Update

Research Focus

Surfing during population expansions promotes genetic revolutions and structuration

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Recent studies have shown that low-frequency alleles can sometimes surf on the wave of advance of a population range expansion, reaching high frequencies and spreading over large areas. Using microbial populations, Hallatschek and colleagues have provided the first experimental evidence of surfing during spatial expansions. They also show that the newly colonized area should become structured into sectors of low genetic diversity separated by sharp allele frequency gradients, increasing the global genetic differentiation of the population. These experimental results can be easily reproduced *in silico* and they should apply to a wide variety of higher organisms. They also suggest that a single range expansion can create very complex patterns at neutral loci, mimicking adaptive processes and resembling postglacial segregation of clades from distinct refuge areas.

Range expansions promote genetic revolutions

A tenet of population genetics is that genetic drift is a very weak evolutionary force in large populations, which should rather evolve under the effect of selection and thus adapt to their environment. Another common assumption is that genetic drift should be very limited in growing populations [1], preventing alleles from going to fixation or being lost [2]. These classical results are not always true. For instance, selection at one locus can lead to genetic drift at other loci (see Ref. [3] and references therein), social factors such as an intergenerational correlation in fertility can lead to founder effects in growing populations [4,5], and in large geographically structured populations, patterns of gene flow will determine whether local adaptation will occur or not [6,7].

In the case of populations having gone through a recent range expansion, which can, for example, be driven by climatic changes [8], classical expectations about levels and patterns of genetic diversity that do not take into account the dynamics and the spatial component of the expansion can, in fact, be very misleading [9]. This is because spatial expansions into new territories can lead to the spread of rare alleles over wide areas where they can reach very high frequencies [10,11]. This phenomenon coined as 'surfing' [11] is due to strong genetic drift occurring in populations located on the edge of the expansion (see Figure 1). Populations at the wave front are characterized by a very low density where random sampling can lead to large frequency changes. The genetic composition of these marginal populations will also determine the genetic diversity propagated by colonizers, which are recruited from the wave front. As illustrated in Figure 1, the genetic makeup of the expanding population can thus rapidly change over time and space, leading to potentially large allele frequency differences between the source and the edge of the spatial expansion.

Such genetic revolutions leading to drastic differences in allele frequencies between geographic regions have often been interpreted as signatures of positive selection [12–15]. Indeed, when a species colonizes new environments, one would expect genetic adaptation to occur, meaning that some rare but newly advantageous alleles would increase in frequency and erase previous diversity [16,17]. Such selective sweeps occurring at a given locus should affect the diversity of nearby linked loci, offering the possibility to look for signs of recent adaptation by performing genome scans to find regions of low diversity (see e.g. Refs [17–20]). For instance, the human microcephalin gene affecting brain size harbors a mutation showing very high frequencies in non-African populations only. This striking spatial distribution has been interpreted as being due to positive selection on the gene after the exit of modern humans out of Africa some 50 000 years ago, potentially bestowing its carriers with higher cognitive abilities [12]. However, whereas follow-up studies have been unable to show any selective advantage associated with this mutation [21,22], simulation studies have shown that neutral surfing during the spatial expansion out of Africa could indeed lead to very similar patterns just by chance [23].

The surfing phenomenon and its consequences are now beginning to be better understood. For instance, new mutations arising on the wave front of an expansion have a much larger chance to surf than mutations occurring within a fully occupied area [11,24], and the center of the final geographic distribution of such new alleles can be far away from their place of origin [10]. Surfing has also been shown to be favored in small and fast-growing populations, and when gene flow is limited between neighboring populations, because surfing alleles then compete less with alleles coming from the interior of the range [11]. Moreover, allele frequency clines can often be found after range expansions along the expansion axis [11,24–28], implying that observed allele clines should not necessarily be interpreted as being due to selection. Deleterious mutations can surf as well, although, naturally, not as often as neutral or beneficial mutations. However, interestingly, deleterious mutations can surf over longer distances [24]. This is

