Advancing impact prediction and hypothesis testing in invasion ecology using a comparative functional response approach

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Abstract Invasion ecology urgently requires predictive methodologies that can forecast the ecological impacts of existing, emerging and potential invasive species. We argue that many ecologically damaging invaders are characterised by their more efficient use of resources. Consequently, comparison of the classical 'functional response' (relationship between resource use and availability) between invasive and trophically analogous native species may allow prediction of invader ecological impact. We review the utility of species trait comparisons and the history and context of the use of functional responses in invasion ecology, then present our framework for the use of comparative functional responses. We show that functional response analyses, by describing the resource use of species over a range of resource availabilities, avoids many pitfalls of 'snapshot' assessments of resource use. Our framework demonstrates how comparisons of invader and native functional responses, within and between Type II and III functional responses, allow testing of the likely population-level outcomes of invasions for affected species. Furthermore, we describe how recent studies support the predictive capacity of this method; for example, the invasive 'bloody red shrimp' *Hemimysis anomala* shows higher Type II functional responses than native mysids and this corroborates, and could

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have predicted, actual invader impacts in the field. The comparative functional response method can also be used to examine differences in the impact of two or more invaders, two or more populations of the same invader, and the abiotic (e.g. temperature) and biotic (e.g. parasitism) context-dependencies of invader impacts. Our framework may also address the previous lack of rigour in testing major hypotheses in invasion ecology, such as the 'enemy release' and 'biotic resistance' hypotheses, as our approach explicitly considers demographic consequences for impacted resources, such as native and invasive prey species. We also identify potential challenges in the application of comparative functional responses in invasion ecology. These include incorporation of numerical responses, multiple predator effects and trait-mediated indirect interactions, replacement versus non-replacement study designs and the inclusion of functional responses in risk assessment frameworks. In future, the generation of sufficient case studies for a meta-analysis could test the overall hypothesis that comparative functional responses can indeed predict invasive species impacts.

Introduction

Invasion biology faces two major challenges with respect to increasing our ability to forecast the ecological impacts of invasive species. Firstly, the discipline needs to move beyond describing and cataloguing case studies of impact towards the development of a mechanistic understanding of impact that would allow for more predictive power, and this in the context of global change (Walther et al. 2009; Dick et al. 2013; Simberloff et al. 2013). Secondly, robust tests of major hypotheses in invasion ecology are often lacking, as evidenced by equivocal support for many such hypotheses (e.g. Catford et al. 2009; Davis 2011;

Jeschke et al. 2012; Ricciardi et al. 2013). This may, in part, be due to a lack of rigour in defining these hypotheses (Heger et al. 2013) and lack of focus on demographic processes. These two major challenges need to be simultaneously addressed to advance the fundamental science of invasion ecology and to provide practical methodologies that prioritize and mitigate invasion threats by, for example, refining risk assessment protocols (Ricciardi and Rasmussen 1998; Parker et al. 1999; Byers et al. 2002; Andersen et al. 2004; Kumschick et al. 2012; Leung et al. 2012) and managing biological communities to provide maximum biotic resistance (Taylor and Duggan 2012).

There have been several attempts to develop frameworks for conceptualizing the mechanisms whereby invasive species cause ecological impacts, with a common theme being how invaders alter communities and ecosystems through resource use (Vitousek 1990; Chapin et al. 1996; Parker et al. 1999). In particular, Parker et al. (1999) opined the need for 'operational generalizations' about impact and stressed the difficulty of assessing the *per capita* effects of invaders. Not all invaders have a major impact because of their *per capita* effects; for example, many invasive plants, through their great abundance or biomass, affect fire regimes (Brooks et al. 2004). Nonetheless, many invaders do generate impacts directly because of *per capita* effects, and a major obstacle to testing impact theories is the lack of standardized methods for determining such effects on use of resources, such as native prey (Ricciardi et al. 2013). Furthermore, we require methods that can reliably explain the ecological impacts of existing invaders, and predict impacts of emerging and future invaders under different or changing environmental circumstances; understanding the corollary, patterns of resistance of natives towards invaders, would also be welcome. Ideally, such methods should be rapid, reliable, inexpensive and applicable across taxonomic and trophic groups, with data collection possible from a variety of laboratory and field-based studies, as appropriate to the organisms and systems involved.

Here, we review and provide a framework for a promising emerging field in invasion ecology that can address these issues: the use of comparative functional responses, whereby the relationship between resource consumption rate (e.g. by a predator) and resource density (e.g. prey) is compared between invader and native species to reveal ecological impact (e.g. see

Dick et al. 2013; Fig. 1a–d). Specifically, we: (1) examine species trait comparisons in invasion ecology and explore advantages of the functional response method in this context; (2) review the historical use of functional responses in invasion ecology and its major hypotheses; (3) introduce our comparative functional response framework and its advantages as a predictive tool in invasion ecology; and (4) outline future challenges of implementing this framework in predicting invader impacts and testing hypotheses, and identify research priorities.

