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FE SPOTLIGHT

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"Winners" and "losers" in the Anthropocene: Understanding adaptation through phenotypic plasticity

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Being able to make accurate predictions about the success of a species in the face of climate change and other stressors is a major focus of ecological research. Integral to the approach is to identify the mechanisms by which organisms respond to change. To persist under new conditions (for example, increased ocean temperatures), a species will either need to shift its geographical distribution (Poloczanska et al., 2013), adapt through genetic evolution (Muñoz, Farrell, Heath, & Neff, 2015) or exhibit adaptive phenotypic plasticity in response to the stressor (Palumbi, Barshis, Traylor-Knowles, & Bay, 2014). Range shifts have been documented for a number of marine species (e.g. Mieszkowska, Firth, & Bentley, 2013); however, for most, the bulk of their geographical distribution will remain unchanged (Munday, Donelson, & Domingos, 2017). Genomic evolution may not be possible for individuals "trapped" in their current distribution, because of a mismatch between generation time and the speed of changes. Studies which assess the genomic and epigenetic mechanisms that underpin species' plasticity in response to rapidly changing environmental conditions are, therefore, particularly relevant. Ultimately, the flexibility and strength of these responses will be critical to becoming a "winner" under unprecedented rates of change.

In this issue of *Functional Ecology*, Clark et al. (2018) report on a creative experiment that takes significant steps towards understanding the molecular basis of phenotypic plasticity. Polar habitats are at the forefront of anthropogenic-driven change, with the Antarctic Peninsula having experienced some of the most rapid warming relative to baseline for any region on Earth (Meredith & King, 2005). It is, therefore, no surprise that scientists have focussed on the ability of polar species to acclimatize. Clark et al.'s selection of the Antarctic limpet *Nacella concinna* to investigate the cellular and molecular mechanisms underpinning plasticity is perfectly aligned to this aim. This species inhabits both intertidal and subtidal zones, with two morphotypes that differ in a suite of physiological and morphological characteristics that make them suited to the specific environment's requirements. Phenotypic variation such as this is not unusual for marine species (e.g. De Wolf, Backeljau, & Verhagen, 1998), but critically, *N. concinna* is a broadcast spawner, producing a planktonic larval stage that disperses over 1–2 months and thus contributing to its genetically homogeneous background across the habitats (Hoffman, Peck, Hillyard, Zieritz, & Clark, 2010).

Gene expression profiles following reciprocal transfer experiments between the two habitats show the upregulation of cellular stress response genes reflects individuals being moved from the relatively benign subtidal to their new stressful intertidal home. However, these changes also persisted in the intertidal animals transplanted to the subtidal. Epigenetic differentiation (methylation patterns) also showed differences after transplantation, thus indicating its role in an organism's ability to respond to new environments and also in habitat-specific phenotype differentiation.

What this study has also carried out, which makes it stands out not only from other polar studies, but also for marine invertebrates generally, was to include a long-term common garden experiment. This has enabled the authors to investigate whether the expression profiles had become fixed. The 9 months of being in aquarium conditions did not remove transcriptomic differences between the subtidal and intertidal groups. The epigenetic differences seen at the start of the transplant experiments did not persist, although the authors do acknowledge that they may have missed some methylation as it can be extensive across the genome (Huang et al., 2017).

Clark et al. (2018) have addressed fundamental issues of adaptation but, as is often the case, the animals did not always stick to the plan. The fact that individuals of both transplanted groups began to move back to their source habitats (travelling several metres) highlights some interesting future research themes, for example: (1) why would an organism return to an environment that is demonstrably more stressful; and (2) how does an organism initiate novel behavioural strategies (i.e. start homing) that contribute to phenotypic plasticity?

Our world is changing rapidly not just in terms of average meteorological quantities, for example temperature and precipitation, but also with variability of these quantities, for example the intensity and frequency of extreme climatic events (Jentsch, Kreyling, & Beierkuhnlein, 2007; Leung, Connell, & Russell, 2017; Thompson, Beardall, Beringer, Grace, & Sardina, 2013). Studies using transcriptomic and epigenetic methods that show species *can* respond to change in relatively short time-scales are currently in the minority, but the results of Clark et al. (2018) and others will have significance as they give hope that many more species have the potential to be "winners". Indeed, rapid stress-induced epigenetic changes are thought to contribute to the fast acclimatization experienced during biological invasions: an extreme form of winning (Huang et al., 2017). However, what is missing from being able to identify "winners" at a broader scale is if the transcriptomic and epigenetic resilience can be routinely passed to offspring. Some marine species have capacity for transgenerational acclimation (Munday et al., 2017; Veilleux et al., 2015), but multigenerational experiments are required for many more marine species in line with mammalian studies (Metzger & Schulte, 2016).

Keystone species from other habitats also need to be investigated. Like Clark et al. (2018), many marine studies have focussed on intertidal rocky shore species for their tractability and obvious exposure to extreme conditions (Mieszkowska et al., 2013), but other benthic habitats are also at risk. Intertidal mudflats are traditionally thought to be buffered to extreme climatic effects, but our own data show that temperatures within the top 5 cm of the sediment (where many of the infaunal species live) are still susceptible to heat waves if emersion corresponds with high solar radiation levels (White, 2018). As sediment is a sink for many pollutants, these habitats have also suffered disproportionately from other toxicological stressors (e.g. Vandegehuchte & Janssen, 2014). Cumulative effects of multiple stressors should, therefore, be a priority for future epigenetic and transcriptomic studies.

Although we are beginning to understand the role of variability (interindividual, interpopulation and interspecies) that discriminates a "winner" from a "loser", it is clear that the Anthropocene is taking us (science, species and communities) into unchartered waters. As Clark et al. (2018) have accomplished for their polar limpet, it is imperative for ecologists to understand if, and how, species can respond to an uncertain future. We can only hope that many species do have the capacity to be future "winners".

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