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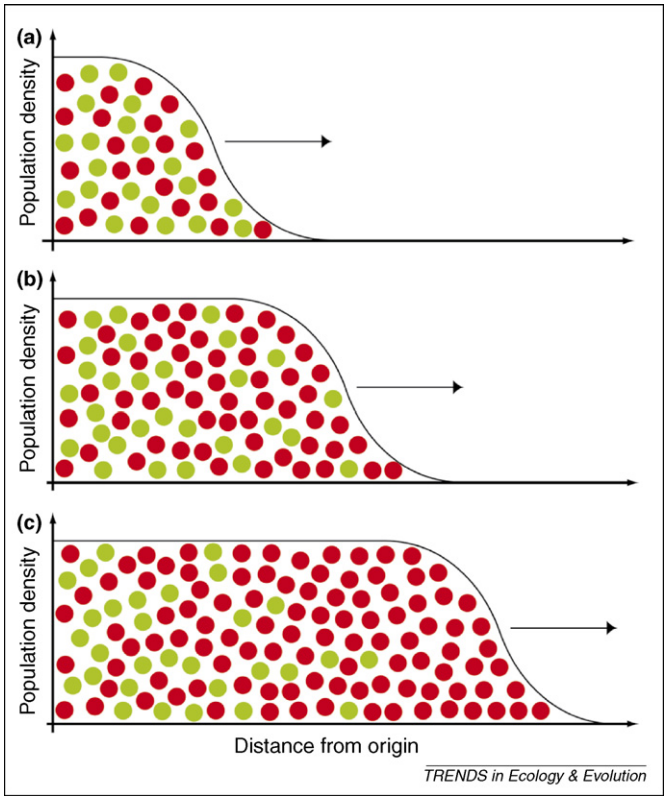

Figure 1. Genetic drift occurring at the wave front of an expanding population, leading to changes in allele frequencies and surfing. **(a)** Initial conditions show an equal proportion of two alleles (red and green) in a spatially expanding population. **(b)** The red allele found by chance at the tip of the wave front in (a) increases in frequency owing to local drift. **(c)** The red allele has become fixed by drift at the wave front, and downstream populations will only carry this allele.

explained by the fact that most deleterious mutations that are able to persist are those which have surfed over long distances and reached high frequencies [24]. Theoretical studies of range expansions in one dimension have shown that genetic diversity should decrease with the progression of the wave as a result of repeated founder effects [29,30], and that the surfing phenomenon cannot be exactly described by deterministic models, such as Fisher's description of the spatial spread of a beneficial mutation [31], because it involves stochastic events (genetic drift) at the wave front [30].

Structuration of the genetic landscape during range expansions

Hallatschek *et al.* [32] have recently studied the genetic consequences of range expansions by monitoring the spatial structure of genetic diversity during the growth of bacteria on an agar plate. In their experiments, they deposited a mixed population of two fluorescently labeled strains of nonmotile *Escherichia coli* in the middle of an agar plate and followed the distribution of the two strains over 4 days. After 36 h, stable sectors harboring a single bacterial strain began to emerge, indicating a complete segregation of the two strains into distinct regions of the plate. These sectors then remained stable and expanded in a radiating fashion, with sector boundaries following a superdiffusive random walk [32] (see Figure Ie in Box 1). These well-defined sectors are thought to have originated from a single founder effect from the edge of the central domain containing the mixed population, as illustrated in Figure 1. The results show that genetic drift on the expansion front can lead to the fixation of a single type of bacteria, which then grows further toward the edge of the plate. This study provides the first direct evidence that surfing can dramatically alter the neutral genetic variability of a large natural population. The authors also performed comparative fitness experiments which show that the fixation of a single strain in a given sector was not a result of enhanced growing abilities of the surfing strains. Whereas previous simulation studies had shown that very patchy gene frequency surfaces could be obtained after range expansion if rare long-distance migration events occurred (see e.g. Refs [33–35]), it appears now that very complex genetic landscapes can also emerge through a continuous range expansion without long-distance dispersal.

