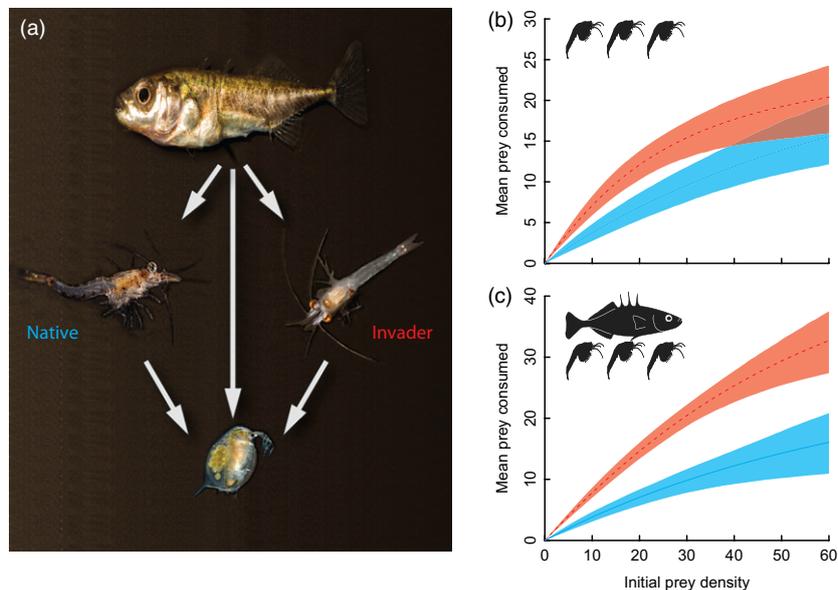


IN FOCUS

Integrating comparative functional response experiments into global change research



(a) Direct feeding interactions between a higher predator (the three-spined stickleback, *Gasterosteus aculeatus*), intermediate consumers (native *Mysis salemaai* and invasive *Hemimysis anomala* mysids), and a basal prey (the cladoceran, *Daphnia magna*). Photo credits: *G. aculeatus* and *H. anomala* by Stephen Potts, *M. salemaai* and *D. magna* obtained from Wikimedia Commons; (b) functional response of three native mysids (in blue) and three invasive mysids (in red); (c) functional response of three native mysids and one stickleback (in blue) and three invasive mysids and one stickleback (in red). Shaded areas are bootstrapped 95% confidence intervals. Adapted from Barrios-O'Neill *et al.* (2014).

In Focus: Barrios-O'Neill, D., Dick, J.T.A., Emmerson, M.C., Ricciardi, A., MacIsaac, H.J., Alexander, M.E. & Bovy, H.C. (2014) Fortune favours the bold: a higher predator reduces the impact of a native but not an invasive intermediate predator. *Journal of Animal Ecology*, **83**, 693–701.

There is a growing appreciation for the importance of non-consumptive effects in predator–prey interaction research, which can often outweigh the importance of direct feeding. Barrios-O'Neill *et al.* (2014) report a novel method to characterize such effects by comparing the functional response of native and introduced intermediate consumers in the presence and absence of a higher predator. The invader exhibited stronger direct feeding and was also more resistant to intimidation by the higher predator. This experimental framework may be incorporated into mainstream global change research, for example, to quantify the importance of non-consumptive effects for the success or failure of biological invasions.

The last 10 years of ecological research have seen incremental integration of multispecies interaction studies with other previously disparate fields (Ives, Cardinale & Snyder 2005; Johnson & Stinchcombe 2007). It is increasingly recognized that studying responses of species in isolation or

within single or two trophic level systems cannot adequately capture the complexity of the interactions found in nature. Multi-species systems are replete with non-trophic interactions (e.g. intimidation, competition, facilitation), whose effects are often stronger than their trophic counterparts (Schmitz, Krivan & Ovadia 2004; Preisser, Bolnick & Benard 2005), leading to calls for greater consideration of non-feeding interactions in the study of

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natural systems (Kefi *et al.* 2012). Indeed, the impacts of global change drivers cannot be predicted by examining direct effects on individual species when interactions strongly influence how those drivers alter individual fitness, geographic ranges and the structure and dynamics of communities (Gilman *et al.* 2010). This is particularly relevant to invasive species research, where competition, parasitism and habitat alteration abound (Levin *et al.* 2002), yet impacts of invaders are typically limited to species diversity and abundance metrics, rather than quantifying the altered interactions that underlie the observed changes. Only by investigating the strength of trophic and non-trophic interactions between native and introduced species, can the true impacts of biological invasions on food web structure and ecosystem functioning be understood (Salvaterra *et al.* 2013).

In the current issue, Barrios-O’Neill *et al.* (2014) present a novel method for quantifying and predicting the strength of consumption exerted by native and invasive consumers and their susceptibility to higher trophic level predators. They employ a comparative functional response framework to estimate attack rates and handling times of consumers in isolation, in combination with conspecifics, and in the presence of higher predators. They show that the functional response of both native and invasive mysid crustaceans in the presence of conspecifics is highly predictable based on experiments carried out in isolation due to the additive nature of the interaction. The invader exhibits much greater top-down control of the cladoceran prey which, coupled with its faster reproductive rate, suggests it may be a far more efficient exploiter of resources, leading to possible competitive exclusion of the native species within the wider community (notwithstanding other possible drivers of displacement in nature, e.g. behavioural effects, disease). This scenario is compounded by the greater susceptibility of the native mysid to the presence of a higher stickleback predator: here, its consumptive pressure on the basal prey is much lower than would be predicted from individual experiments, while the invasive mysid continues to express additive consumption of the prey. Importantly, both mysid species are equally susceptible to direct predation by the stickleback, indicating that the loss of performance in the native species is due to a non-trophic interaction, that is, intimidation in the presence of the higher predator prevents it from feeding as efficiently.

