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Functional responses can't unify invasion ecology

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Abstract Dick et al. (Biol Invasions, 2017) propose that the comparative functional response framework provides a unifying approach for the study of invasive species. We agree that functional responses are an important and powerful quantitative description of consumer effects on resources, and co-opting classical ecological theory to better predict invasive species impacts is a laudable move for invasion biology. However, we fear that the early successes of select examples of the comparative functional response (CFR) approach has led Dick et al. to exaggerate the generality of its utility, and about its ability to unify the field. Further, they fail to provide a convincing argument why CFR is better than existing tools such as invasion history or impact indices, even when considering emerging or potential invaders. In this response we provide details of three conceptual issues stemming from classical ecological theoretical

frameworks and two practical problems that Dick et al. and other CFR proponents need to address.

Keywords Functional responses · Impact prediction · Impact indices · Resource–consumer · Prey–predator · Invasion hypotheses

A conceptual challenge for the application of CFR is that even in relatively simple food webs most consumers share resources with multiple other consumers (Fig. 1). Thus for any resource one could compare any randomly chosen pair of consumers with the result that one of them will always have the higher functional response. However, alone this difference in their functional responses provides little information about the relative importance and impacts of the two species on the shared resource, or on the structure and

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dynamics of their ecological community. This simple thought experiment reveals why the proposal by Dick et al. is flaccid in three ways stemming from classical ecological theoretical frameworks.

First, the goal of the comparative functional response (CFR) approach is to be able to use short-term experiments as a tool to gain insight into the longer term impacts of an invader on native communities. Dick et al. (2017) postulate that the impacts of invasive species can be predicted by comparing the functional response (FR) of a potential invader to that of a putatively similar native counterpart. However, it is unclear whether the assertion that species with higher functional responses have greater impacts on prey populations over longer time scales is at all grounded in theory. Resource–consumer dynamics as embodied in classic theory (e.g., Leibold 1996; Hastings 1998) rely on not only the FR but also on other parameters (e.g., conversion efficiency, background mortality, etc.) that the CFR approach has completely ignored. Yet these parameters could have effects rivaling or even neutralizing effects that arise from differences in the FRs of two consumers. Using classic ecological theory (Rosenzweig and MacArthur 1963), we can directly measure the impact of consumers on resources by determining the resource equilibrium abundance and show that increasing the height of the functional response by either increasing attack rates or decreasing handling time pushes a resource to lower equilibrium abundances, which supports the basic arguments of the CFR approach. However, this argument assumes that consumers have the same conversion efficiency and background mortality, and that changing these parameters has equal or larger influences on resource equilibrium abundance.

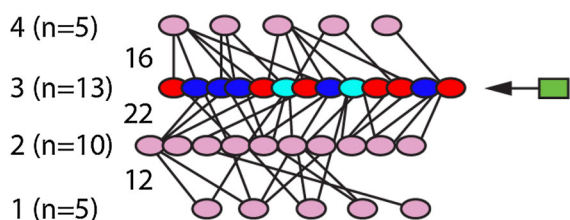


Fig. 1 In this food-web (Arizona montane forest adapted from McDonald-Madden et al. 2016) with four trophic levels, a putative invading generalist predator (*green square* trophic level 3) would need pairwise comparisons with 22 connections to the ten trophic resources at level 2. Predators at level three have either 1 (*red*), two (*blue*) or three (*cyan*) prey connections

Thus, even in this greatly simplified scenario, the fundamental tenet of the CFR approach would only hold under cases where conversion efficiency and background mortality of the invader and native were the same or very similar. Given that invasive species are often released from their natural enemies and that conversion efficiency can vary even among even closely related taxa (e.g., Fenton et al. 2010) we think that the assumptions around this argument of CFR are rarely true. Indeed, looking at these other parameters may provide insights for the cases where predictions of CFR have not been supported (e.g., Guo et al. 2016).

