Current Biology Vol 18 No 6
R246

Dispatches

Biological Invasions: Paradox Lost and Paradise Gained

A new study shows how an invasive snail species accrues elevated genetic variation for key life-history traits through multiple introductions and outcrossing to create genetically novel offspring. Furthermore, the invaders' offspring follow a unique life-history strategy that may enhance their ability to invade.

Ruth A. Hufbauer

With increasing human interference in animal and plant dispersal, biological invasions are wreaking havoc in environments and economies around the globe [1]. The phenomenal success of invasive plant and animal species poses a puzzle that is often studied from an ecological perspective [1]. Recent research, however, has revealed that adaptive evolution plays a crucial role in many invasions [2,3]. One paradox scientists have grappled with is how the founding invaders, which are frequently low in number and thus may experience severe genetic bottlenecks, are able to colonize successfully, adapt and increase to population sizes that can become economically and ecologically threatening. Recent studies of biological invasions, however, show that perhaps there is no paradox: many invasive species are introduced in large numbers or multiple times such that not much of the genetic diversity of the species is lost [4,5]. Even more critically, when individuals from populations that are genetically distinct within their native range are brought together in the introduced range, genetic variation within populations can be higher than in the native range [6]. With sexual organisms, formerly distinct genetic variants brought together in the introduced range can cross, leading to admixed offspring with an entirely novel genetic make-up [7]. Thus, many invaders may actually not be limited by lack of diversity, and indeed may harbor combinations of genes never seen in the native range. However, whether such diversity in invaders, which is mainly measured using molecular markers that are likely to be evolutionarily neutral, corresponds to the ecologically important variation required for adaptive evolution is largely unknown [7]. The effects of multiple introductions and outcrossing on variation in ecologically important traits are the subject of a new study by Facon and coworkers [8] in a recent issue of *Current Biology*.

Crossing between distinct variants within species, like crossing between species, can broadly be considered hybridization. Invaders of hybrid origin are common, and this is used as evidence that hybridization stimulates invasion [9]. In an introduced range, where encounters with novel genotypes may be more frequent, however, hybridization may be predicted *a priori* to be more common than in the native range of a taxon. Thus, high rates of hybridization in invasive species do not necessarily indicate that hybridization is important for their success. Unfortunately, there are remarkably few data on the fitness consequences of crossing among genetically distinct invaders (though see [10]). Often, outcrossing and hybridization produce unfit offspring due to genetic incompatibilities or creation of ecologically intermediate phenotypes where no intermediate habitat exists [11]. However, heterosis and creation of phenotypes outside the range of the parents (transgressive variation) also can occur. It is thus still unclear whether genetic admixture reduces fitness and invasion proceeds nevertheless (e.g. [12]), or if admixture actually promotes invasion.

One reason that data on the ecological consequences of hybridization are lacking is that recombination rapidly mixes genes from different sources and adaptive evolution swiftly culls the initial variation, obscuring the direct effects of admixture. Facon and coworkers [8] have overcome these difficulties by using a unique study system, the Thiarid snail *Melanoides tuberculata*, in which clonal reproduction is the norm, but sex can occur occasionally. This species' mode of reproduction thus essentially slows the process of recombination. Using this system, Facon *et al.* [8] evaluate how individual crossing events influence life-history traits that are fundamental components of fitness. *M. tuberculata* is native to Asia and Africa and has invaded the new world transported largely via the aquarium trade. There is a wide variation of shell ornamentation, allowing visual identification of discrete morphs that correspond to single clonal lineages [13]. Surveys reveal that many locations within the native range contain single morphs, while locations in the invaded range can have many. The freshwaters of Martinique, a veritable tropical paradise, have been invaded by *M. tuberculata*. Martinique now contains five morphs that originated in the native range as well as two morphs created *in situ* via sexual reproduction between three of the five introduced morphs. Facon and coworkers [8] use this remarkably simple system to examine the complex consequences of multiple introductions and admixture in detail, using the asexual reproduction of introduced and sexually formed morphs to generate clonal replicates on which they measured two key life-history traits: the number of offspring (fecundity) and their size. Differences between morphs provide thus a direct measure of quantitative genetic variation in these traits.