Species traits comparisons and the utility of functional responses

Comparisons of species traits between invaders and natives (or unsuccessful/less successful invaders) have in some circumstances been successful in identifying broad determinants of invasiveness in terms of establishment and spread (e.g. Mack 1996; Remanjek and Richardson 1996; Sakai et al. 2001; van Kleunen et al. 2010), however, numerous exceptions to any derived rule dilute the predictive power of such techniques for any one known or potential invader. Trait-based predictions have had some success in predicting plant establishment, invasiveness and impact (e.g. Pyšek et al. 2009; but see Palacio-Lopez and Gianoli 2011), but the distribution of success of such trait comparisons is patchy among animal taxa (Hayes and Barry 2008), with some good predictors of invasion success for birds (Sol et al. 2002; Blackburn et al. 2009), fishes (Marchetti et al. 2004a, b) and mammals (Jeschke and Strayer 2006), often based on propagule pressure and human affiliation. However, consistent predictors of invasion success across animal and plant taxa remain elusive (Hayes and Barry 2008). There has been even less progress in the prediction of the ecological impacts of invaders (Branch and Steffani 2004; Ricciardi et al. 2013; but see Nentwig et al. 2009; Kumschick et al. 2013), with invasion history emerging as a useful but restricted indicator of likely future impact (Kulhanek et al. 2011; Kumschick and Richardson 2013), especially since the method only applies to known invaders with sufficient existing studies of impact. However, we require forecasting methods that can be applied to new and emerging invaders, for
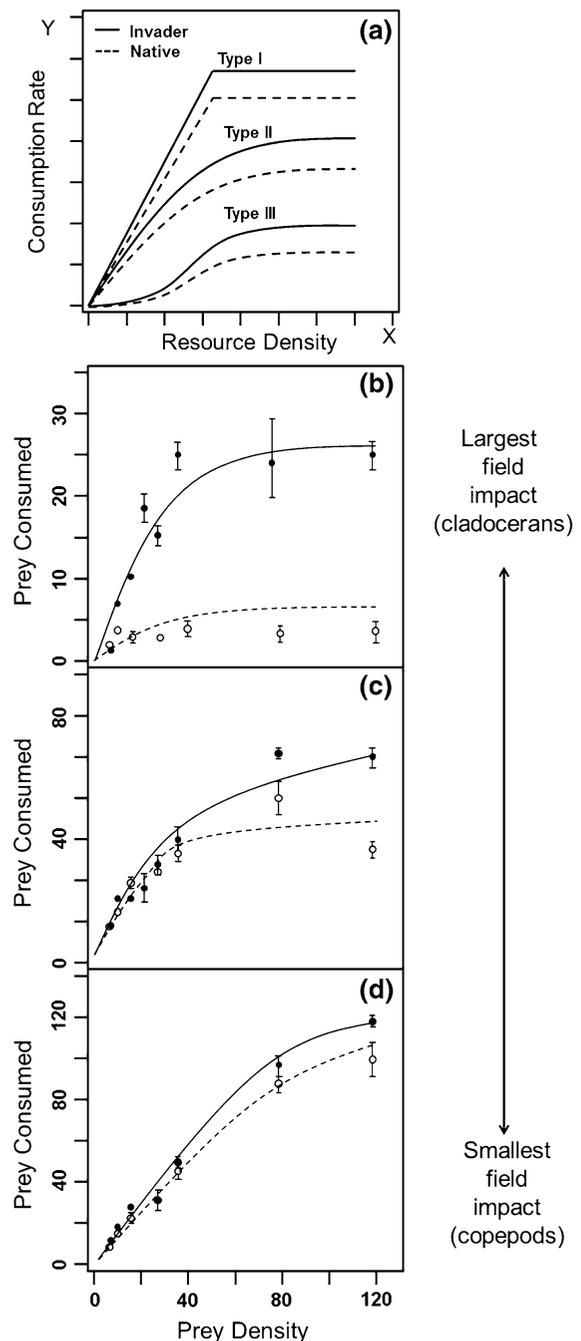
Fig. 1 **a** Functional response types and hypothetical invader/native comparisons; **b–d** Differences in functional responses between an invasive mysid shrimp (*Hemimysis anomala*, *closed circles*, *solid line*) and a native comparator (*Mysis salemaai*, *open circles*, *dashed line*) explains and predicts known field impacts of the invader on zooplankton prey species (redrawn from Dick et al. 2013)

example, where a new species has just arrived or is known to be spreading, or indeed potential new invasive species from known donor region 'hotspots' such as the Ponto-Caspian region (Ricciardi and MacIsaac 2000).

Invasive species are characteristically more able to rapidly and efficiently utilise resources than native species (Vitousek 1990; Strayer et al. 1999; Byers et al. 2002; Funk and Vitousek 2007; Johnson et al. 2008; Weis 2010; Morrison and Hay 2011; Chapple et al. 2012) and thus resources, such as native prey species, are vulnerable to potentially severe declines or extinctions (Clavero and Garcia-Berthou 2005; Snyder and Evans 2006; Salo et al. 2007; Cucherousset and Olden 2011; Roy et al. 2012). Indeed, difference in resource use is a major tenet of 28 of 29 invasion hypotheses identified by Catford et al. (2009). It follows that comparing resource utilisation rates and patterns among known invaders and trophically analogous natives, and perhaps among emerging or new invaders and such natives, could allow more reliable predictions of invader impact. The relationship between resource availability and resource consumption rate is the 'functional response' (Solomon 1949; Holling 1959a, b; Juliano 2001), which usually takes three forms (Fig. 1a), and can be derived for consumers and compared among them (e.g. Fig. 1b–d). Although the functional response is a standard measure utilized in classic behavioural, population and community ecology (e.g. Sabelis 1992; Soluk 1993; Barbeau et al. 1998; Jeschke et al. 2002; van Leeuwen et al. 2007), and also a familiar technique in assessing the potential and efficacy of biological control agents (O'Neil 1990; Van Drische and Bellows 2011; but see criticisms by Lester and Harmsen 2002), the uptake of functional responses in invasion biology has been very limited (see below). Indeed, despite the use of functional responses in testing the efficacy of biocontrol agents towards invasive species (e.g. Carrillo and Pena 2012), it has been employed surprisingly rarely by invasion ecologists who are essentially asking very similar questions about ecological impact. In general, it is reasonable to expect that the functional responses of invaders will determine their impact on resources, as the functional response quantifies the strength of primary ecological interactions (e.g. predator–prey). Further, if invaders show greater functional responses than natives, with which the affected native resources (e.g. prey species) have an

evolutionary history, then the difference in magnitude of invader/native functional responses may explain and predict invader impacts (as with Fig. 1b–d).

There are several advantages to deriving the functional responses of invasive species and comparing them with native species, or among invaders, as a measure of ecological impact. First, the method quantifies the rate of resource uptake and provides parameter estimates for the functional response curves (attack rate, handling time and maximum feeding rate) that describe the mechanisms driving their shape and magnitude (see, for example, Dick et al. 2013). Secondly, however, and perhaps most importantly, the shape and magnitude of the functional response can inform whether the consumer (e.g. introduced predator) will likely regulate, stabilise or de-stabilise the resource (e.g. prey) populations, with implications for population viability. Here, we use a predator–prey relationship to illustrate this point. In a sigmoidal, positive density-dependent Type III functional response (see Fig. 1a), although the predator may regulate the prey population, prey experience a low density refuge with a reduction in risk of mortality as prey densities fall below a threshold level, thus potentially imparting stability to predator–prey dynamics and facilitating prey persistence (Murdoch and Oaten 1975). This is in contrast to the potentially population de-stabilising, inversely density-dependent Type II functional response where most, if not all prey are consumed at low prey densities, potentially leading to prey extinction at a range of spatial and temporal scales (Hassell 1978; Taylor and Collie 2003; Ward et al. 2008; Rindone and Eggleston 2011). Further, counter to the traditional view, functional responses are not fixed for predator–prey species pairs, and functional responses can change from Type II to Type III or vice versa under different circumstances. For example, it is well established that functional responses may change under the influence of a number of environmental variables, such as temperature, light levels and habitat structure (Lipcius and Hines 1986; Eggleston 1990; Koski and Johnson 2002; Jeschke et al. 2004; Alexander et al. 2012, in press). Also, predators may have different functional response types with different prey species (e.g. Moustahfid et al. 2010). Thus, comparative functional response studies in invasion ecology may have a further predictive advantage in that relevant environmental contexts (e.g. global climate change), and differences in abiotic

