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NEWS AND VIEWS

PERSPECTIVE

Population-level traits that affect, and do not affect, invasion success

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What allows some species to successfully colonize a novel environment while others fail? Numerous studies in invasion biology have sought to answer this question, but those studies have tended to focus on traits of species or individuals (e.g. body size, seed size, seed number), and these traits have largely been found to be weak predictors of invasion success. However, characteristics of colonizing populations (e.g. genetic diversity, density, age structure) might also be important for successful establishment, as the authors of a study published in this issue of *Molecular Ecology* show (Crawford & Whitney 2010). By experimentally manipulating the density and genetic diversity of colonizing populations of *Arabidopsis thaliana*, the authors found that genetic diversity, but not population density, increased colonization success. Importantly, the effects of genetic diversity on colonization success were both additive and non-additive, suggesting that traits associated with particular genotypes and complimentarity among genotypes contribute to colonization success. This research highlights the importance of considering within-species variation and characteristics of entire populations in predicting colonization success.

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The arrival and establishment of novel species threatens the integrity of ecosystems in nearly all corners of the globe (Mack *et al.* 2000). As a result, a major focus in ecology has been to identify the characteristics of invasive species that allow them to successfully colonize novel ecosystems. The individual-level traits of invasive, or potentially invasive, species that many investigators have focused on usually include life history traits such as body size, generation time, seed size and number (Rejmanek & Richardson 1996). However, the lack of useful generalizations in predicting which species will become invasive has led to a fair amount of pessimism in the literature (Crawley 1987; Mack 1996).

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One possibility for the lack of generality is that previous investigators might have focused on the wrong level of biological organization. That is, instead of asking what individual-level traits make some species more likely to become established than others, perhaps it would prove fruitful to ask what population-level traits make some populations more likely to become established. In fact, there is a long history in population genetics that focuses on population-level traits and population establishment by species in novel environments and subsequent evolutionary dynamics and consequences over at least several generations (e.g. founder effects, bottlenecks). Experimental tests of how population-level traits, such as genetic diversity and population density, might affect establishment by novel species in ecological time have been largely absent in the literature. The exciting paper by Crawford & Whitney (2010) in this issue of *Molecular Ecology* fills that void.

In a cleverly designed experiment, Crawford & Whitney (2010) manipulated the population density and genetic diversity of *Arabidopsis thaliana* in the greenhouse (Fig. 1) to ask whether these population-level traits influenced colonization success, where colonization success was estimated as seedling emergence rate, biomass production, duration of flowering, and reproduction. Importantly, these responses represent different stages of the life cycle of the plant, and they compared the effects of genetic diversity to population density.

One of the key results of the study is a negative result - that population density did not increase colonization success of *A. thaliana*. Most invasion biologists will find this to be a peculiar result, because, as Lockwood *et al.* (2009) wrote, '… the primary determinant of establishment success is propagule pressure or the number of individuals

Fig. 1 Experimental tests of the effects of population diversity and density of *Arabidopsis thaliana* on colonization success.

introduced'. Indeed, this result from Crawford & Whitney's (2010) study seems to run counter to the notion that a minimum viable population size is necessary if a population is to persist in the face of environmental or demographic stochasticity and overcome Allee effects. So why is there no effect of population density on colonization success *A. thaliana* in this study? One possibility that Crawford & Whitney (2010) allude to is that there was little or no environmental or demographic stochasticity in the controlled environmental conditions of this experiment. Under more natural field conditions, perhaps density would have been related to success, as it is in so many other studies of invasions (Lockwood *et al.* 2009; Simberloff 2009).

Genetic diversity, in contrast to population density, increased colonization success: seedling emergence, biomass, flowering duration, and reproduction were all greater in genetically diverse populations than in genetically depauperate populations. As Crawford and Whitney point out, a number of studies have shown that genetic diversity, usually in plants, can affect a wide variety of community and ecosystem processes, including biomass production (reviewed in Whitham *et al.* 2007; Hughes *et al.* 2008). So it is not that surprising that genetic diversity of *A. thaliana* was positively correlated with biomass; indeed, similar effects of genetic diversity have been known from the agricultural literature (Smithson & Lenne 1996) and from ecological studies for quite some time. Similarly, a handful of other studies have shown how genetic diversity can influence various aspects of fitness (reviewed in Hughes *et al.* 2008), while the results on flower number and duration are mixed at best (Crutsinger *et al.* 2008).

Independently, the effects of genetic diversity on biomass, seedling emergence, flowering duration, or reproduction in *A. thaliana* would not be that exciting. But what it novel about this study is that those life stages were all affected by genetic diversity, and the effects of genetic diversity were compared to another factor, population density. To my knowledge, no study to date has demonstrated such pervasive ecological effects of genetic diversity on a colonizing species. Additionally, few studies have compared the effects of genetic diversity to other factors, as Crawford and Whitney do here by comparing genetic diversity to population density. Moreover, the effects of genetic diversity were not simple additive effects (i.e. the ecological response in diverse plots is not simply the sum of the component genotypes). Instead, the effects were largely non-additive, meaning that, for example, biomass in genotypically diverse plots was greater than expected based on the biomass of component monoculture plots that made up the diverse plot. At least according to several recent reviews and syntheses (Hughes *et al.* 2008; Bailey *et al.* 2009), it seems that evidence is beginning to accumulate that the effects of genetic diversity on a host of community and ecosystem-level processes are non-additive more frequently than not. Such a result begs the question of why and will hopefully spur on investigators in this area to begin to identify, rather than simply speculate about, the underlying mechanisms for non-additive effects of genetic diversity.

Crawford & Whitney (2010) are right to point out that their study has important implications for the study of invasion biology, but I would argue that there are other implications as well. While the number of studies that identify population density or propagule pressure as determinants of invasion success continues to grow (Simberloff 2009), perhaps Crawford and Whitney's important study will lead invasion biologists to pay more attention to the genetics of colonizing species (e.g. Saltonstall 2002; Tsutsui *et al.* 2003). Additionally, the study reminds us that ecological and evolutionary timescales, traditionally considered separate, are intimately linked (Antonovics 1976). Genetic diversity is the lifeblood of evolutionary processes, but important diversity-related effects can play out within a single generation and determine whether the evolutionary consequences of genetic diversity have a chance to be realized. Finally, I hope this study will remind all of us that designing rigorous experiments, even with the lab rat of the plant world, *Arabidopsis*, can inform us about important ecological questions and pressing environmental problems such as the establishment of novel species in new environments.

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