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The ecology of plant populations: their dynamics, interactions and evolution

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What regulates the size and distribution of plant populations? What determines whether a population of plants will increase in size or decline? What allows some species to become aggressive invaders of exotic habitats, and what prevents this from occurring? When do individuals from different species exclude each other from a community by competition, and when do their interactions facilitate coexistence? These are just a few of the questions that arise when one contemplates the ebb and flow of plants across our landscapes, the magnificent diversity one finds in some habitats, or the tendency of one species to exclude all others in habitats that would appear to be very similar. This Special Issue brings together 15 articles presenting recent research bearing on these and other questions that have become, or continue to be, hot topics in the study of plant populations.

The topics covered in this issue range from the epigenetic inheritance of characters that influence defence traits to the abiotic factors and biotic interactions that contribute to community assembly and the coexistence of plant species. Several of the studies consider the ecology and evolution of invasive species. Others address questions about the evolutionary ecology of local adaptation and differentiation in life-history traits, including differentiation between the sexes of dioecious plants. With this breadth, it is perhaps not sensible to look for themes that unite all the papers – beyond the common concern with plant populations. Nevertheless, one theme does echo hither and thither between the contributions made: that ecological interactions take place between organisms that vary genetically, and that the extent of genetic, indeed phylogenetic, divergence between interacting populations can matter.

The integration of a formal phylogenetic perspective into comparative functional ecology represented an important step in the field of plant ecology (Harvey and Pagel, 1991; Silvertown et al., 1997). The point is a simple one: traits may be associated among species either because they are functionally related, or simply because traits are inherited together from common ancestors (or both). It is now accepted that failure to account for the latter possibility is tantamount to pseudoreplication, because species are not independent units, and can lead to spurious conclusions about function. In phylogenetically corrected analyses, trait associations between more closely related species are effectively downplayed in relation to those found between more distantly related species (Felsenstein, 1985; Grafen, 1989; Harvey and Pagel, 1991). But how distant is distant, in an absolute sense?

In this Special Issue, two papers incorporate a phylogenetic perspective into their analyses, the second of which considers this question of phylogenetic distance. But first, in a somewhat provocative paper, Herben et al. (2012) ask whether there is an association between abundance and genome size! Intriguingly, they find a statistically significant link between genome size and abundance for annual plants, but what could this mean? Most likely, the link is indirect, probably caused by association with other traits that have a more direct influence on species abundance. Interestingly, the weak association found between genome size and abundance remains both after taking account of phylogeny, and also after accounting for the other ecologically relevant traits that were included in the analysis, such as seed size and number, plant height and specific leaf area. This would thus suggest that there may be other, unmeasured, traits that contribute to the regional abundance of European annual plants in addition to size, specific leaf area, seed size and number.

In the second paper, Beltrán et al. (2012) reflect on recent discoveries of the importance of phylogeny in explaining whether species that interact by facilitation should be maintained together in the face of competition. The key idea goes back to Darwin (1859): competition is likely to be more intense between closely related species, because they are more likely to occupy a similar niche (or 'place in the economy of nature', as Darwin put it). The corollary is that cases where one species facilitates the establishment of a second species should be more frequent for pairs of species that are phylogenetically more distant from one another. These predictions have been borne out by comparative analysis (Verdú et al., 2009; Violle et al., 2011) but, as is typical, there is noise in the data: in particular, some congeneric species interact and coexist by facilitation. Beltrán et al. (2012) ask why. They suggest that while some cases can be explained by interactions with a third party (e.g. pollinators or mycorrhizal symbionts), others are in fact consistent with Darwin's idea, because congeneric taxa can be very distantly related. Taxonomic rank is of course a poor estimate of evolutionary divergence, and it is ultimately the traits themselves that matter in ecology.