factors such as temperature or salinity regime, can be incorporated into experiments to reveal differences in the type and/or magnitude of the functional response, and hence likely population outcomes for a variety of impacted native species (e.g. see Kestrup et al. 2011). Further, since factors such as parasitism of invaders/natives can be included in study designs, the methodology allows for the robust testing of other major hypotheses in invasion ecology, such as 'enemy release' (see Dick et al. 2010; Fig. 2 as discussed below).

A full assessment of the impact of a consumer on a resource, such as for predators and prey as discussed above, would include alongside the *functional response* an assessment of the *numerical response*, which can involve the demographic and/or aggregative response of the predator to prey density; this combination gives the *total response* (Solomon 1949; Holling 1959a, b). In practice, the functional response is relatively straightforward to derive, whereas empirical derivation of the demographic numerical response is more challenging, and might add little to the predictive power of functional responses if the latter prove overwhelmingly robust in explaining and predicting the ecological impacts of invasive species. Thus, whilst acknowledging the potential to include numerical responses in our framework, we make the case here for a focus on functional responses; however, we make some suggestions as to inclusion of numerical responses and their proxies in impact scoring in the "Challenges, future research and applications" section below.

History of functional responses in invasion ecology

We conducted a systematic search for the use of functional responses in invasion ecology using Web of Science to search for the following: "functional response(s)" AND invader(s); "functional response(s)" AND invasive(s); "functional response(s)" AND exotic(s). We also then utilised each paper's reference list to bolster and track down more obscure literature. What emerges is that, whilst functional responses have a long history in classical ecology and biological control, their use in invasion ecology is more recent and surprisingly sparse (Table 1). The use of functional responses in a comparative approach, whereby invasive and native predators are compared against one another, features even more rarely and, often, the functional

responses of invaders are derived for reasons other than explaining or predicting ecological impact (Table 1). For example, the functional response of the invasive round goby *Neogobius melanostomus* was compared to that of the native mottled sculpin *Cottus bairdi*, with the invader showing a higher functional response, but this was done only as a prelude to another experiment on behavioural interactions between these fish species (Dubs and Corkum 1996; Table 1). A more common use of functional responses in an invasion context, however, comes from studies with either invasive or native predators considered separately, with comparisons made of consumption of native and invasive prey (see Table 1). Such studies have been used to deduce whether a native predator is likely to impact a native prey species more than an invasive prey species, or vice versa, with similar conclusions drawn for invasive predators (Table 1).

Although functional responses have been used to evaluate the biological control potential of introduced parasitoids (Greenberg et al. 2001; Jones et al. 2003), the first explicit test of the hypothesis that a known ecologically damaging invader might display a higher functional response than native and other less damaging invaders was by Bollache et al. (2008), who showed that the invasive 'killer shrimp', *Dikerogammarus villosus*, had a higher Type II functional response than other native and introduced comparator species in Europe. Dick et al. (2010) then used the comparative functional response method within an invasive species, showing that an invasive predatory amphipod, *Gammarus pulex*, had a higher Type II functional response when parasitized with an acanthocephalan worm, counter to the enemy release hypothesis, illustrating the utility of the method in tests of major invasion biology hypotheses (see below). It is again noteworthy that the biological control literature uses comparative functional responses to make such comparisons, but with different questions in mind. Thus, while Dick et al. (2010) explicitly tested the enemy release hypothesis, a study by Farrokhi et al. (2010) on *Wolbachia*-infected parasitoid wasps essentially did the same, but the context was to test the effects of parasitism on the biocontrol efficacy of a control agent (see also Bayoumy 2011).

Jones et al. (2011) used functional responses of an invasive stoat to examine the dynamics of this predator and its mammal prey. In the same year, the co-existence patterns of two intra-guild predators, a native amphipod

Table 1 Contexts and history of functional responses (FRs) in invasion ecology

Reference	Native predator	Invasive predator	Native prey	Invasive prey	Notes
Native versus invasive predators—native prey					
Dubs and Corkum (1996)	Mottled sculpin *Cottus bairdi*	Round goby *Neogobius melanostomus*	Amphipod *Gammarus* spp.		Invasive predator had higher FR than natives
Bollache et al. (2008)	Amphipods *Gammarus duebeni*; *Gammarus roeseli*; *Gammarus pulex*	Amphipod *Dikerogammarus villosus*	Isopod *Asellus aquaticus*		Invader exhibited significantly higher Type II FR
Haddaway et al. (2012)	White-clawed crayfish *Austropotamobius pallipes*	Signal crayfish *Pacifastacus leniusculus*	Amphipod *Gammarus pulex*		Invasive crayfish had higher FR
Dick et al. (2013)	Mysid shrimps *Mysis salemaai*; *Mysis diluviana*	Mysid shrimp *Hemimysis anomala*	Range of zooplankton prey species		FRs of invader higher than native species; consistent across invasive range; Lab data consistent with known field impacts
Native predators—native versus invasive prey					
Barnhisel and Kerfoot (2004)	Lake trout *Salvelinus namaycush*		*Daphnia pulicaria*	*Bythotrephes cederstroemi*	FRs unravelled how invader coexists with natives
Richman and Lovvorn (2004)	Lesser scaup duck *Aythya affinis*		Clam *Macoma balthica*	Asian clam *Potamocorbula amurensis*	FRs revealed invader is better food item
Griswold and Lounibos (2005)	Diptera *Toxorhynchites rutilus* and *Corethrella appendiculata*		Mosquito *Ochlerotatus triseriatus*	Mosquito *Aedes albopictus*	Type II responses; more invasive prey consumed
Zuharah and Lester (2011)	Notonectid *Anisops wakefieldi*		Mosquito larvae *Culex pervigilans*	Mosquito larvae *Aedes notoscriptus*	Type II FR for both; more exotic prey consumed
Invasive predators—native versus invasive prey					
Hooff and Bollens (2004)		Copepod *Tortanus dextrilobatus*	Calanoid *Acartia* spp.	Cyclopoid *Oithona davisae*	FRs used for predatory impact estimation
Buhle and Ruesink (2009)		Japanese drill *Ocinebrina inornata*; Eastern drill *Urosalpinx cinerea*	Olympia oyster *Ostrea lurida*	Pacific oyster *Crassostrea gigas*	FRs revealed predation endangered both oyster species