Increased genetic differentiation after range expansions

Whereas surfing has previously been applied to describe the fate of a single mutant [10,11,24], this experimental study [32] shows that it also occurs extremely frequently for common alleles. In fact, any single gene on the wave front can surf, and therefore the probability of surfing should be directly proportional to the initial frequency of an allele. This frequency should, in turn, determine the final area where this allele reaches high frequencies after a range expansion [32] (see Figure I in Box 1). This study also shows that, unlike in a one-dimensional system, radiating range expansions in two dimensions should lead to an increase in the global genetic differentiation of the population, as measured for instance by F_{ST}. The structuration of the whole population into regions of nearly fixed alleles should indeed lead to very high levels of population differentiation. However, the exact shape of the sectors of low genetic diversity might depend on the particular organism under study. By performing similar experiments in yeasts, Hallatschek *et al.* [32] have indeed confirmed that the expanding front will be divided into sectors, but the number of sectors and their shape differed somewhat from those seen in *E. coli*. This can be a result of interspecific differences in the shape or in the dispersal abilities of organisms, as well as in their exact mode of reproduction (O. Hallatschek, pers. commun.). Interestingly, the division into sectors and differentiation patterns observed by Hallatschek *et al.* [32] can be easily reproduced through spatially explicit simulations (see Box 1).

Perspectives

Hallatschek *et al.*'s [32] study is a perfect example of the usefulness of small-scale 'microcosm' experiments that have wide applications in ecology and evolution [36]. Further studies are needed to understand the exact expansion conditions leading to distinct zones of low genetic diversity and the influence of potential environmental heterogeneity and complex dispersal patterns, but also whether surfing can simultaneously affect several loci at once, and how long sectors can persist after the expansion. A recent epidemiological study of the spread of a rabies virus in North America [37] has shown that the genetic structure established after a spatial expansion can be extremely stable over

Box 1. Simulation of radiating expansions

The prevalence of temporally stable sectors of low genetic diversity after microbial growth has led Hallatschek and colleagues to conclude that the observation of such sectors could be a generic signature of past range expansions in two dimensions. To check that more mobile species could produce similar patterns of genetically homogeneous geographic regions, we have carried out simple computer simulations of a radiating range expansion.

An extended version of the simulation software SPLATCHE [11,54] was used to model the genetic diversity of populations after a spatial expansion on a two-dimensional lattice (of 112 by 112 demes). The expansion starts from an initial set of demes located at the center of the grid. Initially, these 185 central demes are at carrying capacity, and have two alleles at equal frequencies at a given locus. The density of each deme is logistically regulated with an intrinsic growth rate r arbitrarily set to 1 (to indicate a doubling of the population of each generation at low densities). The maximum population size of each deme (the carrying capacity K) is assumed to be uniform over all demes, but varies among simulations. In each generation, a proportion m of the individuals migrate out of each deme and is equally distributed over the four adjacent demes. Allele frequencies drift randomly within demes according to current population densities, and migrant alleles are randomly chosen according to their local frequencies. This process is continued for g generations, which produces a radiating expansion very similar to that observed for bacteria. At the end of the simulation, the allele frequencies are recorded and mapped using a regular shade of gray (Figure Ia–d).

These simulations show that the sectors of low diversity observed for *E. coli* (Figure Ie) can be quite well reproduced when local densities are high and when gene flow is limited (Figure Ib,c), which is the case in microbial populations. However, genetically homogeneous domains are less well defined for smaller population densities ($K = 100$; Figure Ia), and even less clear with higher levels of gene flow ($m = 0.25$; Figure Id), which leads to allele frequency gradients between sectors. Note that even when sharp sectors are initially produced, broad allele frequency gradients also emerge after some time (data not shown), owing to ongoing short-range migrations that slowly erase the initially sharp boundaries between the low diversity domains.

The important point here is nevertheless that the segregation of alleles into genetically homogeneous regions seems to occur for many types of spatial expansions, showing that it could thus occur in a variety of higher organisms.

