

NEWS AND VIEWS

PERSPECTIVE

Up against the edge: invasive species as testbeds for basic questions about evolution in heterogeneous environments

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Yogi Berra is often credited* with having opined that ‘prediction is very difficult, especially about the future’. There is no discipline for which this statement holds with more force than invasion biology, where it has been historically very challenging to predict the fate of introduced species (Williamson 2006). Some species after introduction quickly go extinct. Other relatively similar species may persist, but with little spread from their initial beachheads. Yet others can become aggressive invaders, with devastating consequences for native communities and ecosystems. This lack of predictability may of course sometimes reflect a simple lack of knowledge, both about key features of a species’ basic biology, and about the environmental and community milieu in which invasion occurs (Williamson 2006). However, unpredictability may also arise from a fundamental fact about populations of living organisms – they almost always contain genetic variation, and so are not fixed entities responding to an environmental template, but instead labile in how they cope with the environment, over many spatial and temporal scales. Chance vicissitudes in the origination, maintenance and spatial organization of genetic variation could play a large role in generating the observed unpredictability in the fates of introduced species. The degree to which a particular introduced species becomes ‘invasive’ – to the extent of coming to the attention of worried land managers, governmental officials and the public – may reflect in part its capacity for adaptive evolution across a wide range of environmental conditions.

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*The actual originator of this piquant phrase is the matter of some dispute. Denenberg (2009) lists 25 claimants to the honour, ranging from Groucho Marx to Cecil B. DeMille. The physicist Niels Bohr seems to have the strongest claim. This seems peculiarly appropriate, as he was one of the creators of quantum mechanics, which is based on the fundamental unpredictability of physical processes.

Even ubiquitous and abundant invaders face limits in their ability to adapt to novel conditions. Unravelling the processes that lead to the current edge of an invasive species’ range helps to illuminate the determinants of invasion in the first place, and also may reveal potential constraints on adaptation to novel environments. This is the basic and very important question tackled by Leger *et al.* (2009) in this issue. These authors focus on cheatgrass (*Bromus tectorum*), a noxious invasive over much of the western United States. Cheatgrass, an annual grass that evolved in Eurasia, was introduced into the western US in the late 19th century [Pellant (1996) provides a succinct account of the origin and impact of this species]. It typically germinates in the fall, overwinters, then rapidly grows and prolifically reproduces (usually by selfing) in the spring, leaving behind swards of dry biomass in the summer that provide fuel for intense fires. Cheatgrass spreads easily by wind or mechanical dispersal, is carried by animals, and readily establishes in disturbed habitats, for instance created by over-grazing. It is fair to say that cheatgrass is among the most noxious invasive species inflicting the western states of the US. Cheatgrass has led to an increase in both fire frequency and intensity (Pellant 1990), with consequent massive changes in native species diversity and vegetation cover, at times leading even to severe erosion (Knapp 1999).

However, cheatgrass, although seemingly ubiquitous in much of the West, is not everywhere. For instance, in the Great Basin, this species is scarce or absent at high elevations. Leger *et al.* (2009) exploit this fact to examine the capacity of cheatgrass to adapt to conditions at its range margin. Molecular analysis revealed high levels of genetic variation in both low and high elevation populations, with some evidence for genetic differentiation across the altitudinal gradient. They used reciprocal transplants across the altitudinal range limit on Peavine Mountain in Nevada to ascertain if this distributional boundary was a true limit (rather than say the leading edge of a sluggish invasion front). It is surprising how rarely this procedure is carried out in studies of invasion or range limits. As Geber (2008) has recently noted ‘It is surprising that in the face of hundreds of reciprocal transplant studies assessing local adaptation and ecotypic differentiation within a geographic range ... so few studies have included the range boundary’. The authors clearly demonstrate that survival plummets outside the current range margin, so it is likely this boundary is stable, rather than a gradually moving transient. Moreover, plants originating at low elevations survived better there than did transplants from high elevations, but at high elevations, all plants suffered equally, regardless of origin. When plants were grown in growth chambers, there appeared to be genetic variation within and among

populations in traits such as germination timing and growth rates. However, field estimates of heritability were much lower, which could constrain the scope for adaptive evolution. The authors conclude that there is no evidence that at present the marginal populations are specifically adapted to their local environments. The fact that abundant genetic variation is present at the molecular level could indicate that these populations might eventually be able to adapt to these marginal environments, and the invasion would then continue marching up the mountains. This may be promoted because the species largely selfs (and so can escape the demographic costs or 'migrational load' of gene flow), and also occasionally cross-fertilizes (permitting new gene combinations to be put together). An alternative possibility is that these indicators of genetic variation are misleading because there may be no genetic variation for those key traits that actually determine survival and reproductive success in marginal habitats – a condition that Bradshaw (1991) called 'genostasis'. Only careful analysis of the functional biology of this species as it operates in its natural environments will be able to determine which of these scenarios may be the more likely.

Regardless of the resolution of this issue as an explanation for the altitudinal limit of cheatgrass on this particular mountain slope, a deeper understanding of the factors limiting the ranges of invasive species can shed light on basic questions in ecology and evolutionary biology, such as conservatism and evolution in species' niches (Holt *et al.* 2005). The article by Leger *et al.* (2009) provides a valuable and timely case study of how molecular tools, when combined with laboratory and field studies, provide essential glimpses into the genetic variation present in invasive species and the nature of potential adaptive constraints on the geographical span of an invasion. This is the kind of

multifaceted study that needs to be replicated, across many species and biomes, to gauge the importance of evolutionary processes in explaining the seeming unpredictability of invasions.

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