Traits that affect the coexistence of congeneric taxa are also the focus of the paper by Silvertown et al. (2012), who ask how species within the genus *Restio* are able to coexist in communities of the fynbos vegetation in the Cape of South Africa. Previously, Silvertown and colleagues have demonstrated that species can be maintained together in English meadow communities by subtle but critical niche differentiation along hydrological gradients (Silvertown et al., 1999), and a subsequent recent study demonstrated much the same phenomenon in the highly diverse Cape fynbos (Araya et al., 2011). In the

present work, they now dig deeper using a field experiment in the fynbos to ask how species segregation along hydrological gradients originates in a community in which the clock is, in effect, reset every decade or so by massive disturbance by fire. Their experiments involved reciprocally transplanting thousands of soil plugs (and the seeds within them) at a spatial scale of only metres at two burnt fynbos sites for which they had detailed fine-scale hydrological maps. At one site, they found that transplanted seedlings performed better at the moister microsites, but not at the other site. Perhaps significantly, the site for which they found an effect of hydrology on plant performance was also the site at which they had found evidence for species segregation along the observed hydrological gradients. Their study, and their work on English meadows, suggests that microsite variation in the water table is an important factor contributing to the local coexistence of plant species – and helps to explain the so-called 'paradox of the plankton' (Hutchinson, 1961), the puzzle over how species that effectively all require the same list of resources can be maintained together in a community.

The assembly of a species-rich community ultimately requires the successive invasion and establishment of new species. One would think that, as the niche space gets carved up and used with the arrival of new species over time, the likelihood of subsequent invasions would decline, i.e. that more species-rich communities would be more resistant to invasion (Elton, 1958). Empirical support for this intuitive prediction, however, has been mixed, and there has been a paucity of studies that have added species to natural – as opposed to experimentally constructed – communities that differ in diversity. In this Special Issue, Zeiter and Stampfli (2012) contribute to filling this gap by introducing seeds of species into small quadrats in a regularly mown, old grassland community. Intriguingly, their experiments revealed a positive diversity–invasibility relationship, even though the species they added to their experimental plots were drawn from the same community (but absent from the quadrats) and whose niches ought to overlap with those of the species already resident in the plots; i.e. one should have expected even greater resistance to the invasion of newcomers by those already present. As the authors note, there is clearly still much to learn about community assembly and invisibility.

While the concept of invasibility of communities is fundamental for our understanding of community assembly, it is also a major concern in conservation and restoration ecology: what factors determine whether exotic species will become successfully invasive; and what will determine our success at restoring degraded communities by species reintroductions? Three papers in this Special Issue are to some extent motivated by the former of these two questions. First, Zhang and Shea (2012) take up the question of how disturbance influences the population dynamics of the thistle, *Carduus nutans*, which has become a serious invader in the Americas, Australasia and southern Africa.

Although habitat disturbance may be important in facilitating the invasion of exotic species into native vegetation, its role is not straightforward (Moles *et al.*, 2012). A key point made by Zhang and Shea (2012) is that disturbance is a multidimensional process that needs to be measured along different axes, including intensity, frequency, timing, duration and

extent. In their paper, they ask how the first three of these factors, in combination, affect key life-history traits of *C. nutans* that have a direct impact on the species' population dynamics (and thus invasion potential). Their results confirm the importance of considering more than one dimension of disturbance, with the timing of disturbance and its interactions being particularly important, probably because the absolute amount of biomass removed by a disturbance depends critically on when it occurs during the plant life cycle. This conclusion is clearly relevant for the management and control of invasive species.

