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NEWS AND VIEWS

PERSPECTIVE

The genomics of adaptation, divergence and speciation: a congealing theory

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In this issue, Flaxman *et al.* (2014) report the results of sophisticated whole-genome simulations of speciation with gene flow, enhancing our understanding of the process by building on previous single-locus, multilocus and analytical works. Their findings provide us with new insights about how genomes can diverge and the importance of statistical and chromosomal linkage in facilitating reproductive isolation. The authors characterize the conditions under which, even with high gene flow and weak divergent selection, reproductive isolation between populations can occur due to the emergent stochastic process of genomewide congealing, where numerous statistically or physically linked loci of small effect allow selection to limit effective migration rates. The initial congealing event can occur within a broad range conditions, and once initiated, the self-reinforcing process leads to rapid divergence and ultimately two reproductively isolated populations. Flaxman *et al.*'s (2014) work is a valuable contribution to our understanding of speciation with gene flow and in making a more predictive field of evolutionary genomics and speciation.

Keywords: adaptation, gene flow, population genetics, population genomics, speciation

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Flaxman, Wacholder, Feder and Nosil's new work, 'Theoretical models of the influence of genomic architecture on the dynamics of speciation' (2014), is a simulation-based investigation of speciation with gene flow (SWGF). The established view for many decades was that speciation required external barriers (i.e. geography) to gene flow for incompatibilities between populations to arise and result in reproductive isolation (RI; Futuyma & Mayer 1980). More recent work has challenged the extrinsic barrier-dependent speciation view, showing that under some circumstances, divergent selection can drive speciation between populations experiencing high rates gene flow (Jiggins 2006; Via 2001). Despite advancement in our understanding of the process, theoretical expectations concerning the conditions that allow for SWGF to occur are still being explored. Flaxman *et al.*'s (2014) work makes progress identifying these conditions by modelling population divergence over the entire gene flow continuum (allopatry to sympatry) at the scale of individual genomes within populations.

Genomic architecture is an essential part of Flaxman *et al.*'s (2014) work. To understand the effects of genomic architecture in their simulations, the authors compared two more realistic genome architecture models to a simpler, null, 'beanbag' inheritance model, which allowed them to attribute patterns of divergence and RI exclusively due to genomic architecture. Genomic architecture, defined by the authors as the way loci are distributed across the genome, is in part a consequence of inheritance. Our alleles are not sampled at random from one large pool representing the previous generation, but are instead inherited semi-randomly from two smaller pools (i.e. parents) that possess a subset of all possible alleles present in their population. As the authors showed, their two genomic architecture models allowed for degrees of association between divergently selected loci to accumulate, forming statistical linkage due to shared inheritance (genome only model), and by chromosomal linkage over short recombination distances (physical linkage model). Besides genomic architecture, the authors' simulations included divergent selection among two demes, migration (gene flow), random mutations with randomly chosen selection coefficients, recombination (linkage architecture model only) and drift (see also, Flaxman *et al.* 2013 for further details).

Much of Flaxman *et al.*'s (2014) work concerns the characterization of what they called genomewide congealing (GWC), a sudden, well-defined transition towards genomewide differentiation and RI observed in their simulations. In these simulations, differentiation was slow or nonexistent initially, despite the build-up of substantial potentially adaptive genetic variation. However, after GWC, differentiation was rapid and linear. Note that gene flow was still nonzero even after GWC, consistent with numerous empirical examples of well-defined, divergent sister species that continue to experience low levels of migration.

This well-defined transition was only observed in simulations with genomic architecture (both the genome only and linkage models) and rates of migration greater than the strength of divergent selection, likely due to the accumulation of statistically and/or physically linked loci experiencing divergent selection, which create a feedback towards RI. Gene flow was able to overcome divergent selection until the right combination of architecturally linked alleles could interact. Once this combination of alleles occurred, the genomes of the populations were rapidly pulled towards RI by divergent selection. Chromosomal linkage between divergently selected loci was not

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necessary for the transition to occur as it was also exhibited in the genome only model, but it did cause the transition to be even more rapid. Very few assumptions about the demographics and mechanisms of evolution were needed for GWC to result; periods of allopatry, chromosomal linkage and a large number of strongly divergent loci all decreased the number of generations needed for GWC to occur, but they were not essential to the process. The simple assumptions under which GWC could occur suggests it may be a common result when multiple loci are each experiencing weak divergent selection between populations experiencing gene flow, providing a possible unifying explanation for rapid adaptive radiations observed in nature even in the face of gene flow.

