A postscript on cryotypes

Phylogenetic partitioning of plasticity

Phylogenetic analysis is a theoretical construct that employs a nested hierarchy of 'subroutines' to relate discrete elements ('phyle' from the Greek for 'tribes') to their wider origins ('genesis' from the Greek for 'birth' or 'origins'). Its modern usage ranges from molecular biology to ecology, where it may be used to relate elements not connected by DNA (Wanntorp et al., 1990). Cryotypes may not be conventionally genetically related (in the 'tree of life' sense) but they share a different kind of genetic relation – that of evolutionary physiology (the 'mode of life' sense): the shared acquisition of a specific adaptive suite.

Defining phenotype

I refer the reader to DeWitt and Scheiner's (DeWitt and Scheiner, 2004) remarks concerning one of the definitions of phenotypic plasticity they favour, '...the word "phenotype" is left for individuals to define for themselves.'

Genotypic plasticity

Genotypic plasticity is not 'total phenotypic variance', but, if anything, total genotypic variance – the diversity and extent of variance expressed by all genotypes. But, in most cases where it is examined empirically in low temperature biology, the variance examined is by no means 'total', only, given that a mere handful of genotypes are studied, 'representative' – hence our (Hawes and Bale, 2007) preference for the less ambitious and more general term, 'genotypic plasticity'.

Superplasticity

As to whether the 'superplastic' responses described (Hawes et al., 2007) exceed environmental change: *Halozetes belgicae* changes from warm-acclimated to 'winter' phenotype [lower lethal temperature (LLT) declines from –7 to approximately –27°C] after just two hours at 0°C, whereas the climate in maritime Antarctica takes at least two months to reach winter temperatures – by most temporal reckoning, two hours is somewhat faster than two months.

Survival as the fundamental measure of fitness

For some time it has been widely accepted in our field that fitness has multiple expressions over time and space (e.g. Baust and Rojas, 1985). Nonetheless, when it comes to delimiting the adaptive boundaries of arthropods, one must first determine the parameters of survival before one can proceed to ecological and evolutionary parameters, such as pupation, reproduction and generational effects. Indeed, if one wants to be etymologically literal – the word 'fundamental' comes from the Latin 'fundamentalis', meaning 'of the foundation': LLTs are quite literally the 'foundation' from which all determinations of low temperature fitness originate.

Cryotypes

Linnaeus (Linnaeus, 1751) in his notes on 'Methodi Naturalis' urges his readers to seek out ways of relating organisms. If readers wish they may continue to say, 'arthropods are freeze tolerant (FT) or freeze avoiding (FA), but some use desiccation as their primary strategy; some use both freeze tolerance and freeze avoidance; some use desiccation and freeze avoidance; some use desiccation and freeze tolerance, etc.' To my mind, it is more conceptually coherent to say that, 'four cryotypes are employed and these are defined by their management of internal ice (tolerance, avoidance, removal, or some combination thereof)'.

Plasticity in freeze tolerant cryotypes

In FA cryotypes, the more dynamic their metabolic and cryoprotective machinery is at low temperatures, the lower the temperature they can survive. In FT cryotypes, the primary adaptive suite has an entirely different goal to plasticity: the establishment and maintenance of a state that obviates or mitigates against dynamism – the suspended stasis of freezing. The difference between equilibrium freezing temperatures and LLTs in FT cryotypes are, thus, expressions of the durability of the envelope of stasis they have evolved.

That plasticity declines in FT cryotypes with increasing evolutionary derivation does not mean that LLTs become less plastic with departure from the basal state, but that the FT adaptation does. Thus, on one end of the scale there are the species with the more derived forms of FT, which often possess this capacity permanently and independent of environmental temperatures [see Hawes and Bale (Hawes and Bale, 2007) and references therein]. At the other end of the scale, there are species for which the FT adaptation is 'incomplete' – i.e. they do not survive equilibrium freezing (Todd and Block, 1995).

LLTs may themselves show considerable variability in FT cryotypes – but this is phenotypic plasticity. This extension of the 'stasis envelope' observed in acclimation and/or acclimatization experiments is not associated with the relative derivation of FT (which has occurred over evolutionary time) but with the cues and stimuli responsible for upregulating whatever FT traits it has acquired (i.e. a property of the phenotype). The difference in context should be clear. FA cryotypes incorporate plasticity at the level of cryotype (for such species the acquisition of cold tolerance adaptations is the acquisition of plasticity in relation to sub-zero temperatures). By contrast, FT cryotypes evolve to be static (or relatively so) at the level of the cryotype, with most plasticity incorporated at other levels.

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