The removal of plant biomass as a regulator of growth and reproduction can be caused by physical disturbances such as tree-fall, mowing, ploughing or fire, but also through attack by herbivores and pathogens (Bond and Keeley, 2005). Indeed, a leading hypothesis for the failure of native species to expand inexorably, as they sometimes do when introduced into a new area, is that they are held in check by their herbivores and pathogens, which they escape in their new range (Keane and Crawley, 2002). Escape from pests can have an obvious immediate positive effect on growth and competitive ability, but there is also the potential for a secondary effect that may be of equal significance or more important: the evolution of increased competitive ability ('EICA') by invasive species that are not compelled to allocate their resources towards defence from pests they have left behind (Blossey and Notzold, 1995). In this issue, Joshi and Tielbörger (2012) perform an experiment with *Lythrum salicaria* to add to a growing number of studies that test this idea. *Lythrum salicaria* is native to Europe but has become a serious invader of wetland habitats in North America. In their experiment, Joshi and Tielbörger (2012) grew individuals of *L. salicaria* from populations sampled in both the native and the introduced ranges under full exposure to the native herbivores in Europe and found support for the EICA hypothesis: introduced populations were more vigorous than their native counterparts, and they were more susceptible (though also tolerant) to herbivory.

Given that herbivory may constitute a potentially major disturbance event for plant populations, it may play an important role in the regional dynamics of species maintained in a balance between population extirpation or extinction and their recolonization by long-distance dispersal. In this issue, Hemrová *et al.* (2012) consider the extent to which the regional abundance and maintenance of the polycarpic perennial herb *Scorzonera hispanica* are sensitive to damage caused by ungulate herbivores, which are on the increase in the Czech Republic. The case is particularly interesting as a study of regional dynamics, because herbivores remove inflorescences without damaging the vegetate rosettes, so herbivory ultimately affects just the extent to which plants within an affected (meta-)population contribute propagules (wind-dispersed seeds) to the regional migrant pool. To predict the regional dynamics of *S. hispanica*, the authors used individual-based simulations parameterized using field observations and combining a matrix-based account of local population dynamics, estimates of migration via dispersal kernels, and scenarios of herbivory and stochastic rates of local population extinctions.

The rapid evolution of reduced defence and greater competitive ability in invasive plants, mentioned above, suggests that

invading populations have substantial amounts of additive variation on which selection can act. This might be surprising for species introduced into their new range through what must often be a narrow bottleneck (Prentis *et al.*, 2008). One explanation for this apparent paradox is that successful invasions tend to follow multiple introductions, so that the amount of genetic variation in the establishing populations can in fact be large (Simberloff, 2009). In other words, selection during invasion can act upon standing genetic variation, after all. The paper by Latzel *et al.* (2012) raises the question of whether some of the heritable variation among individuals in defence might in fact also be of epigenetic origin. They report that lineages of *Arabidopsis thaliana* that differ only in the extent to which their genomes were methylated (and not in their nucleotide sequences) showed different phenotypes in terms of growth and response to hormones that typically mediate defence responses. Their results confirm earlier suggestions that some of the variation we find in ecologically important traits might be of epigenetic origin (Herrera and Bazaga, 2011), with the possibility that phenotypically plastic defence responses could be transmitted to progeny that are likely to be exposed to a similar environment.

The relative extent to which invasive species are phenotypically plastic versus genetically variable is also the focus of the paper by Skálová *et al.* (2012), who compare three species of *Impatiens* that have become invasive in Europe, *I. glandulifera*, *I. noli-tangere* and *I. capensis*, and one species native to Europe, *I. parviflora*. They find that the most invasive species in their study, *I. glandulifera*, is also the most plastic, and the less invasive species, while also plastic, are more genetically differentiated among populations. The variation found among these four *Impatiens* species echo the reflections of Beltrán *et al.* (2012) in this Special Issue, cited above, that congeneric species can differ a great deal in their ecological strategies.

The basis of intrageneric variation in plant phenotypes is also considered by Ross *et al.* (2012) in their study of individuals sampled along an altitudinal gradient from a *Senecio* hybrid zone on Mount Etna, Sicily. Here, high-altitude *S. aethnensis* and lower-altitude *S. chrysanthemifolius*, which differ in a number of morphological traits, meet in a hybrid zone at intermediate altitude (Brennan *et al.*, 2009). In their study here, Ross *et al.* (2012) ask whether the temperature dependence of seed germination and early seedling establishment varies along the altitudinal cline in a way that could be interpreted in adaptive terms. They find that the high-altitude *S. aethnensis* tends to germinate better at low temperatures than the lower-altitude species, and to grow faster at warm temperatures, perhaps reflecting an adaptation to a shorter growing season. These results suggest that local adaptation along the altitudinal gradient is at least one contributing factor to the maintenance of the *Senecio* hybrid zone and provide a satisfying illustration of how natural selection tracks environmental variation over relatively small spatial scales despite on-going gene flow.