These findings are important because they clearly demonstrate two mechanisms through which introduced species may cause a decline in native abundance (and potentially diversity) at multiple trophic levels: superior foraging and enhanced resistance to predatory cues. There is an emerging consensus for a higher functional response in invasive predators that out-compete their native counterparts in natural communities (Bollache *et al.* 2008; Haddaway *et al.* 2012; Dick *et al.* 2013). With further research into this promising avenue, there is potential to adopt the comparative functional response framework as

a tool for identifying potentially damaging invaders and taking pre-emptive steps to limit their impacts (Dick *et al.* 2013). In predator–prey combinations where consumptive pressure proves additive, they may also be a useful predictive tool for determining potential impacts of established invaders (Barrios-O’Neill *et al.* 2014). Concordantly, recent advancements in functional response research could be incorporated within this framework to increase its predictability. Given the universal temperature and body mass dependency of functional response parameters (Rall *et al.* 2012), these fundamental characteristics of the environment and the biotic interaction, respectively, which are inherently linked to metabolic rate (Brown *et al.* 2004), should be considered in future comparative studies. There is also a growing appreciation that static descriptions of functional response curves may be inappropriate given the observed shift from type-II to type-III response with increasing predator–prey body mass ratio (Vucic-Pestic *et al.* 2010). Generalized allometric functional response models have recently been proposed to take account of this body mass dependency (Kalinkat *et al.* 2013) and may improve the reliability of parameter estimates. There are also numerous alternative models to the simple Holling type-II functional response that incorporate predator interference and thus might be more appropriate in studies involving multiple predators (Skalski & Gilliam 2001). This would be especially feasible in studies exhibiting replacement of consumed prey, as performed by Barrios-O’Neill *et al.* (2014), but the approach has also recently been demonstrated in experiments with prey depletion (Lang, Rall & Brose 2012; Delong & Vasseur 2013). Similarly, studies comprising multiple prey species should take account of the reduced amount of time available for encountering either of the prey (Sentis, Hemptinne & Brodeur 2013). Such considerations would improve the quantitative and predictive nature of model fitting in functional response studies (DeLong, Hanley & Vasseur 2014).

While there is a large body of research on the importance of predator avoidance and other non-consumptive interactions for determining community structure and the prevalence of trophic cascades (Werner & Peacor 2003; Schmitz, Krivan & Ovidia 2004; Preisser, Bolnick & Benard 2005; O’Gorman, Enright & Emmerson 2008; Zhao *et al.* 2013), this mechanism has rarely been studied in relation to biological invasions. Peacor & Werner (1997) demonstrated that predatory cues can facilitate lower trophic level invasions due to decreased resource suppression by intermediate predators. Invasive crabs also elicit strong behavioural effects in intermediate predators on rocky shores, forcing them to feed less on basal prey by spending more time hiding in refugia (Trussell, Ewan-chuk & Matassa 2006). Some invasive amphipods that exhibit greater predator avoidance relative to native species enhance their survival chances when both are exposed to direct predation pressure from fish (Pennuto & Kepler 2008). Barrios-O’Neill *et al.* (2014) demonstrate an

interesting counterpoint to the latter mechanism, that is, if introduced intermediate consumers spend less time than natives avoiding predators without any additional negative effects of predation pressure, they are at a competitive advantage by spending more time feeding on prey. Clearly, non-consumptive interactions have a critical role to play in the success or failure of biological invasions, with important implications for conservation programmes, demanding more thorough investigation of their strength and ubiquity in nature.

Through innovative experimental design, such as that presented by Barrios-O'Neill *et al.* (2014), both consumptive and non-consumptive effects of interacting species may be enumerated. By coupling these comparative functional response experiments with quantitative descriptions of food webs (Ledger *et al.* 2013), the direct and indirect pathways of energy flow through an ecosystem may be characterized. Comparisons in the presence and absence of introduced species (or other anthropogenic or environmental stressors) will help to elucidate disruptions to the structure and functioning of ecological networks, as well as the altered interactions that cause them. This may be achieved through either before/after and control/impact comparisons of real ecosystems, or experimental manipulation within outdoor mesocosms. Theoretical models based on foraging traits such as attack rates and handling times (Petchey *et al.* 2008) may provide a framework to predict anomalies in the structural properties of invaded ecosystems. Integrating these laboratory, field and modelling approaches will maximize our capacity to understand, predict and resolve the impacts of not only biological invasions, but indeed any of the major global change drivers (e.g. warming, CO₂ enrichment) that we face in our rapidly changing world.

Acknowledgements

Supported by NERC grant NE/I009280/1 and the Grand Challenges in Ecosystems and the Environment initiative at Imperial College London.

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Received 13 January 2014; accepted 12 February 2014

Handling Editor: Graeme Hays