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Dorothy's Dilemma and the Unification of Plant Population Biology

Jonathan Silvertown

A CONSENSUS HAS EXISTED for many years that a greater synthesis should be possible between population ecology and population genetics, but the synthesis is still to emerge. At the British Ecological Society symposium entitled *Genes in Ecology*, held in Norwich, UK, in April this year, the organizers attempted to encourage synthesis by teaming an ecologist with a geneticist in every presentation¹. In fact, rather than bridging it, this bold device emphasized the gap that still separates genetics and ecology. Disappointingly few of the contributors reflected at all on why the gap exists. Specifically in plant population biology, there is a dilemma that few interested in a synthesis of ecology and genetics have yet confronted.

Synthesis between plant genetics, physiology and ecology was one of

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the goals of the recently concluded interdisciplinary study of the genus *Plantago* in The Netherlands, and it is now a central objective of the European Network in Population Biology². If the synthesis is still elusive, this is not because of any lack of desire on the part of plant population ecologists to take an evolutionary view. Some have suggested that the problem will be solved when we can identify and track genotypes more easily and they look forward to the fruits of molecular and other techniques that will make this possible^{3,4}. These methods will certainly yield a huge quantity of new information, but will they lead to a *qualitative* advance over what we already know from the use of less-sophisticated genetic markers? The barrier between population genetics and population ecology may be mainly conceptual, not technological.

For any synthesis to occur between two disciplines they must share a

common set of core variables. The components of fitness (fecundity and survival) are demographic variables, so on the face of it the conditions do exist for the merger of population genetics with population ecology, but population ecologists who census individuals and geneticists who census alleles still seem to be having trouble finding common ground. A large part of the problem arises from a fundamental difference in the relative importance that population genetics and plant population ecology accord to population structure.

Key genetic concepts such as the founder effect, genetic drift, genetic differentiation, gene flow, shifting balance, allopatric speciation, neighbourhood area, effective population size and the hierarchical organization of genetic diversity all assume that populations have spatial structure or are organized into metapopulations. Metapopulations, or networks of populations linked by migration, are a familiar concept in population genetics and animal ecology, but plant population ecologists usually ignore this kind of spatial structure, though it is everywhere we (don't) look. At present, plant population ecology has a limited vision, bounded by the population edge. Most plant population studies concentrate on a small

scale and treat different parts of the population as replicates or as entirely separate entities, not as potentially interdependent units. Unlike in animal population ecology, migration between local populations, population colonization and extinction are all routinely ignored.

Dorothy's dilemma

Convenient justification for this myopia is found in the typically leptokurtic dispersal curve for plant seeds, which shows that vanishingly few ever travel far from the parent⁵. However, the dispersal curve *does* have a distant tail, though it is as difficult to find as the end of the rainbow. In the Wizard of Oz, Dorothy's dilemma is to find a way to the end of the rainbow, or at least to imagine what it would be like. Plant population ecologists have to have the same imagination⁶, and to think beyond the horizon of the population to the metapopulation (*sensu* Levins⁷). What they will find there is a map of population structure that may form a basis for the unification of population ecology and genetics. We must get away from the inward focus that, ironically, terms an individual plant a 'metapopulation' (*sensu* White⁸). If population ecologists can address processes that give rise to the kind of spatial structure that appears in population genetics, we will have found a common set of variables.

In making a similar point, Antonovics and Levin⁹ suggested that ecologists calculate ecological neighbourhoods or zones of influence around individual plants as analogues of the genetic neighbourhood. Unfortunately, the parameters of ecological neighbourhoods have not turned out to be particularly powerful predictors of individual plant performance¹⁰ or of population dynamics¹¹. In monocultures, interactions between the time a plant emerges relative to its neighbours, its size and the size of its neighbours can introduce strong nonlinearities into these relationships¹⁰. We should now focus our attention on a larger scale. Spatial structure at the metapopulation level has received very little attention in plants, but offers better prospects for unification. How could it be done?

The yellow brick road

To anyone seeking directions to the rainbow's end, the reply 'If I was going there, I wouldn't start from here' may seem singularly unhelpful, but we cannot hope to find the all-important tail of the seed-dispersal curve by starting at the seed source.

Instead, we need to survey potential colonization sites in the areas around existing local populations and watch for new populations to show up. Potential colonization sites have to be identified experimentally by the addition of seeds to likely areas, and colonization rates measured as a function of distance from seed source by creating artificial sites. Population extinction rates need to be measured by monitoring large numbers of natural or artificial local populations. One of the very few such studies to date showed that local populations of semelparous perennials in a sand-dune system in The Netherlands had high extinction rates¹². These experiments and observations would provide parameters for ecological models in which spatial structure is explicit, and this spatial structure would provide the basis for genetic measurements of gene flow, genetic differentiation and so on.

An obvious objection to this scheme is that it is based upon the assumption that local populations have a high turnover rate, and that for long-lived plants such as trees, monitoring extinction rates is no more possible than finding the end of the rainbow (both endeavours will see the experimenter in heaven). However, these problems are not peculiar to a metapopulation approach and apply equally to studies of the local population dynamics of trees, so the same solutions may be applied. For example, population structure and population projection models can be used to determine extinction rates for local populations. In fact, because forest trees require canopy gaps for successful recruitment and because these colonization sites are easily identified and counted, tree populations are highly suited to a metapopulation approach. A recent ecological study of the metapopulation dynamics of the neotropical pioneer tree *Cecropia obtusifolia* in Mexico¹³ is a good example. This was not a genetic study, but rates of seed dispersal measured between old and new sites could easily be used to estimate gene flow between local populations. Of course, other genetic parameters could also be measured within the explicit spatial structure elucidated by such an ecological study.

Genecology in the land of Oz

Olivieri *et al.*¹⁴ have pointed out that the metapopulation perspective has the advantage that 'it allows the study of constant disequilibrium within populations'. Phenomena that are a nuisance to the population ecologist studying a limited number of

populations, such as the fact that some populations are expanding and others contracting, or that populations are prone to sudden extinction before the study is finished (most ecologists seem to have an unpublished story of this kind), become significant when viewed at the metapopulation level. For example, certain life history traits such as semelparity and seed heteromorphism are difficult to understand for local populations in a supposed steady state, but become easier to explain as soon as it is appreciated that populations are ephemeral in any one place, and sites permitting colonization are patchily distributed¹⁵⁻¹⁷. Semelparous perennials are favoured over annuals in a deteriorating environment such as a sand-dune succession¹⁸. Similarly, seed heteromorphism, which is very common in the Compositae but also occurs in *Viola*, *Impatiens* and other genera, permits plants to disperse a fraction of their seeds locally and a fraction to a greater distance. Dispersal between ephemeral sites is vital to the long-term fitness of plants occupying them, and both of these life history syndromes clearly imply the existence of a metapopulation structure.

Much of the complaint about the failure of ecology and genetics to unite comes from geneticists who plainly believe in the fundamental significance of their subject. However, because of this failure it is still unclear, for example in explaining the distribution and abundance of a species, when genetic structure matters and when it does not. In the meantime it would be no bad thing for ecologists to keep an open mind on such questions. A hierarchical view of life suggests that phenomena at the level of the population and above can be independent of the lower levels where genetic structure is shaped. If we can resolve Dorothy's dilemma by widening our attention from local populations to metapopulations we may hope to address such issues.

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