Table 1 continued

Reference	Native predator	Invasive predator	Native prey	Invasive prey	Notes
Native predator—invasive prey					
Monserrat et al. (2005)	Buzzard-eagle *Geranoaetus melanoleucus*; horned owl *Bubo magellanicus*; red-backed hawk *Buteo polyosoma*			European hare *Lepus europaeus*	Native predation may regulate invasive hare
Kushner and Hovel (2006)	Predatory gastropod *Pteropurpura festiva*			Asian date mussel *Musculista senhousia*	FRs revealed patterns of biotic resistance
Twardochleb et al. (2012)	Signal crayfish *Pacifastacus leniusculus*			Mud snail *Potamopyrgus antipodarum*	Type III FR; snail predicted to invade at low crayfish density
MacNeil et al. (in press)	Amphipod *Gammarus duebeni*	Amphipod *Gammarus pulex*		Amphipod *Crangonyx psuedogracilis*	FRs reveal differential biotic resistance
Invasive predator—invasive prey					
Mistri (2004)		Mud crab *Dyspanopeus sayi*		Asian date mussel *Musculista senhousia*	Type II FR may be de-stabilizing to invasive prey
Invasive predator—native prey					
Ruscoe et al. (2005)		House mouse *Mus musculus*	New Zealand beech seed *Nothofagus solandri* var. *cliffortioides*		Type II FR not modified by alternative food
Griffen and Delaney (2007)		European green crab *Carcinus maenas*; Asian shore crab *Hemigrapsus sanguineus*	Mussel *Mytilus edulis*		FRs reveal second invasive predator has more impact than first

FRs = functional responses

and an invasive amphipod, were partly explained using the comparative functional response method, which revealed that the native species withstood replacement by the invader by preying more heavily on the invader's juveniles (Kestrup et al. 2011). Authors then began explicitly comparing invader and native species with functional responses, such as Haddaway et al. (2012), who showed an invasive crayfish has a higher functional response than a native. However, this study, as with most others (see Bollache et al. 2008; Dick et al. 2010), did not explicitly link differential functional responses to actual field patterns of impact on particular prey species; rather, the prey species were chosen to illustrate the methodology and general pattern of higher functional responses of invaders compared to natives. More recently, however, Dick et al. (2013) demonstrated that the invasive 'bloody red' shrimp *Hemimysis anomala* has a higher functional response to several prey species than trophically analogous native species (that are also themselves invasive in some regions) and, more intriguingly, that the greatest invader/native differentials in functional responses were associated with the greatest field impacts of the invader (Fig. 1b–d). Further, Dick et al. (2013) showed that differential functional responses are consistent across the invader's geographical range (see also Lohrer et al. 2000), thus demonstrating that this technique offers advantages over other trait-based predictions, since other traits often vary across an invader's range (Olden et al. 2006; Rossong et al. 2012; Parker et al. 2013).

At present, there are insufficient studies to perform a formal meta-analysis to test the overall hypothesis that ecologically damaging invasive species have higher functional responses than comparator native species (see Table 1). However, of the n = 4 studies in Table 1 that have such a comparison, all support the hypothesis. Further, if we include from those studies the comparison of one invader with multiple native comparators (Bollache et al. 2008) and invader/native comparisons using multiple prey species (Dick et al. 2013), we have n = 12 comparisons, of which 11 support the hypothesis; the one comparison of the invasive *Hemimysis anomala* with the native *Mysis diluviana* that showed no difference in functional responses involved a prey species that is not impacted by the invader in the field (Dick et al. 2013). Further data, from both functional response comparisons and actual field corroborations of levels of impacts on natives, will allow more powerful tests of the hypothesis and we encourage research in this area.

Functional responses are increasingly being incorporated into tests of major hypotheses in invasion ecology, such as 'enemy release' (Dick et al. 2010; see above) and 'biotic resistance' (e.g. Twardochleb et al. 2012). Further, we agree with Heger et al. (2013) that many of these hypotheses need to be "branched" into more specific and testable hypotheses. Thus, whilst functional responses have been used in testing the 'biotic resistance' hypothesis and studies of the impacts of resident on invasive species (e.g. Zuharah and Lester 2011; Twardochleb et al. 2012), MacNeil et al. (in press) argue that true support for this hypothesis requires: (1) demonstration by field studies that resident species restrict the range, density or abundance of an invader; and (2) that some form of population regulation or de-stabilising interaction occurs between resident and invading species (e.g. in their predator/prey relationship). This was shown to be the case with a North American invasive amphipod, which is strongly negatively associated with two resident predatory amphipods in Europe (MacNeil et al. in press). In the laboratory, both resident species displayed potentially population de-stabilising Type II functional responses towards the invasive prey, even in the presence of habitat complexity, which often drives more stabilising Type III responses (see Alexander et al. 2012, in press). Additionally, as the functional response methodology examined predation rates over a range of prey densities (see below), it was able to demonstrate that the resident predator with the stronger negative field association with the invader had a significantly higher functional response than the other resident predator (MacNeil et al. in press). Importantly, these latest studies (Dick et al. 2013; MacNeil et al. in press) show remarkable congruence of laboratory derived functional responses with actual field patterns of invader and resident predator impacts. Further demonstrations of such congruence will provide great confidence that the methodology has real value in predicting field patterns of impact (see "Challenges, future research and applications" section below).