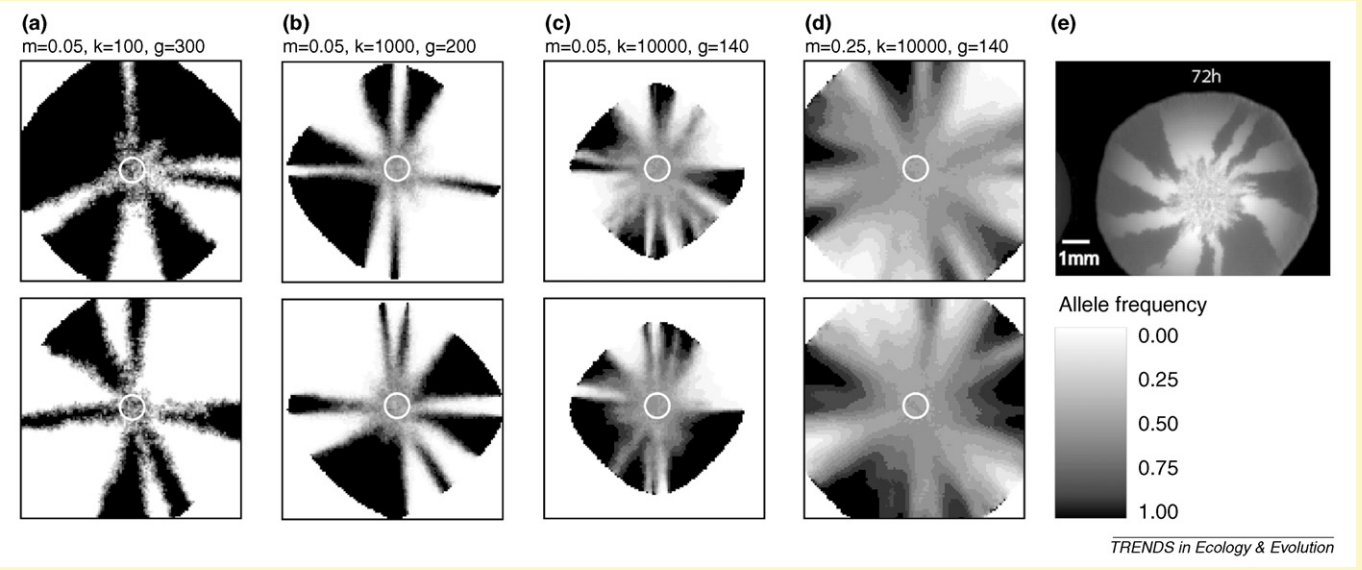

Figure I. Simulation outputs of the spatial segregation of two alleles during a radiating range expansion **(a–d)**. See Box 1 for methodological details. Two random replicates are shown for four simulation conditions, which have been chosen to illustrate the effect of increasing carrying capacities ([a] $K = 100$; [b] $K = 1000$; [c] $K = 10\,000$) and migration rates ([a–c] $m = 0.05$; [d] $m = 0.25$). White circles in (a)–(d) represent the initial zone seeded with an equal proportion of both alleles. **(e)** Fluorescent image of real bacterial colonies after 72 h of growth, starting from an equal mixture of two cell strains (dark and light) (Figure 1a in Hallatschek *et al.* [32], Copyright (2007) National Academy of Sciences, U.S.A.).

time, and that observed phylogeographic patterns are mainly determined by the initial colonization wave. However, due to short-range migrations, any sharp boundary between genetic sectors should be progressively eroded by gene flow [38], leading to the transient observation of allele frequency gradients between sectors. It is therefore interesting to note that spatial expansions can lead to allele frequency gradients that are not only parallel [11,24] but also orthogonal to the expansion axis. These latter clines could actually occur over a wide geographic area (see Figure Ic,d in Box 1), and could easily be misinterpreted as being due to or maintained by selection [39]. For instance, a north-south cline could emerge between two sectors after the expansion of a species along an east-west axis, and a natural interpretation of this observation would be that the cline results from a climatic gradient. It therefore appears necessary to be more careful when equating the observation of allele frequency clines with selection.

