

Phenotypic plasticity, the flexibility that animals and plants show in the face of varying environments, remains a central theme in ecology, evolution and developmental biology. It is incorporated across scales in our explanation of the causes and consequences of variation among and between species². Predator induced phenotypic plasticity is a popular and exciting form of plasticity highlighted by ecologists, evolutionary biologists and developmental biologists. An emerging question in research on predator induced plasticity is how prey integrate their response to multiple predator threats, within a seasons and across morphological and life history traits. We examined the integration of predator induced behavioural, morphological and life history traits to spatial variation from multiple sources of predation risk in the classic system of water fleas (Cladocera) and its array of predators (predatory fish and phantom midge larvae (*Chaoborus spec.*)). The main objectives were :

(i) *within and between predator regimes*, to test the hypothesis that predators of different size selectivity will generate different trade-offs among a suite of life historical and morphological traits. Studying plastic responses in the solitary presence of different predator species, we develop a picture of the integrated strategy of each prey-predator combination, genetic variability (cross-clone) in this strategy and variation along the prey body size and predator hunting mode gradient.

(ii) *under multiple predator regimes.*, to evaluate how prey responds to multiple predator pressure. We tested the hypothesis that multiple predators induce additive effects on trait integration. The alternatives are that multiple predators that induce different responses in multiple traits will produce phenotypes that are not the sum of the reactions to each predator but represent either a generalised phenotype being intermediately effective, a phenotype ineffective to multiple predators or a phenotype being only effective against the most dangerous predator.

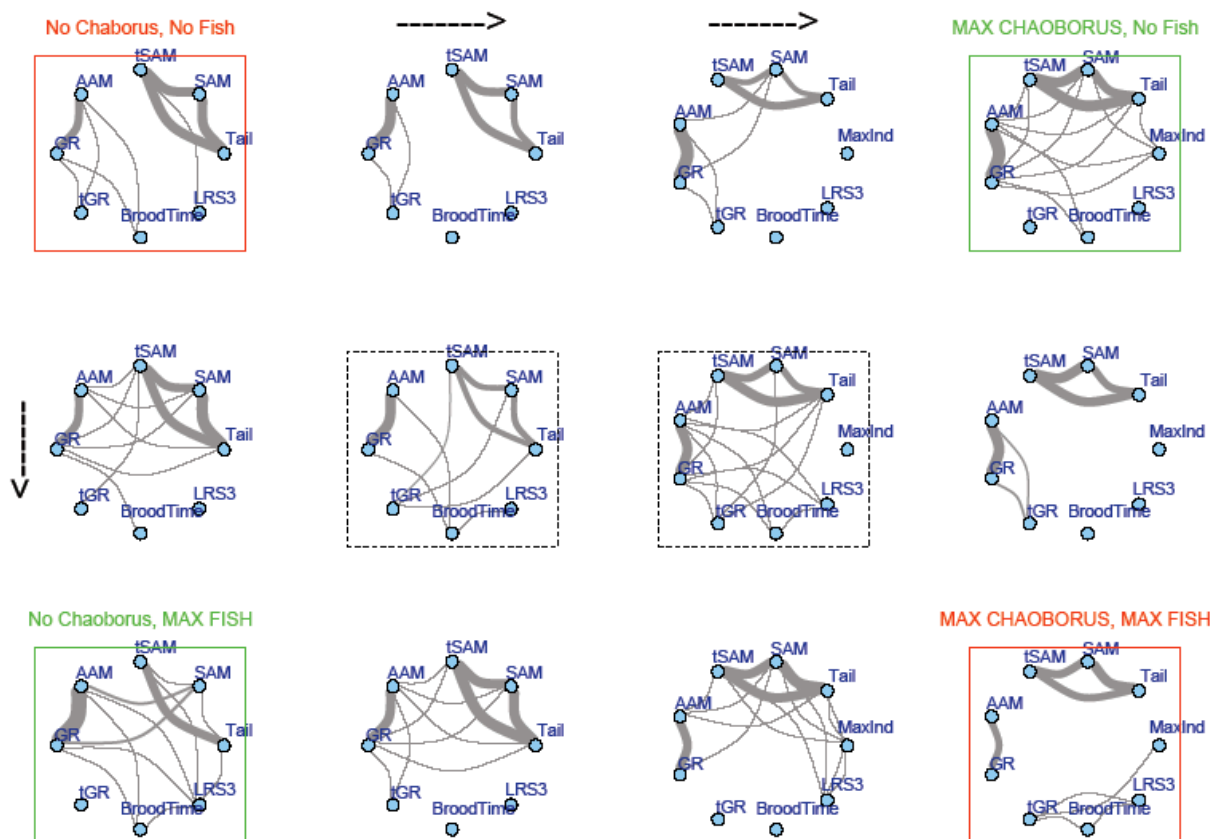


Figure 1. Partial correlations of 8 traits in *Daphnia pulex* across a gradient of *Chaoborus* (No Chaoborus to MAX CHAOBORUS) and predatory fish (No Fish to Max Fish) densities.

