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Functional responses can unify invasion ecology

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Abstract We contend that invasion ecology requires a universal, measurable trait of species and their interactions with resources that predicts key elements of invasibility and ecological impact; here, we advocate that functional responses can help achieve this across taxonomic and trophic groups, among habitats and contexts, and can hence help unify disparate research interests in invasion ecology.

Keywords Functional responses · Resource use · Impact prediction · Predator–prey · Invasion hypotheses · Species-traits · Biological control · Context-dependency · Risk assessment

Invasion ecology is fragmented and lacks truly unifying principles across taxonomic and trophic groups, with many widely cited invasion hypotheses

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biased towards plants or animals in their development and testing (Catford et al. 2009; Jeschke et al. 2012). Further dis-unity is evidenced with respect to habitats; for example, freshwater and marine invasions conferences consistently fail to amalgamate (e.g. ICAIS versus Marine Bioinvasions) and responsibility for introduced species is often delegated according to a freshwater/marine/terrestrial divide (e.g. in France). Propagule pressure has been suggested as a unifying concept to understand general patterns of invasion success and impact (Ricciardi et al. 2011), but lacks predictive power to explain much of the context-dependent variation that currently impedes risk assessments of invader ecological impacts. Also, whilst the invasion history of a species can help predict its impacts in new locations (Kulhanek et al. 2011; Kumschick et al. 2015), this is of no use for emerging or potential invaders, and again suffers from myriad context-dependencies (Ricciardi et al. 2013). Further, whilst explored extensively, no single species trait, or combination of traits, has thus far provided excellent explanatory or predictive power with respect to the invasiveness and ecological impacts of introduced species (Ricciardi et al. 2013; Dick et al. 2014).

This lack of unity is also manifested in disparity in the language, definitions, concepts and statistical approaches used by invasion ecologists. In particular,

animal ecologists use the “functional response” concept (resource use in relation to resource availability) with analyses based on Holling’s disc and Rogers’ random predator equations (e.g. Alexander et al. 2014), whereas plant ecologists generally use Michaelis–Menten kinetics and talk of resource “uptake curves” (e.g. Rossiter-Rachor et al. 2009), “resource use efficiency” (RUE; Funk and Vitousek 2007) and “nutrient responses” (e.g. King and Wilson 2006). In addition, the Fluctuating Resource Availability hypothesis of plant community invasibility (Davis et al. 2000) has parallels with functional responses, as both relate resource uptake to resource supply in determining invasion risk. Further, whilst animal ecologists use functional responses in terms of impact on resource populations (usually prey), the “functional resource utilization response” as used by Tilman et al. (1977) explicitly brings resource use rates, at least in plants, into the realms of interspecific competition (see also below). Both plant and animal invasion ecologists are therefore working on the same principle, that of resource uptake and its predictive capacity for many aspects of invasions. Indeed, resource uptake rate—whether predator/prey, herbivore/plant, plant/nutrient, or in fact any organism/resource interaction—is truly fundamental to all species (see also Real 1977). We thus propose that functional responses (and their namesake variants) have the potential to unify invasion ecology across taxa, trophic levels and habitats as a measurable species trait and resource interaction with significant predictive capacity. This could clearly extend to the majority of hypotheses in invasion ecology, as resource use is a central mechanism in 28 of 29 hypotheses listed by Catford et al. (2009) to explain invasion success, and resource use also features in several hypotheses listed by Ricciardi et al. (2013) to explain spatio-temporal variation in ecological impact.

Comparative functional responses, whereby the relationship between resource availability and resource uptake rate is derived and compared among species (Dick et al. 2014), have thus far consistently revealed that high ecological impact invaders have higher maximum feeding/consumption rates than trophically analogous natives—whether animal (predator or herbivore), plant, vertebrate or invertebrate, aquatic or terrestrial (Fig. 1). This is also often accompanied by higher attack rates (classically curve

