats up

Many recent studies have suggested that as a consequence of global climate change there will be an increase in the incidence of vector-borne diseases, such as malaria, yellow fever, dengue fever and tick-borne encephalitis. This is based principally on the idea that, as the planet warms and parasite and vector development rates speed up, transmission will be possible at increasingly higher latitudes. However, two new papers by Sarah Randolph and David Rogers challenge this notion and suggest that due to the complex nature of most host–vector–parasite interactions it may be extremely difficult to make good generalizations about the future distributions of vector-transmitted diseases.

In a paper published in *Science*, Rogers and Randolph explore the effects of global climate change on the future incidence of cerebral malaria, a life-threatening disease caused by *Plasmodium falciparum* and transmitted by anopheline mosquitoes[1]. Earlier models had predicted that cerebral malaria would spread northwards through Europe and would invade large tracts of North America. These predictions were based on models that incorporated details of the biology of the *Plasmodium*–mosquito interaction (such as temperature-dependent parasite development rates) into the forecasts produced by global circulation models (GCMs). In contrast, Rogers and Randolph used a two-step multivariate statistical approach. First, they used maximum-likelihood methods to map present day malaria distributions by determining the key climatic variables associated with the presence or absence of disease. Second, these results were used to predict the worldwide distribution of cerebral malaria in the year 2050, based on a widely accepted GCM scenario. This predicted that changes in the distribution of *P. falciparum* will largely be restricted to the tropics and sub-tropics, with just as many people being freed of the risk of infection as being newly exposed.

In a second paper, published in *The Proceedings of the Royal Society*, Randolph and Rogers took a similar approach to predict the future distribution of tick-borne encephalitis virus (TBEv) in Europe[2]. Again, they produced a multivariate description of the current distribution of disease risk and applied the identified predictor variables to various GCM scenarios for the future. This predicted that although TBEv would extend its distribution northwards, the overall range would decline as a result of global climate change, possibly culminating in TBEv disappearing completely from central and eastern Europe by 2080. The biological interpretation is that climate change may alter the seasonal dynamics or survival of the ticks, so disrupting virus transmission between the two immature tick life-stages co-feeding on rodents.

These two studies are interesting not only because they make predictions that run counter to conventional wisdom, but also because they use multivariate statistical methods that incorporate predicted changes not only in temperature but also rainfall, humidity, and their interactions. In so doing, they appear to be able to capture more of the constraints on parasite transmission and development. Of course, these models are not perfect. For example, they do not allow the parasites to evolve in response to changing selection pressures. It is possible, for example, that reduced opportunities for transmission of non-systemic infections of TBEv between co-feeding ticks might lead to the evolution of alternative transmission routes or to changes in virulence. However, it is likely that models like these will be particularly useful in identifying areas where vector-borne diseases are likely to expand their distributions.

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Conflict begets diversity?

There is a long tradition in evolutionary biology that views reproductive isolation as a by-product of gradual species divergence over time. However, many studies have recently demonstrated that traits involved in reproduction, especially postmating-prezygotic characters, diverge rapidly among closely related species. These studies have not only generated a lot of interest over the evolutionary processes underlying this rapid divergence, but they have also raised important questions about the effects of these processes on speciation, and consequently on patterns of species diversity. For example, sexual conflict

