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NEWS AND VIEWS

PERSPECTIVE

Within-genotype epigenetic variation enables broad niche width in a flower living yeast

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Niche theory is one of the central organizing concepts in ecology. Generally, this theory defines a given species niche as all of the factors that effect the persistence of the species as well as the impact of the species in a given location (Hutchinson 1957; Chase 2011). Many studies have argued that phenotypic plasticity enhances niche width because plastic responses allow organisms to express advantageous phenotypes in a broader range of environments (Bradshaw 1965; Van Valen 1965; Sultan 2001). Further, species that exploit habitats with fine-grained variation, or that form metapopulations, are expected to develop broad niche widths through phenotypic plasticity (Sultan & Spencer 2002; Baythavong 2011). Although a long history of laboratory, greenhouse and reciprocal transplant experiments have provided insight into how plasticity contributes to niche width (Pigliucci 2001), recent advances in molecular approaches allow for a mechanistic understanding of plasticity at the molecular level (Nicotra *et al.* 2010). In particular, variation in epigenetic effects is a potential source of the within-genotype variation that underlies the phenotypic plasticity associated with broad niche widths. Epigenetic mechanisms can alter gene expression and function without altering DNA sequence (Richards 2006) and may be stably transmitted across generations (Jablonka & Raz 2009; Verhoeven *et al.* 2010). Also, epigenetic mechanisms may be an important component of an individual's response to the environment (Verhoeven *et al.* 2010). While these ideas are intriguing, few studies have made a clear connection between genome-wide DNA methylation patterns and phenotypic plasticity (e.g. Bossdorf *et al.* 2010). In this issue of *Molecular Ecology*, Herrera *et al.* (2012) present a study that demonstrates epigenetic changes in genome-wide DNA methylation are causally active in a species' ability to exploit resources from a broad range of environments and are particularly important in harsh environments.

Keywords: DNA methylation, epigenetics, fungi, MS-AFLP, niche theory, phenotypic plasticity

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Herrera *et al.* (2012) studied the nectar-living yeast *Metschnikowia reukaufii* (Fig. 1, Pozo *et al.* 2011), which is an ideal organism for plasticity studies because it reproduces clonally and is easy to replicate across different environmental treatments. Additionally, the natural ecology of *M. reukaufii* lends itself to the investigation of factors influencing niche width because it exploits the nectar of a huge number of plant species (e.g. Fig. 2). The nectar of *M. reukaufii*'s host flowers is a highly diverse, fine-grained environment where *M. reukaufii* is passively introduced via pollinators (Brysch-Herzberg 2004; Herrera *et al.* 2010). The authors demonstrated that *M. reukaufii* has evolved a broad niche width and has considerable plasticity in resource use by characterizing floral nectar and use on a total of 2,359 nectar samples from 94 plant species in 31 families. *Metschnikowia reukaufii* occurred in the nectar of 48% of species and 52% of families surveyed. Herrera *et al.* (2012) next characterized the broad intra- and inter-specific variation of the nectar environments detecting approximately threefold variation in sugar concentration and high variation in sugar composition in a subset of 12 species. Then, Herrera *et al.* (2012) conducted experiments on cultures of five genotypically distinct strains of *M. reukaufii*, which were obtained from floral nectar of different host species. Strains were replica-plated on media differing in a factorial design of sugar concentration and composi-

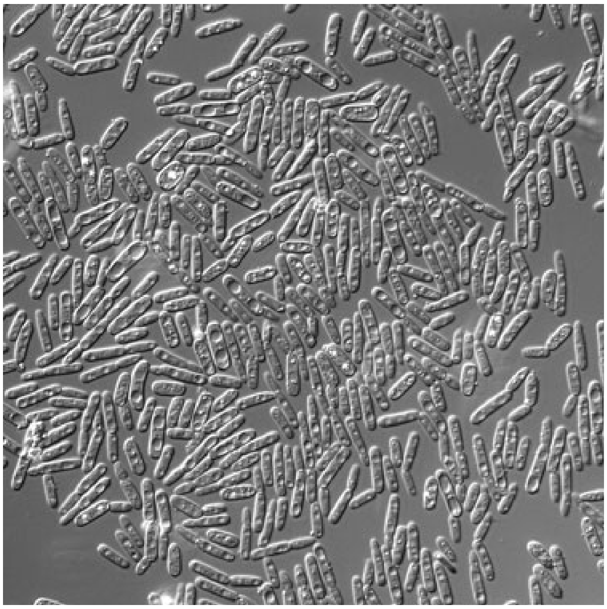

Fig. 1 The nectar-living yeast *Metschnikowia reukaufii*. Image courtesy of Carlos M. Herrera.