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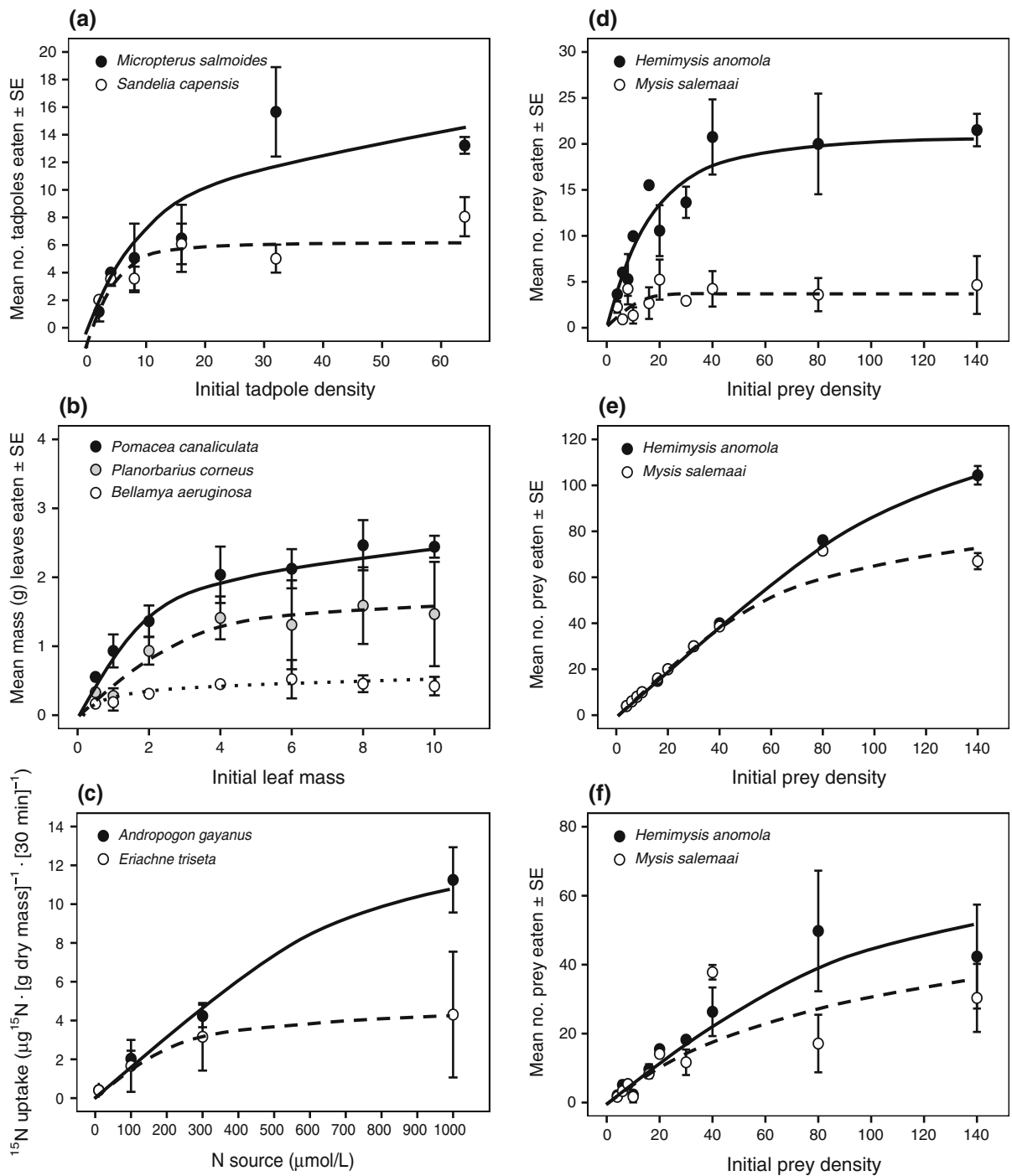


Fig. 1 Functional responses of ecologically damaging invaders have higher asymptotes compared to those of native analogues, across taxa, trophic groups and habitats: invasive/native comparisons are **a** Largemouth bass/Cape Kurper; **b** Golden apple snail/Chinese snail (*middle curve* is emerging invader, the greater ramshorn snail); **c** gamba grass/Australian grass; **d**–

f bloody red shrimp/opossum shrimp. In this latter example, the degree of difference in invader/native functional responses correlates with degree of actual field impact of invader on cladocerans (high impact; **d**, **e**) and copepods (low impact; **f**). Redrawn from Alexander et al. (2014), Xu et al. (2016), Rossiter-Rachor et al. (2009) and Dick et al. (2013)

parameter “a”) and differences in curve shape, generally variants of Type II and III functional responses, which have implications for resource population stability (see Dick et al. 2014). We therefore propose that functional responses, and their equivalents in terms of, for example, nutrient uptake curves, are inherently measurable species traits of invaders and natives, and their interactions with resources, that can truly unify the drive to increase explanatory and predictive power in invasion ecology. For example, while most invader/native functional response comparisons to date have examined predator–prey systems (e.g. Dick et al. 2013), there are emerging studies involving herbivore–plant (Xu et al. 2016) and plant–nutrient interactions (see Rossiter-Rachor et al. 2009). The latter study, by using completely different terminologies, led to the existence of essentially similar thinking by animal and plant invasion scientists—who, thus far, have had little collaborative interaction or consideration of each other’s research.

