

NEWS AND VIEWS

PERSPECTIVE

Genotypes on the move: some things old and some things new shape the genetics of colonization during species invasions

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Abstract

When we set a species loose outside of its historical range, we create opportunities to test fundamental questions about how populations establish, adapt, disperse, and ultimately define range boundaries. A particularly controversial issue here is how genetic variation among and within populations contributes to the dynamics of species distributions. In this issue of *Molecular Ecology*, Rosenthal and colleagues (2008) seize an opportunity to examine how multiple introductions create genetically distinct establishment events and how these are incorporated into invasive spread. Their findings suggest that a particular recombinant lineage of *Brachypodium sylvaticum* may be responsible for most of the recent expansion of this invader, highlighting the potential importance of genetic novelty and historical context for colonization success.

Keywords: colonization, genetic bottlenecks, hybridization, non-native species, novelty, pre-adaptation, range limits

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Brachypodium sylvaticum, or false brome, is in a relatively early stage of invasive spread, and fairly restricted in its non-native distribution. Its invasions are centred on three North American sites: two in Oregon and one in California, with small satellite populations surrounding the Oregon introductions. This phase of an ongoing invasion is ideal for investigating the interplay between genetic variation and population expansion, and represents an unusual opportunity as genetic studies of invasions at this stage are rare (Dlugosch & Parker 2008b). Rosenthal *et al.* (2008) use nuclear (microsatellite) and chloroplast genotypes of native and invading individuals to identify the most probable sources of the introductions, track changes in genetic

diversity across the invasion, and assess evidence for recombination among lineages.

What should we expect to see in terms of genetic variation in an invader? On the one hand, species introductions are sampling events and should often generate genetic bottlenecks. On the other hand, introductions from multiple sources in the native range could enhance genetic variation. Rosenthal *et al.* (2008) do find evidence of multiple introductions of *B. sylvaticum* from Western Europe into North America, although allelic variation is approximately one-third lower in introduced populations relative to native ones. One group of novel multilocus genotypes dominates the Oregon satellite populations, suggesting that a new intraspecific hybrid may be particularly successful at invading there. This would imply that novel genotypes, rather than diversity per se, are contributing to invasive behaviour (Ellstrand & Schierenbeck 2000). Given that invasive species display a loss of genetic variation on average, and that most invaders probably pass through genetic bottlenecks at some point, it seems likely that genetic variation is not itself a driving force of many invasions (Dlugosch & Parker 2008a), and recombination among source genotypes might play a more important role. Nevertheless, the contribution of particular novel genotypes to invasive spread has yet to be demonstrated directly. The *B. sylvaticum* system offers an exceptional opportunity to explore this question further, because the traits of recombinant Oregon genotypes could be contrasted with those of the nonrecombinant California invaders.

Regardless of whether genetic variation is high or low in invading populations, its geographical distribution will also have important consequences for its maintenance and availability for local adaptation into the future. Previous studies of invasive plants have suggested that genetic differentiation among invading populations is often greatly diminished relative to differentiation in the native range (Novak & Mack 2005). This study of *B. sylvaticum*, as well as another recent study of a young plant invasion (Dlugosch & Parker 2008b), finds instead that invading populations have high F_{ST} values, comparable to differentiation among native populations. These results reveal that separate introductions can establish unique gene pools through founder effects, drift, and/or responses to selection at different locations, before homogenization through gene flow. Such differentiation, even if transient, has important consequences for invasion genetics, because several isolated populations will ultimately preserve more genetic variation than a single gene pool (Lande 1995). This might ameliorate the loss of variation due to bottlenecks during individual introductions. For *B. sylvaticum*, allele frequency distributions show stronger deficiencies of rare alleles at (inferred) sites of initial introduction than elsewhere, consistent with the idea that gene flow during range expansion diminishes some of the negative consequences of founding events.

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David Rosenthal indicates an invading population (background) of *Brachypodium sylvaticum* (inset) in Oregon, USA. New populations are dominated by genotypes that are recombinants of multiple introductions from northern Europe, the native range. (Photos: E. Bonhomme, background; MB Cruzan, inset.)

Gene flow among populations in the new range can also shape the range boundaries of the invasion as a whole. The amount of gene flow into peripheral populations is a key parameter in evolutionary models of species' range limits (e.g. Kirkpatrick & Barton 1997; Gomulkiewicz *et al.* 1999), with potentially contradictory effects. Gene flow acts to homogenize differences generated during the introduction events themselves, and thus relatively high gene flow from the invasion foci into satellite populations could limit further spread by preventing edge populations from becoming locally adapted to changing ecological conditions. However, lack of gene flow into edge populations could also inhibit spread, if edge populations lack adaptive genetic variation in ecologically limiting traits (Kawecki 1995; Barton 2001). The dominance of satellite populations by just a few genotypes — as in *B. sylvaticum* — might limit the invasion to those habitats to which these genotypes are best suited, although support for the idea that low genetic diversity defines range boundaries is not particularly strong among non-invasive species (Eckert *et al.* 2008). Studies of species at different stages of invasion will be invaluable for identifying the factors associated with the creation of range limits and for evaluating the dynamics of genetic variation at range margins during expansion.

Finally, our focus on the evolutionary dynamics within invasions should not obscure the importance of the broader context of these range expansions. Invasion biologists have speculated that species that are more widespread or competitive in their native ranges might spawn better invaders if introduced elsewhere. This has not proved to be generally true (Sax 2001), but perhaps it will be fruitful to evaluate this hypothesis at the level of genotypes rather than species. Rosenthal *et al.* (2008)

note that the chloroplast haplotype of *B. sylvaticum* that has invaded North America is the same as that which has putatively expanded into much of Europe since the last glacial cycle. This haplotype might be a marker for a lineage that is particularly good at colonization, and/or the chloroplast itself may have major effects on adaptive traits (Cruzan & Arnold 1993; Sambatti *et al.* 2008). Nevertheless, *B. sylvaticum* does not appear to be an aggressive colonizer in its native range, and the invasive haplotype is also the most common there. It is possible that this haplotype was introduced merely by chance and has no colonization advantage over the others. Our inference is hampered in this case and in most invasions by a lack of knowledge of the breadth of genotypes that had the opportunity to invade. As we amass more studies that describe the phylogeography of both the native and invading ranges of introduced species, it should be possible to evaluate the potential for past patterns of expansion to preselect colonizing genotypes from native centres of diversity. Common garden studies that explore the relative performance of native lineages in this context will be particularly informative. In order to understand when and how invasions arise, it is critical that we quantify how invaders benefit both from pre-adaptation for colonizing ability in the native range and from genetic novelty that arises within introduced populations themselves.

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