While Ross *et al.* (2012) study phenotypic variation over relatively small spatial scales in a perennial herb, Santos-del-Blanco *et al.* (2012) consider the evolution of local adaptation over climatic gradients at a scale of the Iberian Peninsula, and beyond, in the long-lived tree, *Pinus pinaster*,

again in the face of on-going gene flow. Using a large common-garden experiment with genotypes sampled from 23 populations across the species' range, they analyse population differentiation in a number of early growth traits, in particular the size at first sexual reproduction. After accounting for background genetic differentiation at probably neutral loci, they report an association between key life-history traits and a measure of environmental 'harshness'. Because *P. pinaster* is monoecious (produces both male and female cones), they were able to assess differences in the size at which individuals first reproduced through their male versus female functions. Interestingly, plants behaved relatively uniformly among populations in terms of their male function, but those sampled from harsh sites tended to begin reproducing through their female function at smaller sizes. This study reminds us that fitness accrues through both sexual functions in hermaphrodites, and that selection can act to maximize fitness under different environments rather differently for male versus female function (e.g. Yu *et al.*, 2011). It also represents a rare case of the assessment of variation in sex allocation over the range of a long-lived tree species.

Although most plants are hermaphrodites and allocate to both sexes over the course of their lives, separate sexes have evolved numerous times and dioecious species are found in approximately half of all plant families (Barrett, 2002). Given the observation, such as that of Santos-del-Blanco *et al.* (2012) for *P. pinaster*, that the costs and benefits of male and female functions in hermaphrodites trade off rather differently with one another, one might expect males and females of dioecious species to occupy different niches in the communities in which they necessarily co-occur and compete for common resources. There has been some evidence for differences in competitive abilities between the sexes of dioecious plants, both at the seedling stage (i.e. before any costs of reproduction have been exacted; Mercer and Eppley, 2010) and later during reproduction (Ågren *et al.*, 1999). However, the effects are typically small. In this issue, Varga and Kytöviita (2012) add to this work by testing for differences in competitive ability in the dioecious herb *Antennaria dioica* over a period of 3 years. In common with other studies, they find only small differences in the effects of competition on males versus females, except that the probability of flowering was suppressed by competition only in females growing with other females. Their results indicate that females are the stronger competitors, as commonly found (Sánchez Vilas *et al.*, 2011), and that plants may buffer their growth status by regulating their flowering frequency.

Varga and Kytöviita (2012) also report that 10 % of plants in their experiment showed 'sexual lability' during the course of the experiment, i.e. produced flowers of the opposite sex. Sexual lability is common in plants with separate sexes, a phenomenon that might sometimes be related to a plant's resource status (Lloyd and Bawa, 1984; Delph and Wolf, 2005). An interesting implication of such lability is that it may confer a benefit of reproductive assurance on plants that happen to find themselves alone. This raises the possibility that plants might have evolved mechanisms that allow them to adjust their sexual expression in response to the sexuality of their neighbours. Some homosporous ferns provide a striking example of this neighbourhood-dependent sexual lability:

