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IN FOCUS

Admixture is a driver rather than a passenger in experimental invasions

Genetic admixture propels invasions of *Callosobruchus maculatus* across experimental landscapes.

In Focus: Wagner, N.K., Ochocki, B.M., Crawford, K.M., Compagnoni, A. & Miller, T.E.X. (2017) Genetic mixture of multiple source populations accelerates invasive range expansion. *Journal of Animal Ecology*, **86**, 21–34.

In this issue of *Journal of Animal Ecology*, Wagner *et al.* (2017) demonstrate that genetic diversity can alter the course of spread of biological invasions. They employ *Callosobruchus* seed beetles in a clever array of linked habitat patches to compare experimental invasions using individuals from single population sources or from mixes of two, four or six population sources. By taking a model-selection approach, they find that any amount of mixture propels growth rates and spread of introduced populations. This suggests that heterosis alone can alter the course of an invasive range expansion.

The genetics of colonizing species has been a focus of study since the famous edited volume of that name (Baker & Stebbins 1965; Whitney & Gering 2015). Bottlenecks in population size, which reduce genetic variation and can lead both directly and indirectly to low fitness, are a hallmark of founding populations (Dlugosch & Parker 2008). Data collected from natural populations show that admixture, outcrossing between individuals from genetically distinct source populations, is not uncommon in introduced populations. Such admixture may help populations overcome the problems associated with bottlenecks (Estoup *et al.* 2016; Rius & Darling 2014) and may be the key that allows founding populations to successfully establish and spread. However, the role that genetic variation plays in biological invasions remains murky (Dlugosch *et al.* 2015). A growing number of studies in which level of genetic diversity is experimentally controlled in founding groups demonstrate that genetic diversity promotes initial establishment (Forsman 2014). Experimental evidence is also accumulating that demonstrates that founders with high genetic diversity produce populations with high growth rates (Szűcs *et al.* 2014). Thus, genetic diversity appears to be crucial in population establishment and dispersal from the point of introduction.

A vital missing piece to the puzzle is information about the role of genetic diversity in the subsequent spread of colonizing populations. While Szűcs *et al.* (2014) demonstrated that diversity can increase movement in the first generation of establishment, the longer term effects of diversity on range expansion have, until now, yet to be documented. Do populations founded by more genetically diverse individuals spread faster than those founded with less diverse individuals? Wagner *et al.* (2017) are the first to fill in this missing puzzle piece. In their study, they examine the influence of genetic diversity on the speed of range expansion. They work with *Callosobruchus* bean beetles as a model system, creating linear landscapes made

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of habitat patches (beans in Petri dishes) connected by dispersal corridors (tubing). They created experimental groups of founders with individuals from one of the source populations, or with a mix of individuals from two, four or six of the source populations. They worked with 10 source populations in all and drew randomly from those 10 to create their mixtures, thereby minimizing identity effects of particular source populations to focus on number of sources per se. Their key result is that populations founded by mixtures of sources spread further than those founded by single sources, and thus, genetic mixture alters the course of range expansion.

There are a number of non-exclusive mechanisms that might underlie this exciting result, as genetic diversity could enhance spread across a landscape in several ways. First, and most directly, high diversity could facilitate *spatial selection*. Spatial selection is the process whereby the individuals that disperse furthest and are thus on the edge of a range expansion mate with other individuals that also have dispersed far (Phillips, Brown & Shine 2010). If dispersal ability is heritable, then their offspring should have higher dispersal ability than offspring of individuals at the core of the range, leading to a runaway process whereby each generation, high dispersal ability is selected for at the expanding edge. As the response to selection is expected to be proportional to the amount of additive genetic variation (Fisher 1958), dispersal in the expanding edge might evolve more quickly in more diverse populations than in less diverse populations.

Secondly, *adaptation* to the landscape environment itself may also proceed more quickly with more diverse founders. As populations adapt to the landscape, their growth rate would rise, and an increase in growth rate alone can directly lead to increased spread (Fisher 1937).

Thirdly, *complementarity* among genotypes (Crawford & Whitney 2010) could lead to higher population growth rates among more diverse populations, and thus increased spread.