Functional responses can be viewed partially as inherent characteristics of species with the strength and shape of interactions modified by the various resources in question and extrinsic context-dependencies. Although abiotic and biotic context-dependencies have been a major challenge to ecological impact prediction in invasion ecology (Ricciardi et al. 2013; Kumschick et al. 2015), we contend that functional responses can go a long way to mitigate this problem. By explicitly incorporating relevant context-dependencies into functional response study designs and hypothesis testing, both explanatory and predictive power are enhanced (Dick et al. 2010; Paterson et al. 2015; Barrios-O’Neill et al. 2016); for example, functional responses of invasive meso-predators may be affected by the presence of higher predators (Barrios-O’Neill et al. 2014) and impact predictions from such studies can be made even with regards to the complex world of real communities. Similarly, consideration of changes or differences in the physical environment, such as habitat complexity and water chemistry, can allow impact prediction, owing to shifts in the shape and magnitude of functional responses under such context-dependencies (e.g. Alexander et al. 2015; Iacarella and Ricciardi 2015; Laverty et al. 2015). Whilst not all potential contexts and their interactions can be captured in such studies, those identified as the most relevant can be, and this

approach has facilitated the development of general ecological impact models with functional responses at their core (e.g. Iacarella et al. 2015).

We have encountered a number of confusions, misunderstandings and questions with respect to what comparative functional responses can actually do for invasion ecology. For example, we do not explicitly relate functional responses to resource competition between the invader and native trophic comparator. This is because displacement of a native by an invader may be driven by interactions other than competition; for example, while the invasive amphipod *Gammarus pulex* has higher functional responses towards shared prey than the native *G. duebeni celticus* which is displaced (Laverty et al. 2015), it is intraguild predation rather than competition that drives this replacement process (Dick 2008). The higher functional responses of the invader correlates with its impact on the broader ecological community, which might invoke interspecific competition, but this is not explicit in the functional response studies to date. Nevertheless, we foresee incorporation of functional responses into competition theory and experimentation, since resource consumption is central to both concepts. Indeed, there is some dis-unity with respect to animal and plant studies of competition, evident when considering that Tilman (1977), for example, explicitly utilised resource uptake rates in plant competition studies, yet this use of functional responses is missing from animal competition studies. Further, incorporating the results from functional response experiments into models of the functional niche (Leibold 1995) of a potential invader might allow for a more mechanistic prediction of the likely impacts of such species.

In addition, while comparative functional responses may be directly related to impacts on the resources in question (e.g. prey species impacted in a predator–prey system), the impacts of the invader may be diverse and not only on the resource itself; for example, invasive gamba grass (*Andropogon gayanus*) impacts communities through changes in fire regimes, but its identification as a successful invader with high-impact could still be predicted by its higher functional response (see Fig. 1c). This raises the further issue as to what stages of invasion (see Blackburn et al. 2011) could be better understood by functional response studies. We suggest that functional responses could shed light on which species

(with feeding stages) can survive transportation (e.g. in ballast water tanks) and become established in new locations—where resources might be in short supply or already being utilised by existing native species. Similarly, invader establishment and spread may be facilitated by resource use patterns, again measurable by functional response studies, and species invasiveness as distinct from ecological impact (see Ricciardi and Cohen 2007) may also be correlated with functional responses (see Bovy et al. 2015; Xu et al. 2016). One aspect that might considerably improve the use of functional responses in such contexts would be incorporation of abundance, as per Parker et al. (1999), which is essentially the numerical response that, together with the functional response, gives the total response (or total uptake rate; see Dick et al. 2014). Finally, studies relating functional responses to actual field impacts show great promise in explanatory and predictive power (Dick et al. 2013) and thus we believe that they will guide further development of invasion theory, such as the mechanistic bases for ecological impact, and the roles of prey naiveté, eco-evolutionary experience and history in invasion ecology (Saul and Jeschke 2015).

Risk assessment of invasion threats would naturally consider probabilities and degrees of establishment and impact, both of which could be elucidated by functional responses (Dick et al. 2013, 2014). We advocate that current and emerging invaders of concern, such as those identified by national and international regulatory agencies (e.g. new EU Regulation 1143/2014) be tested for functional responses in a standardized way, analogous to tests of target specificity and efficacy of biological control agents (see Fernández-Arhex and Corley 2003; Finlay-Doney and Walter 2012). Indeed, the biological control community has essentially been asking the same question as invasion ecologists for many decades (and indeed using functional and numerical responses) of what are technically beneficial introduced species based on their predicted impact when released into the environment.

With facilities already existing around the world, such as individual university research laboratories and dedicated biological control research facilities (e.g. CABI), the routine functional response testing of introduced species (current, emerging and potential future), across all taxa, trophic groups and habitats, is surely feasible. This has the potential to not only unite

invasion ecology, but provide a truly predictive science with greater real-world applicability.

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