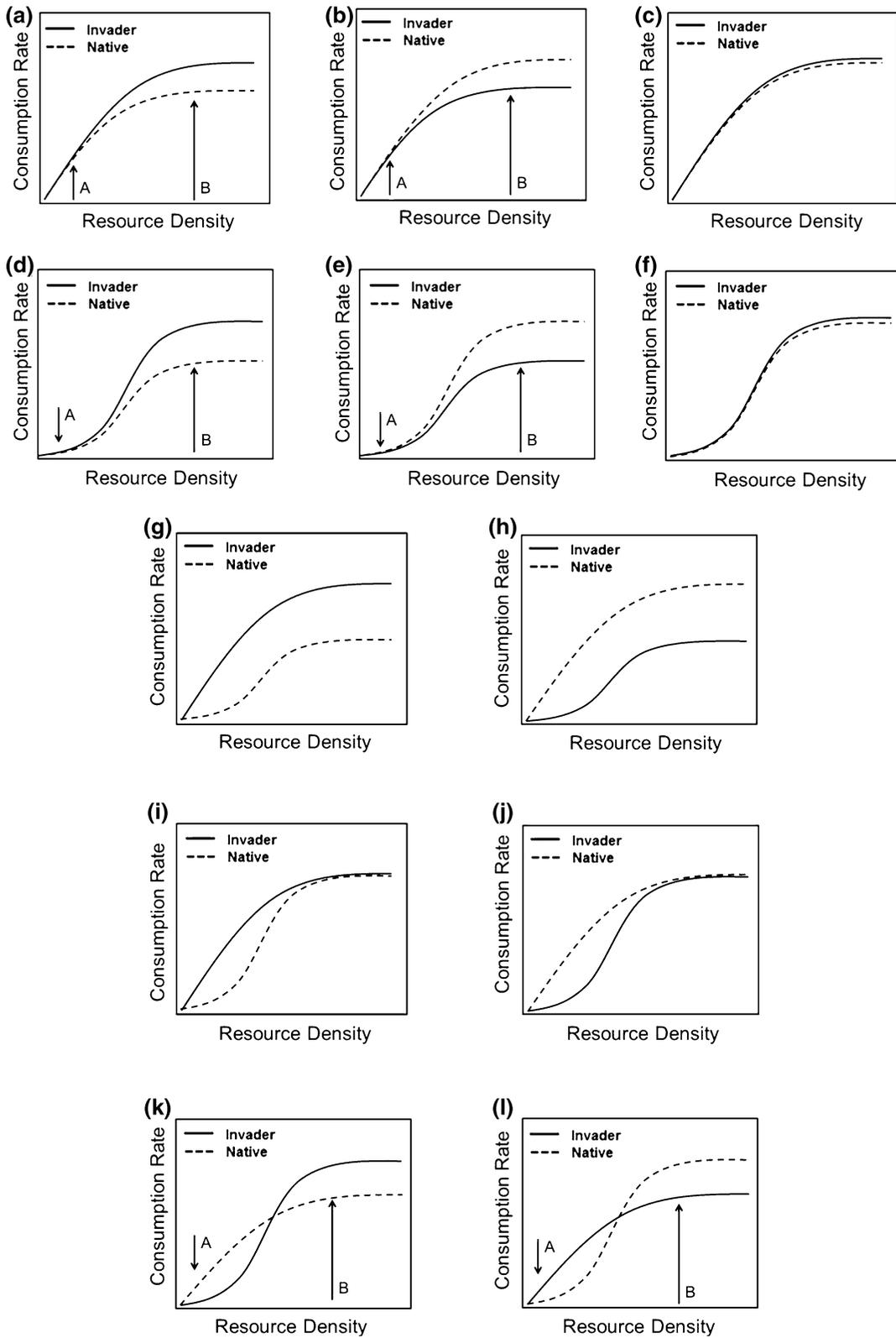## A comparative functional response framework for invasion ecology

In Fig. 2a–l, we present a framework for comparative functional responses in invasion ecology, whereby the

comparisons are between an invasive and a native species of functional response Types II and III (statistical methods available in e.g. R; frair package, Pritchard 2013); however, this could also be comparisons of multiple invasive species, multiple populations of the same invasive species, or an invasive species under differing environmental conditions (e.g. temperature) or states (e.g. parasitism; see Dick et al. 2010). Further, derivation of functional responses can include other context-dependencies, such as multiple predator effects and trait-mediated indirect interactions (see "Challenges, future research and applications" below). We use the maximum feeding rate asymptote on the Y axis to vary the magnitude of these hypothetical functional responses, while also varying their shape, that is, Type II and Type III functional responses, in all their potential combinations. In Fig. 2a–c, the invader can be judged as having a higher, lower or similar Type II functional response compared to the native (the same can be said of two invaders, two populations of invaders, or an invader under two environmental conditions, or with/without parasites, for example). In Fig. 2d–f, the same argument as above applies for Type III functional responses. Then, Fig. 2g–l show combinations of Type II and Type III functional responses; the benefits of using these schemes when applied to invader impacts are explored below. Our narrative, for simplicity, tends to refer to predator/prey functional responses, but we recognise that other trophic interactions, such as herbivore/plant, are also applicable (see "Challenges, future research and applications" section).

With respect to the feeding rates of invaders in comparison to natives, studies most often choose a prey density, or provide prey in excess, and measure prey consumed per unit time (e.g. Kelly et al. 2002; Fielding et al. 2003; Renai and Gherardi 2004; Rehage et al. 2005; Olden et al. 2009; Stoffels et al. 2011). The same is true with other feeding rate comparisons, such as between two invaders (Lohrer and Whitlatch 2002; DeGraaf and Tyrrell 2004; Tyrrell et al. 2006); between parasitized and unparasitized invaders (Fielding et al. 2003); investigations of individual invader species impacts (e.g. Bourdeau and O'Connor 2003; Brousseau and Baglivo 2005; Pintor et al. 2009; Pangle and Peacor 2009; but see Hooff and Bollens 2004); and native species predation of invaders and biotic resistance to invaders by natives (deRivera et al.