Results show that the solitary presence of either predatory fish or *Chaoborus* increased integration measured as the overall number of partial correlations (Fig. 1). In absence of any predator, two independent character modules exist with traits being able to change independently across modules, however, dependent changes occurring within modules. The increase of threat of predation by density predatory fish and *Chaoborus* let vanish these modules and resulted in an overall higher integration (increase in number of partial correlations). This indicates that the presence of single predator types increase levels of trait integration enabling prey to react to the threat of predation in a combined multiple trait manner. However, the simultaneous presence of both predators differing in size-selectivity does not increase the level of integration but lead to new trait modules (Fig. 1). The presence of two predators with opposing selective direction (predatory fish selecting for small and *Chaoborus* selecting for large individuals) let daphnids decrease the level of integration and form new character modules. This provides evidence that the threat of multiple predators is not a sum of the reactions to each predator but rather a product of specific environmental combinations by e.g. predators.

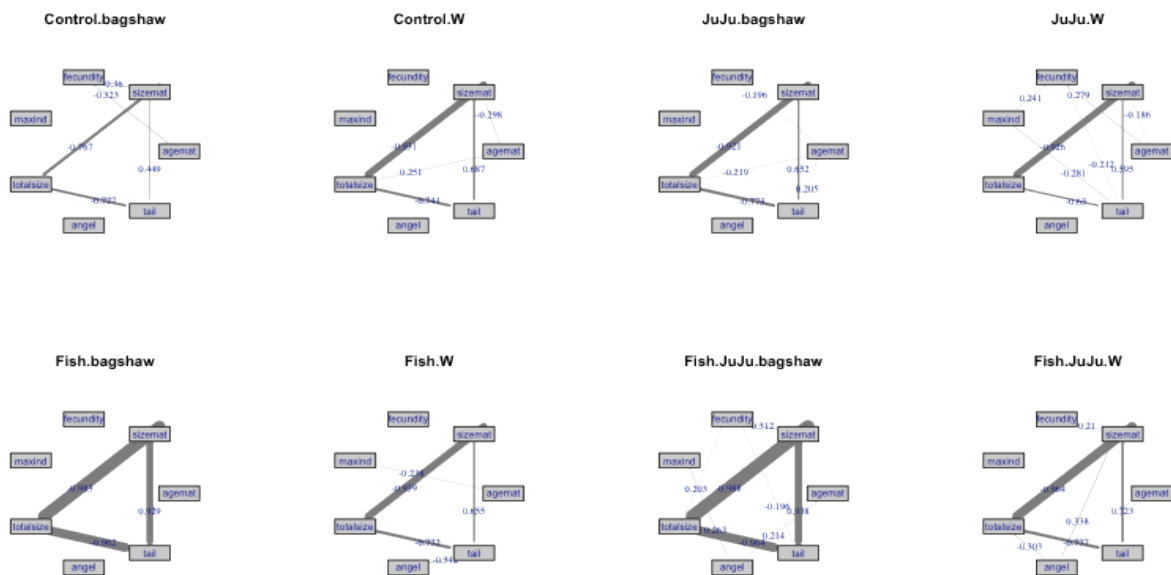


Figure 2. Partial correlations across 7 traits of *Daphnia pulex* clones from two different populations („Bagshaw“ and „W“) in the presence of *Chaoborus* (JuJu) and/or predatory fish (Fish).

However, pattern of trait integration towards multiple predators differed across populations (Fig. 2). Whereas daphnids from population W increase trait integration in the presence of *Chaoborus*, daphnids from population Bagshaw showed no such response. However, both populations again do not increase integration towards a combined threat of predators. Since both population differ in their selective regime, with Bagshaw being dominated by predatory fish and W by *Chaoborus*, pattern of trait integration do not only dependent on the current selective regime but reflect long term selective trends.

The use of “integration” as a tool to examine the phenotypic plasticity is useful and intriguing as it provides substantial evolutionary insight into the network of life history and morphological traits that make a responsive phenotype. Beyond the basic evolutionary insight, such detail provides further understanding about trait mediated effects – a central theme in community ecology and population dynamics. Usually, single trait changes are studied to understand changes in species composition within communities. However, our approach suggests that this may only explain small parts of the overall variation. Since prey alter several different traits in response to different predators with distinct pattern of character integration across a gradient of predators, our approach will be valuable in the context of ecology, resource management and evolutionary biology.