Generally, there is a known trade-off between the number and the size of progeny: due to energetic and time constraints, organisms cannot produce both many and large offspring. Rather, species reproduce on a continuum between few, large offspring and many, small offspring. The introduced snail morphs on Martinique show a remarkable degree of variation in life-history strategies, even within a single location, illustrating how multiple introductions enhance the genetic variation of the invaders.

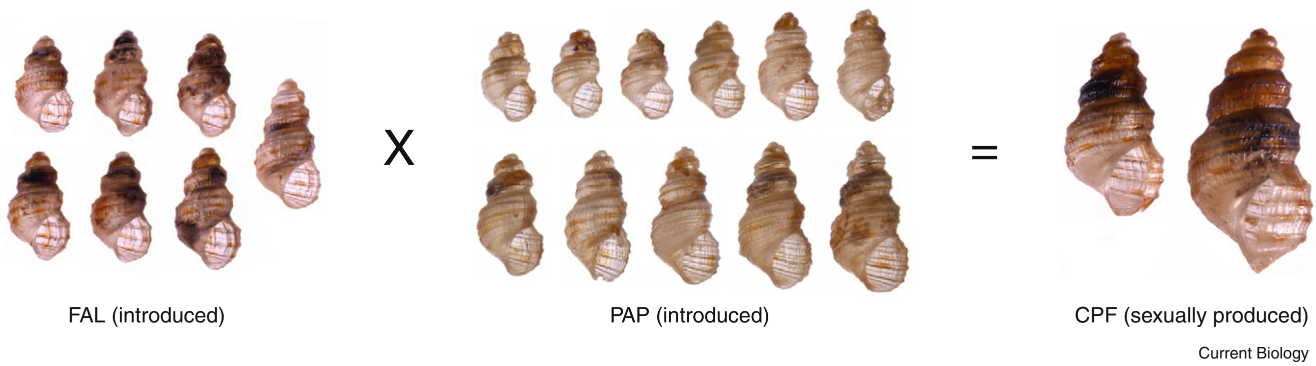

Figure 1. Morphs of the freshwater snail *Melanoides tuberculata* that have invaded Martinique.

Average fecundity (as the number of individuals produced during one week) and size of two invasive morphs (FAL and PAP) as well as their sexually produced offspring (CPF). The sexually produced morphs are significantly bigger and may also have a fitness advantage based on increased genetic diversity stemming form multiple invasions. (Photographs kindly provided by Laurent Soldati and Benoit Facon.)

Furthermore, the new work demonstrates a shift in the life-history strategy within the two new sexually produced morphs: they have lower fecundity but their offspring are larger than that of the parental morphs. For example, one cross between two introduced morphs yielded a morph with a mean fecundity of less than half that of its parents, while the mean size of the offspring has more than doubled (Figure 1). The sexually produced morphs have replaced their progenitors in several streams of Martinique, suggesting that this new life-history strategy provides higher total fitness in this environment [14]. Thus, the multiple introductions of distinct morphs provided a dramatic range of phenotypic variation, while outcrossing created entirely new, transgressive phenotypes, perhaps through polyploidization.

This new research [8] supplies, for the first time, evidence that transgressive variation created via hybridization can facilitate invasion. It further strengthens growing evidence that multiple introductions and genetic admixture can have real evolutionary consequences for invasive species [7,15], with the potential to radically alter the expression of key life-history traits and provide variation for further fine-tuning to a new environment [16]. Biological invasions can no longer be seen as genetic paradoxes. Rather, they are crucibles for evolution.

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Department of Bioagricultural Science and Pest Management and Graduate Degree Program in Ecology, Colorado State University, Fort Collins, Colorado 80523-1177, USA.
E-mail: hufbauer@lamar.colostate.edu

DOI: 10.1016/j.cub.2008.01.038

Cytokinesis: Catch and Drag

Recent studies of actomyosin-ring assembly in fission yeast have suggested that an intricate web of membrane-bound nodes containing myosin and the actin nucleator formin is pulled together into a tight ring through a 'search-and-capture' mechanism.

Mithilesh Mishra and Snezhana Oliferenko*

Actomyosin-based 'rings' underlying the plasma membrane are assembled between segregating copies of genetic material during eukaryotic cell division. Sliding of actin filaments by myosin motors leads to ring constriction, which in turn is thought to permit cortical ingression and individuation of daughter cells. The actomyosin rings are dynamic, complex structures and their assembly and constriction in the plane orthogonal to mitotic spindles are