2005; Bishop and Peterson 2006; Veiga et al. 2011; but see Griswold and Lounibos 2005; Twardochleb et al. 2012). However, the problem with arbitrarily setting one particular level of prey availability is that, because of its 'snapshot' nature, any differences in predatory impact may be missed as no opportunity is given for functional response types and magnitudes to emerge and perhaps diverge. Figure 2a, for example, shows that, depending on an arbitrarily set resource density, an invader might be judged as having a similar (Arrow A) or higher (Arrow B) feeding rate. The scheme of Fig. 2 may also be applied in other contexts, such as comparisons of invaders that are either parasitized and unparasitised. Thus, for example, one study (Fielding et al. 2003) showed that parasitized and unparasitized male invasive amphipods were no different in their predation rates; however, this was because both predator groups effectively ran out of prey in the experimental trials, thus driving the non-significant difference (i.e. the prey density chosen was too low on the potential functional response curve; see Arrow A, Fig. 2a). On the other hand, when prey densities were increased in a functional response experimental design for the same invader and parasite system, the divergence of predation rates of those individuals parasitized and unparasitized was evident and significant (Dick et al. 2010; see Arrow B, Fig. 2a). This type of situation might also be evident with Type III functional responses (see Arrows A and B in Fig. 2d). Thus, invading and native species may have similar types of functional response (II or III), though with different or similar magnitudes (Fig. 2a–f); however, single prey density 'snapshot' experiments cannot reveal such differences, and indeed, different conclusions could be derived depending on the arbitrary densities chosen by the experimenter (see Fig. 2a,b,d, e). Whilst many studies ensure that prey are not totally depleted during experiments by supplying the prey in excess (e.g. Rehage et al. 2005; Veiga et al. 2011), functional response types can still not be revealed by such studies because, with only one prey density examined, the shape of the curve is not known. Thus, impacts on prey populations in terms of the functional response type are not discernible from 'snapshot' study designs.

If we now examine mixed Type II and III functional responses of invader and native species, we could find that an invader has a higher Type II functional response and a comparator native a lower Type III

functional response (Fig. 2g), or vice versa (Fig. 2h). While the former might predict that the invader will impact native prey more so than the native, the latter predicts the opposite. In another scenario, the invader and native species could have similar maximum feeding rates (curve asymptotes; Fig. 2i, j), but either the invader displays a Type II and the native a Type III functional response (Fig. 2i) or vice versa (Fig. 2j). Thus, whilst maximum feeding rates are similar, the population-level outcomes could be quite different, as the former scenario predicts a de-stabilising effect of the invader and stabilising effect of the native, whereas the latter scenario predicts the opposite. Note also that an experiment that simply provides sufficient prey density such that prey depletion is not a problem could still be misleading, as the functional response types can be very different even when maximum feeding rates are similar (Fig. 2i, j). Finally, as in Fig. 2k, an invader could have a higher maximum feeding rate than a native, but the invader has a Type III functional response and the native a Type II functional response; or, as in Fig. 2l, the invader could have a lower maximum feeding rate than the native, but the invader has a Type II functional response and the native a Type III functional response. In the former scenario (Fig. 2k), the higher maximum feeding rate of the invader may be misleading with respect to impact on the prey, as the invader functional response is in theory (and in the absence of other mitigating factors) more stabilising and the native more de-stabilising (see Murdoch and Oaten 1975); in the latter scenario (Fig. 2l), the lower maximum feeding rate of the invader may be misleading with respect to impact on prey, as the invader functional response is more de-stabilising and the native more stabilising. It is particularly clear from Fig. 2k & l that the use of a single prey density could have very misleading conclusions. For example, at point A on Fig. 2k, the native species has a higher feeding rate than the invader, whereas at point B the opposite is apparent

(and feeding rates would be judged equal where the curves cross over); however, if the curves depicted were real data, we would predict strong prey population regulation by the invader but potential prey extinction by the native. In Fig. 2l, points A and B again illustrate the problem of choosing just one prey density, with the invader having a higher feeding rate at point A and the opposite at point B (and equal where the curves cross over). However, in this case if the curves depicted real data, we would predict the native would regulate but the invader could drive extinction.

A major issue with regards to deriving functional response curve shapes and parameters is the design of studies where prey (or other resources) are replaced or not replaced as they are consumed (see Alexander et al. 2012). There are statistical measures to account for non-prey replacement that can allow better estimates of curve parameters (see Alexander et al. 2012), but this does not help distinguish between two predators which may have been differentially constrained in their prey consumption. This is outlined in Fig. 3a, whereby in a non-replacement design, at low prey densities (see Arrow), most if not all prey are consumed and, since prey are not replaced, the slope of the curve is necessarily constrained in its early phase (dotted line, Fig. 3a). On the other hand, if prey are replaced, the same predator can potentially consume more prey and the early part of the curve rises more steeply (solid line, Fig. 3a). The asymptote, or maximum feeding rate, may be the same, but important information on the predator's impact may be missed, especially since prey population viability is increasingly sensitive to predator effects as prey densities fall. We illustrate in Figs. 3b–g how such replacement designs might be more able to discriminate between invaders and natives (and other combinations outlined above) with respect to functional response shapes, parameters and hence predictions of impact. Taking Fig. 2c as a potential outcome of the comparison of an invader and a native where prey are not replaced, a replacement design (Fig. 3b) might show that in fact the invader, whilst having a similar maximum feeding rate to the native comparator, reaches that asymptote with a much steeper initial slope (Fig. 3b). Figure 3c–g illustrate a range of outcomes where invader and native are compared within a replacement design: Fig. 3c illustrates an invader exhibiting a higher maximum feeding rate and steeper initial slope, with the latter unlikely to be revealed in a non-replacement