Fig. 2 Six focal species from which flower nectar sugar environments were studied: from left to right, top row, *Digitalis obscura*, *Gladiolus illyricus*, and *Aquilegia vulgaris*, bottom row, *Helleborus foetidus*, *Atropa baetica* and *Primula vulgaris*. Images courtesy of Carlos M. Herrera.

tion, which mimicked the natural variation faced by *M. reukaufii*.

Although several authors have suggested correlating changes in MS-AFLP markers with phenotype to document the relationship between phenotypic plasticity and epigenetics (Bossdorf *et al.* 2008; Richards *et al.* 2010a; Richards 2011), Herrera *et al.* (2012) may be the first attempt to do so. To demonstrate the importance of environmentally induced changes in DNA methylation in response to the diverse nectar environments, Herrera *et al.* (2012) screened genome-wide DNA methylation at 120 MS-AFLP loci. Sugar composition, sugar concentration and their interaction significantly influenced the mean probability of MS-AFLP loci changing from unmethylated to methylated in cultured strains, yet methylation status did not vary significantly among strains. Also, the overall proportion of methylation was significantly related to sugar concentration, the lowest methylation at 30% and the highest at 50%. Changes in methylation status were predictably associated with 8 of 120 loci. These eight loci had a great deal of variation in response, yet for all, the probability of being methylated was significantly affected by nectar environment.

A distinguishing component of the study by Herrera *et al.* (2012) is that they went beyond showing that plasticity in resource use was correlated with changes in methylation. In addition, they showed that inhibiting methylation with the nucleoside analogue 5-azacytidine significantly depressed the growth of *M. reukaufii* in sugar containing media, but had no detectable effect on growth of *M. reukaufii* in control media. A direct relationship existed across sugar x concentration experimental levels that linked 5-azacytidine with mean per loci probability of methylation. Thus, the greater the changes in genome-wide methylation profile the stronger the impact of 5-azacytidine on growth. These results clearly indicate that phenotypic plasticity of resource use via epigenetic changes in DNA methylation became more important as environmental conditions became harsher.

Herrera *et al.* (2012) conclude that '… plasticity based on variable DNA methylation... might, under such circumstances, be subject to selection in and of itself'. This has long been a goal of evolutionary ecologists, but demonstrating that plasticity can be selected and therefore potentially adaptive has been notoriously difficult and only rarely accomplished. A rigorous demonstration that plasticity is adaptive requires establishing the same elements necessary for demonstrating that any trait is the result of evolution by natural selection: it must be heritable, there must be variation for it, and that variation must be related to fitness (van Kleunen & Fischer 2005; Richards *et al.* 2006; Nicotra *et al.* 2010). Herrera *et al.* (2012) are able to show that while controlling for genotype, artificially reduced plasticity that results from methylation inhibition with 5-azacytidine is correlated with decreased fitness in stressful environments. This beautifully demonstrates that plasticity is correlated with epigenetic changes and also adaptive. However, epigenetic effects offer a special challenge in that some changes that are elicited by stressful environments are not reset in the next generation but are actually inherited, potentially as a mechanism underlying so-called transgenerational plasticity (e.g. Scoville *et al.* 2011). Differentiating the ability to adjust epigenotype within a single generation (as in Herrera *et al*. 2012) versus the inheritance of an environmentally changed epigenotype (e.g. Verhoeven *et al.* 2010) will require further manipulations of the next generation (Richards *et al.* 2010b). These types of studies will be also critical to determine how much of phenotypic plasticity is because of epigenetic effects, which may not be involved in cases of passive phenotypic plasticity (see van Kleunen & Fischer 2005; Nicotra *et al*. 2010; Richards 2011).

This study makes a significant contribution to the growing body of work concerning the importance of epigenetic variation to ecology and evolution. The major contribution is that it elegantly connects within-genotype epigenetic variation that changes in response to the environment, phenotypic plasticity and a conferred advantage to populations in the same system. As such, this study makes a clear case for the importance of epigenetic variation in ecology and evolution.

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Schrey's research focuses on epigenetic variation among populations, population genetics, and conservation genetics. Richards' research incorporates genomics and epigenetics tools into robust ecological experiments to understand how organisms respond to the challenges of stressful and changing environments.

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