spores develop as hermaphrodites by default and release the hormone antheridiogen into their environment that causes neighbouring spores, if there are any, to develop as males (Banks, 1997). This process, which involves intersexual signalling and causes density-dependent sex expression, favours outcrossing when potential mates are available but allows selfing when they are not (Haig and Westoby, 1988). Density-dependent sex choice was also reported for an androdioecious population of the angiosperm herb *Mercurialis annua* in southern Spain, where hermaphrodites co-occur with males, some of which were capable of becoming hermaphroditic at low density (Pannell, 1997). Now, Sánchez Vilas and Pannell (2012) follow up on the earlier study by looking for a possible signal that might cause gender switching in *M. annua*, this time using genotypes sampled from Morocco. By irrigating plants with leachate passed through the soil of other males or females, they attempt to discover whether a chemical signal in the rhizosphere might be responsible for communication between individuals. While they found what was probably a nutrient effect on the sex allocation of hermaphrodites (Delph, 2003; Sánchez Vilas and Pannell, 2011), they failed to observe any treatment-dependent gender switching. *Mercurialis annua* is remarkably variable in its sexual expression across its geographic range, and the authors conjecture that their failure to find gender switching in Morocco might reflect a further manifestation of interpopulation variation in sex allocation.

The Special Issue ends with two papers on plant mating and pollination ecology. Scheepens *et al.* (2012) investigate the patterns of gene flow brought about by bumblebee pollination of the alpine plant *Campanula thyrsoides*. They report that the probability of successful mating between individuals decreased with distance within the large focal population, and that the spatial location of individuals in the populations strongly influenced their mating success, as has been frequently found by paternity analysis of insect-pollinated populations (e.g. Meagher, 1991; Oddou-Muratorio *et al.*, 2005). Their data also point to substantial gene flow among populations, which are nevertheless strongly differentiated at microsatellite loci. This apparent discrepancy between observed levels of gene flow among populations over the short term and long-term migration rates inferred on the basis of population genetic differentiation reminds us that natural populations seldom conform to simple models of population structure and dynamics (Whitlock and McCauley, 1999).

In the concluding paper of the issue, Chamorro *et al.* (2012) review what is known about the distribution of plant sexual systems and the natural history of pollination in the Galápagos Islands. A number of interesting points emerge from their paper. Foremost is perhaps the simple fact that, even for iconic localities such as the Galápagos, which have long attracted the attention of natural historians, we still know very little about plant mating and the structure of plant pollinator networks: of the 557 native plant species on the islands, pollination observations have been recorded for only 89, and for only 26 of the 825 exotic species that have become naturalized (Chamorro *et al.*, 2012). Similarly, nothing concrete is known about the sexual systems of more than 80 % of the flora. Nevertheless, if we assume that those species that have been studied are in any way representative

of the flora of the islands, two observations stand out regarding plant reproductive systems. First, in common with other isolated oceanic islands (Bawa, 1982; Cox, 1989), the Galápagos flora has a large proportion of self-compatible species, a pattern consistent with 'Baker's Law', which predicts high rates of self-compatibility in floras that have become established through long-distance dispersal, presumably as a result of selection for reproductive assurance by selfing in the absence of mates or suitable pollinators (Baker, 1955). And second, in a pattern that stands out as rather unusual among oceanic island floras, the proportion of dioecious species is remarkably low; whereas Hawaii and New Zealand have 28 and 15 % dioecious species, respectively, the Galápagos have less than 2 % (Chamorro *et al.*, 2012). It is not clear why the Galápagos should be so different, but the authors point to their relatively young age as a possible explanation. Nevertheless, given the rapidity with which plant and animal populations can evolve (a fact highlighted by several other papers in this Special Issue), it seems unlikely that the evolution of dioecy (ultimately just the spread of male and female sterility mutations) would need more than several million years to evolve if selection favoured it.

It is difficult not to think of Charles Darwin when reading the review of plant–pollinator interactions on the Galápagos by Chamorro *et al.* (2012). Darwin was, of course, a pioneer in the study of plant population ecology and spent a great deal of time, particularly later in life, doing experiments with plants in his garden at Down House, in the south-east of England. Several of the themes that echo among the papers collected in this issue resonate with Darwin's thoughts, but the study of plant populations has come a long way since then, not least in terms of its increasing overlap with ideas in population genetics. It is hoped that the papers assembled in the pages that follow serve not only to highlight a few of the many directions the study of plant populations have taken since Darwin's experiments, but also to stimulate new work in these areas, and perhaps new directions.

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