Fig. 3 a–h An illustration
of the comparative
functional response
framework utilising
'replacement' study designs
(see text for details)
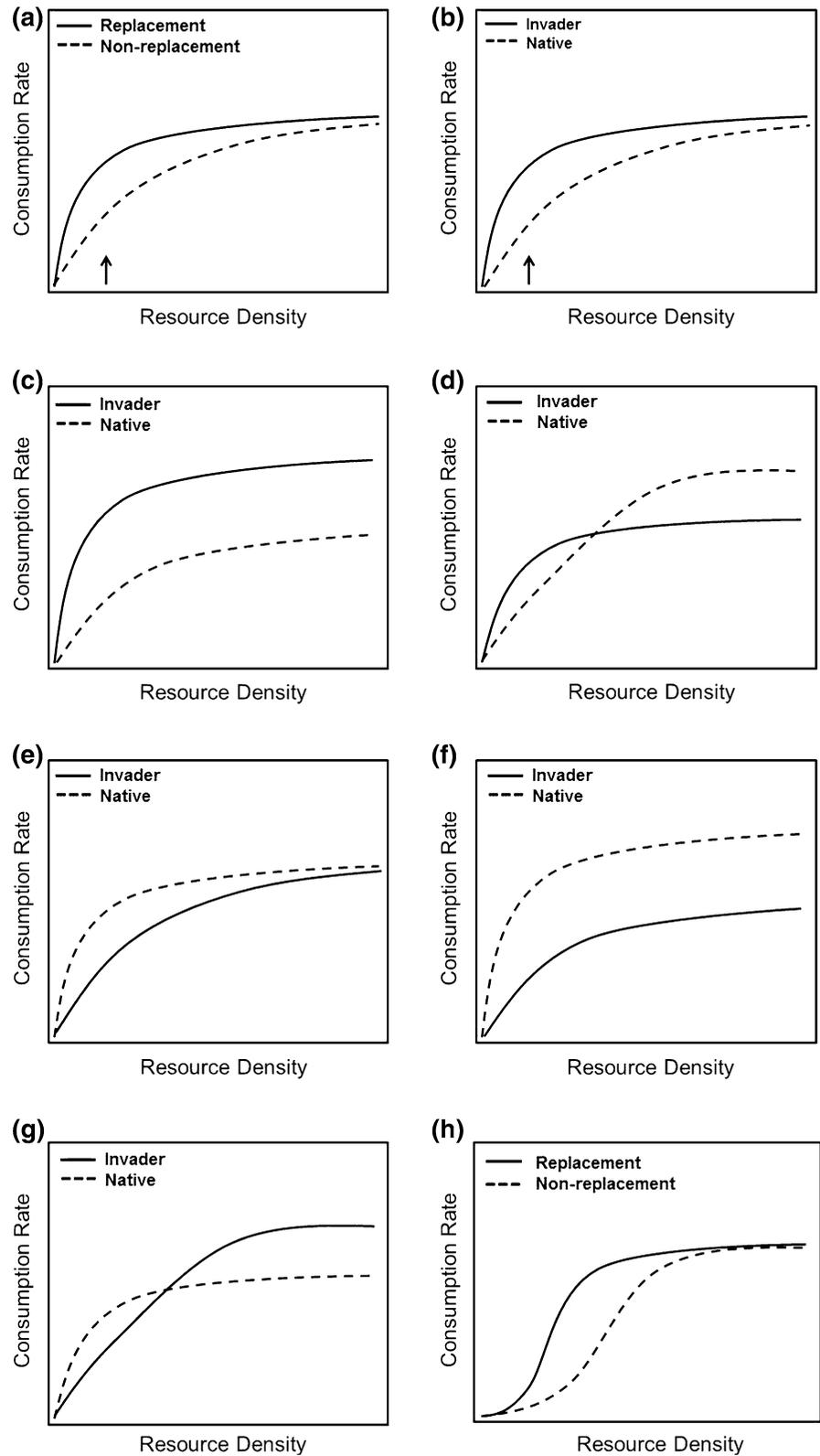
design (cf Fig. 2a); Fig. 3d illustrates a native exhibiting a higher maximum feeding rate but an invader a steeper initial slope, again not revealed in a non-replacement design (cf Fig. 2b); Fig. 3e illustrates invader and native having similar maximum feeding rates but the native a steeper initial slope (cf Fig. 2c); Fig. 3f illustrates a native with both a higher maximum feeding rate and a steeper initial slope (cf Fig. 2b); Fig. 3g illustrates an invader with a higher maximum feeding rate but a native with a steeper initial slope (cf Fig. 2a). Similar arguments would hold if replacement designs were applied within Type III functional response comparisons (see Fig. 3h). The choice of replacement versus non-replacement designs is often due to practicalities, as the former are more labour intensive and the latter a pragmatic solution. However, we encourage replacement designs where feasible (see, for example, Alexander et al. 2012) but, certainly, where non-replacement designs are used and no difference in functional responses are found, any conclusions should be caveated.

Challenges, future research and applications

While functional responses could theoretically be derived for any consumer of any resource, since we are interested here primarily in the population level outcomes for that resource, we have assumed resources are living. However, where non-living resources are concerned, such as nutrients as resources for plants, invader/native comparisons of functional responses could still be useful in determining reasons for, and perhaps predictions of, the success and ecological damage associated with invasive plants. Such resource use is a challenge to measure directly and, in any case, resource use efficiency, as measured indirectly (e.g. photosynthetic rate), has been shown to associate with invasiveness in plants (Funk and Vitousek 2007). Further, while our narrative tends to stress the functional responses of predators towards prey, our intention is not to limit the framework to this trophic interaction; for example, herbivores clearly show functional responses to vegetation (Farnsworth et al. 2002). In addition, there needs to be more imagination in the ways in which functional responses are derived; although many would view this as a laboratory procedure, many functional responses can be derived from field data (e.g. Moustahfid et al.

2010), and techniques such as stable isotope analyses and perhaps even qPCR (see Dick et al. 2013 for further discussion).

Our framework requires extensive and varied empirical testing. We could, for example, ask: When invaders show greater magnitudes of functional responses, that is, higher maximum feeding rates within a functional response type (e.g. Fig. 2a,d), does this concur with field patterns of high invader impact? Which of the individual parameters of functional responses (classically attack rate 'a', handling time 'h' and maximum feeding rate 'T/h') are the best predictors of invader impacts? We already have evidence that high maximum feeding rates and values of 'a', plus lower values of 'h', can all predict invader impact in one invasion scenario, that of the invasive Ponto-Caspian 'bloody red' shrimp *Hemimysis anomala*, which shows higher Type II functional responses than native mysid species. Remarkably, the magnitude of difference in maximum feeding rates is tightly correlated with degree of known field impact (Dick et al. 2013; Fig. 1b–d). Further demonstrations of such congruence will provide greater confidence that the methodology has real value in predicting field patterns of invader impacts, but we need sufficient case studies for a formal meta-analysis.

What is also challenging is designing studies that not only make relevant comparisons among invaders and natives, but detect and discriminate between functional response Types II and III and relate these to field patterns. This is challenging because functional response type can be sensitive to environmental variables (Jeschke et al. 2004), such as substrate type (Alexander et al. 2012). However, we stress that it is the comparison of invader with native (or other comparisons outlined above) that are important, and that the use of comparative functional responses as outlined here is phenomenological rather than strictly mechanistic (c.f. Jeschke et al. 2002). This is reflected in the use of functional responses as tools rather than as true reflections of the processes generating their shape (i.e. Types II and III). An interesting avenue for future research will be to extend the current framework such that it is connected to mechanistic functional response models (see e.g. Jeschke et al. 2002). Also, we must caveat conclusions about functional response types and population consequences (e.g. not all Type II responses will lead to extinction of prey; Twardochleb et al. 2012), but at the same time ask if

real invasions and their impacts are explicable, and thus potentially predictable, from functional response comparisons as outlined in the framework of Figs. 2 & 3. Further, as mentioned earlier, a full assessment of consumer-resource dynamics (such as predator–prey) requires assessment of the demographic and/or aggregative numerical response (and hence total response). However, this may be impractical and moves away from our intention of providing a framework for the rapid assessment of invaders through comparative functional responses, which might be overwhelmingly able to provide ecological impact prediction. A number of proxies of the numerical response might, however, be available to improve the assessment of overall impact of invaders/natives, such as abundance and density data that are a reflection of the numerical response. This also helps with derivation of total ecological impact of invaders as proposed by Parker et al. (1999), that is, the *per capita* effect multiplied by abundance and range. Thus, for example, functional responses could be combined with abundance data to provide an overall score of impact (actual or predicted) as this describes the product of *per capita* effects with the number of individuals acting as consumers.