Fourthly, admixture among populations could lead to heterosis by masking genetic load. Genetic load is reduced average fitness relative to a theoretical optimum and is fundamentally caused by recessive deleterious alleles being found in the homozygous state. In finite populations, genetic load can increase over the course of relatively few generations by genetic drift (‘drift load’; Glémin, Ronfort & Bataillon 2003) and inbreeding (‘inbreeding load’; Szulkin, Bierne & David 2010). *Heterosis via directional dominance* arises when alleles present in one parent mask the deleterious alleles present in the other. It is thought to be the main source of heterosis that occurs in nature (Szulkin, Bierne & David 2010). Alleviating genetic load with admixture would increase population growth rates and thus spread rates, and it could also directly increase dispersal ability in heterozygous individuals.

Fifthly, closely related to the fourth, rather than directional dominance masking genetic load, *overdominance* could be acting. With overdominance, heterozygous individuals outperform both forms of homozygotes (thus, both homozygotes with the deleterious allele and homozygotes with the alternative allele have lower performance than heterozygotes). In sexually reproducing organisms, heterosis caused by overdominance will be more transient than that caused by directional dominance, but with both mechanisms, fitness benefits degrade over time as inbreeding ensues. Increases in population growth rate via overdominance are expected to be the most temporary (i.e. the ‘catapult effect’; Drake 2006).

With spatial selection, the speed of spread should increase over time, as dispersal ability increases in the expanding front, up to a point (fig. 1a of Wagner *et al.* 2017). The rate of increase could depend upon genetic background, such that more diverse groups responded more quickly.

With adaptation and complementarity, more diversity may also increase the magnitude of the response. If this is the case, then populations founded with individuals from six sources should attain the highest invasion speed and distance spread, then populations founded with individuals from four sources and so on.

For heterosis via dominance or overdominance, any amount of admixture could enhance population growth rates; thus, all admixed populations, whether founded with individuals from two, four or six sources, should perform better on average than populations founded from a single source. The speed of invasion should increase one time (e.g. fig. 1b of Wagner *et al.* 2017), and not over several generations, as with spatial selection.

Using a model-selection approach, Wagner *et al.* (2017) find that any amount of admixture produced experimental populations that spread further on average than populations from single sources. Support for models in which the number of sources was either coded as a continuous effect or as discrete factors was weaker. The bulk of the difference in spread between populations founded from a single source and mixed populations seemed to occur in the first generation after population founding, with enhanced population growth rates, supporting the hypothesis that inbreeding depression and/or genetic load were relieved by admixture. By examining the data on patch-level extinction and growth rates closely, Wagner *et al.* (2017) are able to infer that mixing of population sources may have reduced the potency of Allee effects (positive density dependence). This facilitated persistence and increased subsequent population growth even at low population sizes.

Direct analyses of dispersal suggest that there was not a consistent increase in dispersal at the expanding edge, as would be found if dispersal ability or propensity evolved in response to spatial selection. There is good support for spatial selection driving the evolution of dispersal in the cane toad invasions in Australia (Phillips, Brown & Shine 2010). It may be that to observe spatial sorting processes in this model, experimental system would require more time or greater differentiation between core and edge populations. It is not known whether cane toad response to spatial selection would differ with more or less genetic variation, and thus, additional work along the lines of Wagner *et al.* (2017) over longer landscapes or additional generations could prove interesting.

Interestingly, mixes of six sources dispersed poorly at the start of the experiment, in a pattern similar to that seen in populations from single sources. This is an intriguing result that warrants further exploration. Dispersal in the focal species has been shown to increase as a means of reducing competition among kin (Downey *et al.* 2015). Thus, it may be that the propensity to move was reduced as relatives (members of the same source population) were at the lowest frequency in the population from six sources. Dispersal of the populations from a single source may have been reduced due to inbreeding depression or high genetic load. A similar pattern could thus be produced by two different mechanisms.

In summary, the evidence supports the hypothesis that heterosis drives faster spread in this experimental study of invasive range expansion. This does not mean, however, that the other mechanisms could not also act (Perkins *et al.* 2013). As Wagner *et al.* (2017) point out, if populations were invading a distinctly novel habitat, then selection to adapt should be stronger than for a habitat with altered spatial structure but that are otherwise similar, and it may be that under those circumstances, different mechanisms would play a stronger role. As studies build upon this first experimental foray into quantifying the role of admixture in spread, further exploration of these and other mechanisms will reveal how often, and by what means, evolution is a driver rather than a passenger in range expansions and invasions.

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