Second, while one species will always have the highest FR, one cannot infer the impact of that species without considering the complex network of interactions within which the two chosen species exist (Smith-Ramesh et al. 2016; McDonald-Madden et al. 2016; Fig. 1). This is because the functional response is not a trait of a consumer *per se*, but instead is a measure of the interaction strength between a consumer and a specific resource in a particular environment. Dick et al. assert that the FR is an inherent characteristic of a species, but even for a particular pairwise consumer–resource interaction the FR depends on circumstances like consumer size (McCoy and Bolker 2008), consumer density (predator interference; Rall et al. 2008), resource size (McCoy et al. 2011), morphology (Altwegg et al. 2006), presence of parasites (Haddaway et al. 2012) and other resources/consumers/predators (Kratina et al. 2007). The CFR only holds if these modifying effects cannot change the rank order of the FR between the species being compared. Indeed, most invasive species are generalists (McKinney and Lockwood 1999) and so making inferences about impacts from the interaction strength between a single consumer and resource combination is rarely justified.

Dick et al. also propose that FRs provide a means to identify context dependence and improve predictive power in invasion biology, but it is not clear how this will be accomplished. Context dependence typically refers to unpredictable changes in the interaction strength between species that emerge as a result of changes in the phenotype of the interacting species or in response to a third species (i.e., interference). For example, the FR (or the parameters) might change when the native and invading species are (possibly temporarily) coexisting, due to interference (e.g., the Beddington–DeAngelis FR) or other indirect or

emergent processes. While there is nothing inherent in CFR that permits us to quantify such context-dependence, it may be possible to incorporate some additional complexities into FRs (McCoy et al. 2011), and to incorporate emergent dynamics over time (Okuyama and Bolker 2012); but doing so requires such considerable experimental effort and quantitative expertise that it further questions the practicality of the CFR approach as a general tool.

The third challenge for the CFR approach is that neither the invasive nor the comparator species is chosen randomly and so there is no appropriate null model or null expectation for making inferences about effects of invasive consumers. Dick et al. cite a number of studies where a successful invader showed a higher maximum FR than the native species it was compared to a posteriori. However, it is not clear how well this would work to determine impact a priori. Since in a two-species comparison one species always has a higher FR, we would expect the putative invasive species to have a higher FR half of the time just by chance, even if there is actually no difference between the two species, leading to a false positive rate that seems to make the method hardly useful in practice. Also, the functional response only describes resource uptake rates of a given consumer, while ecological theory about community invasibility and coexistence are predicated on the ability of the invader to increase in abundance when rare, and/or when resources are scarce (conversely, CFR only considers maximum intake rate at high resource abundance). Lastly, the FR only provides information about the invasive species and not about the ecosystem being invaded, which can strongly influence the potential success and impacts of the invader (Elton 1958; Levine et al. 2004; Hui et al. 2016; Smith-Ramesh et al. 2016; McDonald-Madden et al. 2016).

Dick et al. fail to make a convincing case that CFR is a practical tool to predict emerging or potential invaders. Aside from the ecological principles (provided above), they ignore the simple exponential increase in the number of comparisons of equivalent taxa that are needed as all potential invaders are tested (Fig. 1). Moreover, nothing is proposed for situations when no equivalent local taxon exists to compare to a potential invader, which is common on islands (e.g., the Brown Tree Snake *Boiga irregularis* on Guam) and not uncommon in continental systems (e.g., the Burmese python *Python bivittatus* in Florida or the

coypu *Myocastor coypus* in Europe). Finally, Dick et al. propose to start characterizing FRs for invasive species identified by national and international regulatory agencies. Paradoxically, all lists of which we are aware consist of species with known impacts based on their invasion history (Kulhanek et al. 2011), which were already rejected by Dick et al. as lacking predictive power. Despite, the failure of invasion biologists to find unifying principles to predict impact in alien species, invasive species' histories do act as an excellent proxy to assess their impact in other climate matched areas (e.g., van Wilgen et al. 2009). Using impact indices (e.g., Blackburn et al. 2014) may not be bulletproof, but is likely to provide a far more practical way for invasion biologists to inform regulatory authorities about high impact invasive species.

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