The largest impediment to prediction in invasion ecology is arguably the context-dependency of the success and impact of introduced species (Parker et al. 1999; Ricciardi 2003; Thomsen et al. 2011; Ricciardi et al. 2013). Much of this contingency is driven by organismal responses to variation in abiotic and biotic conditions across space and time (Ricciardi 2003; Strayer et al. 2006; Branch et al. 2010). Thus, we would expect that, despite the consistency of functional responses demonstrated for a trans-Atlantic invader (*Hemimysis anomala*; Dick et al. 2013), functional responses of invaders will vary across environmental gradients. Indeed, we tested the Environmental Matching Hypothesis of Ricciardi et al. (2013) and showed that the optimal maximum feeding rates as derived from functional responses are close to optimal growth or preferred temperatures of invasive species (Iacarella et al. unpubl. data). Further, rather than viewing environmental influences on the shape and magnitude of functional responses as a nuisance (see above), relevant environmental variables can be incorporated into study designs and explored for their main and interactive effects, hence perhaps refining predictions of invasive species impacts under global change. To more

fully develop this predictive approach, we must also account for inter- and intra-population variation among individuals, and, especially, differences between populations in native versus invasive ranges (see van Kleunen et al. 2010). Extensions of the concept may include determining temporal changes in functional responses of individuals over time since invasion (as a result of adaptation by the invader and native prey, e.g. Carthey and Banks 2012; see also Wright et al. 2010); and examining phylogenetic variation in functional responses to determine the extent to which the functional responses and impacts of invaders can be predicted from the functional responses of closely-related species.

Further context-dependencies that require inclusion in comparative functional response assessments are the effects on individuals of the wider community within which they are embedded. Hence, functional responses of individuals might be influenced by the density of conspecifics (Pintor et al. 2009) and emergent multiple predator effects or MPEs (see Griffen 2006), whereby the presence of other individuals (be they conspecifics or other predator species) might lead to interference or facilitation (see Medoc et al. 2013). Also, intermediate consumers might be influenced by higher trophic-level predators through trait-mediated indirect interactions (TMIIs); for example, functional responses can both decrease and increase due to TMIIs and their interaction with habitat heterogeneity (e.g. in a fish-amphipod-isopod system; Alexander et al. in press). Indeed, in the most recent study, the difference in functional responses between the invasive *Hemimysis anomala* and native *Mysis salemaai* was exacerbated by the presence of a higher trophic-level predator (Barrios-O'Neill et al. in press). Derivation of functional responses thus require attention to the myriad effects of threats to the individual, the so-called 'landscape of fear' (see Laundré et al. 2010) or 'ecology of fear' (see Clinchy et al. 2013). Finally, whilst not essential in the overall goal of comparing functional responses of invaders and natives towards prey, disentangling the relative roles of predator 'novelty' and prey 'naievete' (see Sih et al. 2010) would provide insight into reasons for the higher functional responses of invaders and hence insight into ecological impact.

A measure of the utility of the comparative functional response methodology, or any of its derivatives, will be its adoption into tests of major hypotheses in invasion ecology. We have discussed

above that tests of the 'enemy release' hypothesis with functional responses revealed that parasites, rather than decreasing the feeding rate of hosts (and thus perhaps decreasing competitive ability/ecological impact) were shown to actually increase host feeding rates and potential impact of the invader (Dick et al. 2010). Also, functional responses have been successfully adopted as a method of revealing and predicting 'biotic resistance' (Twardochleb et al. 2012; MacNeil et al. in press). With 28 of the 29 hypotheses described by Catford et al. (2009) involving some element of resource use, and hence the potential to measure functional responses, we are confident that functional responses can help better formulate and test such hypotheses. For example, such hypotheses involve elements of how 'competitive' invaders are compared to natives, the ability of invaders to dominate resources in communities, their growth and reproductive potentials, whether invaders are specialists or generalists, their role as ecosystem engineers and the effect of disturbance in altering invader as compared to native resource use (see Catford et al. 2009).

Finally, there are challenges in the incorporation of any theoretical or empirical advances in invasion ecology into applied methodologies that can reduce the risk of future harmful invasions. Refining risk assessment (RA) protocols is one such major challenge for the management of invasive species (Ricciardi and Rasmussen 1998; Parker et al. 1999; Byers et al. 2002; Andersen et al. 2004; Kumschick et al. 2012; Leung et al. 2012; Kumschick and Richardson 2013), and impact is usually not satisfactorily included in RAs (Kumschick et al. 2012). Including comparative functional responses in risk assessments for invasive species could be a useful way of improving the prediction of ecological consequences, namely impact (measures of *per capita* effects; Parker et al. 1999) of species introductions and therefore increase the predictive power of RA. This would require studies conducted prior to the introduction of a species, similar to those performed for putative biological control agents. However, in contrast to the discipline of biocontrol, the colonization and impact potential of probable future invaders are rarely assessed (see Ricciardi and Rasmussen 1998), a difficult task, considering the enormous number of plant and animal taxa transported around the globe. However, for some groups of species, such as those used in aquaculture and those commonly found in ballast water, comparative functional responses would

be a valuable additional framework to consider for RA, especially given that (1) they can be derived from a variety of laboratory and field methods (see Dick et al. 2013) and (2) there is evidence that differentials in functional responses are conserved across the geographical range of invasive species. The application of this approach might also serve as an early warning method for identifying potentially problematic invaders residing in donor region 'hotspots' (e.g. the Ponto-Caspian; Ricciardi and MacIsaac 2000), or among those predicted to exploit emerging vectors and pathways.

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