NEWS AND COMMENTARY

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Early insights into the genetic consequences of range expansions

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All species experience range expansions at some point in their history. Such episodes are typically short-lived; however, they can leave strong and persistent signatures in the genetic structure of the species. This realization came surprisingly late. In population genetics, ‘equilibrium’ models had been designed to be independent of history, therefore ignoring episodes of range expansions. The first attempts to consider the historical settings when interpreting the genetic structure of populations were by geneticists with a strong naturalist background. For instance, the editors of the classic symposium volume *The Genetics of Colonizing Species* (Baker and Stebbins, 1965) were plant evolutionists with a particular interest in biogeography and palaeoecology. Their work predated by some 15 years the development of phylogeography in the early 1980s, which relied mostly on empirical methods. Quantitative approaches to study the genetics of colonization began later still. Although metapopulation models can be seen as representing a first step in this direction, they deal with local colonization balanced by extinctions, not pure expansions (Slatkin, 1977). The first quantitative studies of the genetic consequences of colonization of a new territory were published some 15–25 years ago and relied initially on simulations (Rendine *et al.*, 1986; Nichols and Hewitt, 1994; Ibrahim *et al.*, 1996), with analytical approaches following shortly after (Austerlitz *et al.*, 1997; reviewed by Excoffier *et al.*, 2009). Below, we consider one of these papers, published 14 years ago in *Heredity* (Ibrahim *et al.*, 1996), which turned out to be particularly influential, with over 300 citations reported to date in ISI Web of Science, most of them after 2001.

This paper was written while Kamal Ibrahim worked as a postdoc with Godfrey Hewitt at the University of East Anglia, in collaboration with Richard Nichols at Queen Mary, University of London. The three authors used individual based, spatially explicit simulations of the genetics of populations

(a rarity in this field at the time) to investigate the spatial patterns of genetic variation generated during range expansion. They showed that different forms of dispersal bring about contrasting population genetic structures, with stratified dispersal (involving both short- and long-distance dispersal), resulting in a distinct patchy genetic structure. The paper is cited as being ‘in prep’ in Godfrey Hewitt’s highly cited (>1200 times) paper entitled ‘Some genetic consequences of ice ages, and their role in divergence and speciation’, which was published the same year (Hewitt, 1996). By providing a brief and accessible account of the study by Ibrahim *et al.*, Hewitt’s paper certainly contributed to its success.

Another work published 2 years earlier by the same group (Nichols and Hewitt, 1994) had prepared the way for the paper by Ibrahim *et al.* However, the study, which had been stimulated by surveys revealing genetic mixing between races of a grasshopper in the Pyrenees, was dealing with a more specific question (the admixture between genetically differentiated populations) and did not attract as much attention.

The study by Ibrahim *et al.* differs significantly from earlier work on the genetic consequences of colonization (such as Rendine *et al.*, 1986) because it considers not only colonization by diffusion but also by ‘leaps and bounds’, that is, involving long-distance dispersal events. At this time, ecologists were starting to realize that long-distance dispersal events are necessary to account for the rapidity of the spread of trees and of other organisms after the last ice age, as anticipated by Reid at the end of the nineteenth century (Reid, 1899; Kot *et al.*, 1996; Clark *et al.*, 1998). The interest in long-distance dispersal was therefore particularly high. Ibrahim *et al.* actually cite a number of studies showing that dispersal is often leptokurtic, with a more acute peak around the mean (that is, a higher probability than a normally distributed variable of values near the mean) and fatter tails

(that is, a higher probability than a normally distributed variable of extreme values).

The realization that range expansions result in a persistent genetic signal also led the authors to point out the limits of models relying on equilibrium assumptions to estimate levels of gene flow. Gene flow estimates that depend on equilibrium conditions were still very popular at the time, even if they had started to be questioned (Boileau *et al.*, 1992). Altogether, this combined interest in long-distance dispersal and in non-equilibrium conditions made the study by Ibrahim *et al.* particularly timely.

Surprisingly, Ibrahim *et al.* is often cited to back interpretations of empirical population surveys that find a decline in genetic diversity during colonization, even though changes in levels of diversity during colonization were not reported in the paper (only measures of genetic differentiation were reported). Subsequent studies have shown that during expansions involving rare long-distance dispersal, genetic diversity can decline faster than in expansions involving pure diffusion, especially in narrow corridors, as a consequence of the ‘embolism’ effect (the growth of genetically uniform populations ahead of the main colonization front that inhibit subsequent gene flow (Bialozyt *et al.*, 2006)). However, the conditions for this are rather narrow. In many cases, long-distance dispersal during colonization instead helps preserve high levels of diversity, by reshuffling alleles across the landscape and propelling them far ahead of the colonization front (Bialozyt *et al.*, 2006; Fayard *et al.*, 2009). To simulate long-distance dispersal events, Ibrahim *et al.* had combined a normal curve with small variance with another one with large variance. Such a dispersal kernel is called a Gaussian mixture. It appears that Gaussian mixture kernels differ fundamentally from ‘true’ fat-tailed kernels, characterized by power-law behavior in the tails (Fayard *et al.*, 2009). In particular, fat-tailed dispersal kernels preserve genetic diversity better than exponentially bounded Gaussian mixture kernels, thereby questioning the generality of the association between long-distance dispersal and the loss of genetic diversity during colonization.

Retrospectively, it is curious to realize that, in the study by Ibrahim *et al.* and in related studies (such as that by Le Corre *et al.*, 1997), simulations of the genetic consequences of simple diffusion are used only as a baseline for comparisons

with models including long-distance dispersal, considered to be biologically more relevant. Spatially explicit studies entirely dedicated to the genetic consequences of short-distance dispersal (Edmonds *et al.*, 2004; Klopstein *et al.*, 2006) appeared much later than those focusing on the genetic consequences of long-distance dispersal (Nichols and Hewitt, 1994; Ibrahim *et al.*, 1996). They led to the characterization of the 'surfing' phenomenon, that is, the possibility for rare variants to rapidly increase in frequency as a consequence of strong genetic drift occurring in populations located on the edge of the expansion (Excoffier and Ray, 2008).

Another curiosity is that Ibrahim *et al.* had refrained from including selection in their simulations, even though their computer program would have allowed it, as they point out in their Methods section. It is only in the last 3–4 years that researchers have started to explore in detail the interaction between selection and colonization during range expansions, especially in conjunction with the surfing phenomenon (Travis *et al.*, 2007; Excoffier *et al.*, 2009). We will never know for sure, but it might be that, had Ibrahim *et al.* included selection in their simulation study, their paper would have not fared so well, because most researchers would have been unprepared.

In summary, the paper by Ibrahim *et al.* can be regarded as a forerunner of a suite of studies that completely changed our perspective on the origin of the genetic structure of populations, as it shifted from a purely ahistorical view, where drift-mutation-gene flow equilibrium prevailed, to a view where

brief events in the remote past have shaped much of the neutral diversity and part of the adaptive diversity that we see today. Such a radical change in our paradigm finally gained wider acceptance thanks to insightful and pioneering studies such as that by Ibrahim *et al.*

Conflict of interest

The author declares no conflict of interest.

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