

NEWS AND COMMENTARY

Speciation

Flowering time and the Wallace Effect

J Ollerton

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Reproductive isolation between groups of individuals would appear to be a *sine qua non* for the evolution of new species, without which gene flow between those individuals would maintain genetic coherence and prevent speciation. How this reproductive isolation is achieved has been the focus of considerable debate, and now a new study on page 198 of this issue, by Jonathan Silvertown and colleagues at the Open University and Rothamsted Research in the UK, provides strong evidence for a controversial proposal. Their work suggests that natural selection can reinforce reproductive isolation within what is essentially one population (Silvertown *et al*, 2005).

The study focused on a species of grass, *Anthoxanthum odoratum*, growing in plots within what is the longest running ecological experiment currently in existence, the Park Grass Experiment at Rothamsted Experimental Station, Harpenden, UK. These plots were originally set up in 1856 to test the reactions of meadow vegetation to different fertilizer applications, procedures which continue to this day and which have generated enormous amounts of data on plant physiological responses, population dynamics and community ecology. Building on previous work (eg Snaydon and Davies, 1976), Silvertown *et al* (2005) have shown that there has been a shift in flowering time of *A. odoratum* at the border between adjacent experimental plots. Crucially, this 'inverse cline' of flowering is a signature of the first steps along a particular road to speciation, that has been predicted by modelling studies exploring how natural selection against hybrids could contribute to reproductive isolation between populations in proximity. It suggests that some species within adjacent plots in the Park Grass Experiment are not exchanging genetic material via pollination as frequently as would be expected. The genetic outcome of this reproductive isolation was tested by using Inter

Simple-Sequence Repeat (ISSR) markers, which confirmed that there had been genetic divergence between adjacent plots at these neutral marker sites. Reproductive isolation and genetic divergence, the first phases of speciation, had been confirmed.

The cause of the shift in flowering and the resulting genetic differentiation in *A. odoratum* remains obscure. It is likely to be due to the difference in pH across the boundaries, with selection against 'hybrids' (with different pH tolerances) formed in that region, though the authors acknowledge that for this to be the case, there must be some link '*...between the traits under direct selection (eg pH tolerance) and the isolating mechanism (eg flowering time)*'. This is clearly a line of research that could be pursued in the future.

The mechanism of reproductive isolation caused by natural selection against hybrids within adjacent populations is generally called 'reinforcement', sometimes termed the 'Wallace Effect' (Silvertown *et al*, 2005) due to its championing by Alfred Russell Wallace at the end of the 19th century (Wallace, 1889). History has been unkind to Wallace, who is often perceived as a lesser figure in Darwin's shadow, rather than as an important scientist and natural historian in his own right. The 'Wallace Effect' is therefore an appropriate honorific which should be more widely used in the search for additional examples of this elusive and important phenomenon.

As is often the case in evolutionary ecology, mathematical models have outpaced empirical data and the theoretical basis of the Wallace Effect has been established in more than 100 mathematical models (Silvertown *et al*, 2005). Supporting field data are less common, however, and are rarely unambiguous. Part of the problem is in not knowing the origin of the supposedly split populations: the only way properly to test the basis for sympatric speciation would be to experimentally manipulate a population, but the timescales of

speciation are too long for such a study to observe incipient speciation within the lifespan of a single research project. That is one of the reasons why the Park Grass Experiment, which next year will have been running for a century and a half, is so important: it has demonstrated that we can observe the initial effects of sympatric speciation on time-scales that can be scientifically documented. This in turn gives weight to the idea that sympatric speciation may be as important as allopatric speciation in driving evolution by natural selection.

Allopatric models of speciation emphasise the role of geographical separation in achieving reproductive isolation between populations, and are currently considered to be the best candidates for understanding most speciation events. Sympatric models, conversely, state that reproductive isolation can be achieved between incipient species if they are in close, even mixed, proximity. Such circumstances are harder to envision, because proximity normally implies gene flow. Although there are many examples of apparent sister species living sympatrically, it is unclear whether this is the end point of sympatric speciation, or if we are seeing the outcome of allopatric speciation with later sympatry due to shared habitat requirements. As an evolutionary snapshot, sympatric sister species provide us with evidence that may be circumstantial rather than conclusive. Identifying *in situ* reproductive isolation between taxa beginning the long road to speciation is therefore difficult. In fact, as a falsifiable hypothesis, it may be untestable using field observations because the sceptical allopatric evolutionist can always fall back to a position of ancient allopatry followed by more recent sympatry. The research by Silvertown *et al* shows relatively unambiguously, following experimental manipulation, that sympatric speciation can potentially begin via the Wallace Effect. That it should be discovered in a wind-pollinated plant, and therefore an essentially panmictic population, is a surprising result. Animal-pollinated species are more often thought to be better candidates for sympatric speciation, via mechanisms such as differences in pollinator behaviour (eg Warren and Diaz, 2001) or changes in pollen placement (eg Maad and Nilsson, 2004), as well as shifts in flowering time (eg Gustafsson and Lonn, 2003).

We often take the timing of the appearance of flowers for granted (bluebells in the spring, ivy in the autumn), though recent research showing earlier

flowering phenologies due to climate change has challenged our perceptions with hard data (eg Fitter and Fitter, 2002). The long-standing interest in variation in flowering time goes back at least to Charles Robertson's observations of seasonal flowering time in relation to pollinator activity (Robertson, 1895). That interest has waxed and waned, but the effects of climate change, and their potential to disrupt the maintenance of populations via reduced reproductive success, has reinvigorated the attention of ecologists. Within this context, Silvertown *et al* have produced a significant contribution to the our knowledge of how changes in flowering time can contribute to genetic isolation

even at modest distances. Much more specifically, it is important to debates about reproductive isolation within and between populations, and the mechanisms of speciation.

J Ollerton is at the Landscape and Biodiversity Research Group, School of Applied Sciences, University College Northampton, Park Campus, Northampton NN2 7AL, UK.

E-mail: jeff.ollerton@northampton.ac.uk

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