The structuration of the geographic space into regions of low diversity separated by sharp frequency gradients after range expansions could also potentially lead to a reinterpretation of broad phylogeographic patterns observed in many species. For instance, the observation of very distinct lineages in various regions of Europe for many animal and plant species has been interpreted as signals of range expansions from genetically differentiated refuge areas [8,40,41]. Although this interpretation is certainly valid for most species, the results of Hallatschek and colleagues suggest that an expansion from a single refuge area followed by surfing and structuration can lead to the same

pattern as several expansions from geographically distinct refuge areas. Note also that expansions from different refuge areas with similar genetic diversity could lead to geographic areas harboring distinct phylogenetic clades. It therefore appears that distinct phylogeographic lineages do not need to have evolved in allopatry after range contractions in distinct refuge areas, or be the result of specific environmental adaptations [40]. It would be worth reexamining hypotheses about the location of refuge areas for some species in the light of these results, for instance by verifying that phylogeographic patterns are similar at several, unlinked loci. However, because heterogeneities in a geographic landscape can induce surfing events (e.g. in the case of spatial bottlenecks [24]), it is also likely that recently colonized but geographically isolated areas might exhibit private phylogenetic lineages at several loci.

The observed spatial division of the microbial habitat into sectors, in the absence of any selective pressure, is reminiscent of the 'area effect' initially described in the grove snail *Cepaea nemoralis* [42], and defined at the molecular level as 'regions of relative genetic uniformity separated by steep clines in allele frequencies' [43]. Such zones of genetic or phenotypic uniformity that are not associated with clear environmental or selective factors have always puzzled evolutionists, and the role of history versus selection for creating these patterns has long been debated [44,45]. Such area effects have been mainly observed in other land snails (see e.g. Refs [44,46]) or in a flightless bushcricket [47], which might be due to the limited dispersal abilities of these species effectively 'freezing' the genetic structure resulting from a range expansion. The prevalence of the structuration phenomenon in natural population thus remains to be more precisely assessed, but will certainly require a very detailed sampling over relatively large areas. Although the frequency of neutral alleles can drastically change during range expansions, it has been shown that traits associated with increasing dispersal can also be selected for during population expansions (see e.g. [48–51]), and interact with other life-history traits (e.g. population growth or adaptability to new environments [52,53]), suggesting that selection pressures for faster dispersal must be very strong to overcome drift at the wave front. However, because range expansions can promote genetic revolutions at both neutral and selected loci, distinguishing between these two types of loci will present a challenge for association studies.

Conclusions

The study by Hallatschek and colleagues [32] convincingly shows that the genetic makeup of expanding microbial populations can drastically change over time and space. Genetic drift occurring at the front of the expansion indeed often promotes the surfing of particular alleles over large areas, leading to patches of low genetic diversity separated by sharp allele frequency gradients. Computer simulations show that similar patterns can occur for a variety of organisms with smaller effective size and higher mobility than growing microbial colonies. This suggests that a range expansion might lead to multiple genetic revolutions and promote neutral and random sweeps of distinct extant alleles in different portions of the range of a species. This mechanism could potentially explain many complex phylogeographic patterns, such as the geographic segregation of distinct phylogenetic lineages within species, that are often interpreted as evidence of range expansions from distinct refuge areas. It also shows that range expansions can create patterns commonly attributed to the effect of adaptive selection such as allele frequency clines or the observation of drastic gene frequency differences between the source and the target of an expansion. Because ongoing and past climatic changes have certainly promoted many range expansions [40], it seems important to take these expansions into account to correctly interpret current patterns of genetic diversity.

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Letters

Does double-blind review benefit female authors?

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Peer review is widely held to be essential for enhancing the quality of scientific communications [1]. Opinions differ, however, as to how to ensure that reviews are as fair and objective as possible. Most ecology and evolution journals employ a single-blind system, which conceals reviewer, but not author, identity. An alternative is double-blind review (both author and reviewer identity is concealed), which, surveys of authors and reviewers suggested, is popular [1] despite the fact that many of those surveyed actually had not experienced the system and that reviewers often like to know the identity of an author so that new work can be placed in context [1,2]. Editors, too, have resisted a switch to double-blind review [1,2], citing a lack of evidence that it is really beneficial [2]. A recent claim of Budden and colleagues [3] that double-blind review favours increased representation of female authors is important, therefore, as it promises tangible evidence in favour of this system.

Budden and colleagues base their conclusion on the journal *Behavioral Ecology* (*BE*), which switched to double-blind review in 2001; they compare the number of male and female first authors immediately before and after this switch for *BE* and five other journals. We summarise the trend across all six journals in Figure 1. Testing each journal separately, Budden and colleagues conclude

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