By specifying the degree of LD among divergent loci a priori, the authors were able to identify combinations of selection (s), gene flow (m) and the number of divergent loci (L) that would result in alternative stable states: non differentiated—well mixed—populations or GWC. For particular combinations of s, m and L, which stable state resulted was dependent on LD between divergently selected loci (Fig. 1). The authors derived equations to estimate the upper and lower bounds of s that resulted in the occurrence of the two stable states over varying rates of m and L. The exploration of this parameter space showed that the strength of divergent selection need not be greater than the rate of migration when the number of loci experiencing divergent selection is moderate to large. Importantly, GWC

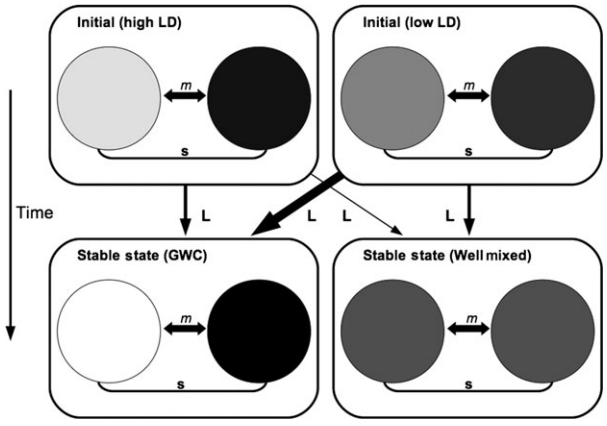

Fig. 1 When two alternative stable states are possible given a fixed combination of selection at each locus (s), effective migration rate (m) and number of divergently selected loci (L), which alternative stable state results depends on the initial LD between divergently selected loci within the two populations. Low LD will result in a well mixed stable state, while high LD will result in GWC. However, with a different combination of s, m and L (here signified by variation in the size of the L arrows), only one stable state may be possible, regardless of the initial LD (i.e. high initial LD in populations will result in a well mixed stable state, while populations with low initial LD will result in GWC). See Flaxman *et al.* (2014) for equations that estimate the upper and lower bounds of s for a given combination of L and m that result in two alternative stable states.

was still observed when $m = 0.5$ with weak selection acting on a relatively small number of divergent loci (Flaxman *et al.* 2014, fig. 5). In addition to showing the conditions that lead to alternative stable states, this work provides valuable insights as to when GWC is sensitive to standing genetic variation and the amount historical gene flow previous to divergent selection pressure.

Previous theoretical works have shown both the importance of recombination to SWGF (Felsenstein 1981), as well as the emergence of barriers to gene flow due to multilocus effects (Barton & de Cara 2009; Barton & Bengtsson 1986). Flaxman *et al.*'s (2014) simulations expanded on this previous work in two important ways. Firstly, the authors' simulations did not require assortative mating among demes, meaning RI resulted directly from fitness consequences of new mutations at divergently selected loci and the LD among them. Secondly, the authors' whole-genome individual-based simulation approach allowed for a more detailed exploration of the conditions that can result in RI, which allowed them to determine when alternative stable populations genomic states would result.

Flaxman *et al.* (2014) built upon previous work by characterizing the patterns of genomewide divergence during the GWC process in their linkage architecture simulations and in doing so identify genomic islands of divergence. They used Ripley's K function to locate chromosomal regions where loci are more clustered across recombinational space than would be expected by chance, finding a region of local divergence that was associated with a nonrandom overclustering of divergently selected loci. Using Ripley's K, the overclustered loci were identified as a genomic island of divergence whose formation, once stable enough to overcome gene flow, quickly pulled the entire genome towards divergence. In the supplemental material (Flaxman *et al.* 2014, video S1), animations of this process illustrate that many ephemeral islands form as simulated generations pass, only to be washed away by gene flow and recombination. After many generations, one beneficial mutation eventually persists long enough for others to join nearby, too close together be broken apart by recombination, and fortunate to overcome drift and gene flow. This characterization and exploration of how genomic islands emerge and the central importance of these divergent blocks in reducing genomewide effective migration rates confirms and explains the importance of these linked regions in facilitating or even driving speciation.

The authors' exploration of SWGF was possible because of the production of a massively complex individual-based model capable of simulating the huge number of interactions that take place in populations of evolving genomes. It has been said that '*The best material model of a cat is another, or preferably the same, cat.*' (Rosenblueth & Wiener 1945). Flaxman *et al.* (2014) and other recent work show that the best models for generating hypotheses and understanding the genetic underpinnings of speciation are not necessarily evolving organisms, but sophisticated simulations of organisms and their genomes *in silico*. This work, and future work that is sure to follow, will pave the way to a field of

speciation genomics where we have the ability to accurately predict the alternative future states of evolving populations.

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