


A trophic interaction framework for identifying the invasive capacity of novel organisms

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Abstract

1. The likelihood and impacts of invasions by novel organisms (e.g. non-native species, genetically modified organisms) on the composition and functioning of receiving biological communities hinges on their capacity to exploit resources and/or avoid predation relative to resident counterparts. While assessment of invasion risk based on the comparison of functional responses (per-capita consumption rate as a function of resource density) of novel species with native analogues has been gaining popularity, it may be undermined if alternative prey and potential predators are not represented realistically.
2. Here, we propose a conceptual framework that enables rigorous identification of trophic traits conducive to invasion success by novel organisms—irrespective of their trophic position—and their likely ecological impacts, given their arrival and establishment. We focus on consumption here, but our framework can also be used for autotrophic energy acquisition, and extended to non-trophic and indirect interactions.
3. The framework enables a structured and prioritized selection of subsets of trophic links for invasion risk assessment. It is based on foraging theory and advances in comparative functional responses in invasion ecology. It can even be used in the absence of a resident comparator organism and when resources or predators are only partly known.
4. Our approach enhances the predictive power of species screening, and thus advances prevention and management of invasions under a common framework for all types of novel organisms.

KEYWORDS

alien species, dietary generalism, ecological novelty, functional responses, GMO, invasion success, predator–prey trophic interactions, risk assessment

1 | INTRODUCTION

Predicting biological invasions (i.e. the spread of non-native species beyond the point of introduction) and managing their impacts (i.e. quantifiable alterations of the receiving ecosystem) remain key challenges in ecology (Simberloff et al., 2013). This demands improved

understanding of the mechanisms of invasions. Human-assisted species translocations entail transfers across barriers that limit natural dispersal, and thus between environments which can have substantially different eco-evolutionary histories. Thus, introduced organisms can impart a high degree of ecological novelty to a system, which is conducive to invasiveness (Saul, Jeschke, & Heger, 2013). Organisms arriving

in new environments enter resident ecological interaction networks, and the identification of their interactions within resident communities is important for understanding community dynamics. Predicting the attributes of these novel interactions is crucial for prioritizing management of existing and anticipated invasions, and for assessing the side effects of intended introductions. Novel organisms (including translocated, but also range-expanding, genetically modified, synthesized or resurrected organisms; Jeschke, Keesing, & Ostfeld, 2013), whose ecological traits contrast with the eco-evolutionary experience of their resident interaction partners (Saul & Jeschke, 2015), can potentially transform resident interaction networks through, for example, altering strengths, spatio-temporal patterns or other functional attributes of interactions (Downing et al., 2012; Mayer et al., 2013; Mitchell et al., 2006; Penk, Irvine, & Donohue, 2015).

Predation is a particularly important interaction type that can have strong impacts on community dynamics. This is primarily because it affects both predator fitness and prey biomass directly, potentially causing trophic cascades (O'Connor, Emmerson, Crowe, & Donohue, 2013; Terborgh & Estes, 2010) and food limitations for competitors (Strayer & Malcom, 2007). Introduced predators can therefore affect resident prey populations significantly (Downing et al., 2012; Hays & Conant, 2007; Strayer, 2009), with efficient exploitation of resources being conducive to high population growth, likely invasion success, and potentially considerable ecological impacts. Resource density is a key determinant of the feeding rate, and this relationship is characterized by "functional response" curves (Holling, 1959). For instance, decreasing prey density can reduce predator encounter rates with prey and thus offer a density-dependent prey refuge in a predator-prey system with a sigmoidal (i.e. Type III) functional response, but not with alternative functional response shapes where high proportions of prey are killed at low prey densities (Types I, II or their variants; Holling, 1959; Jeschke, Kopp, & Tollrian, 2004; Jeschke & Tollrian, 2005). Thus, the height—in particular the maximum feeding rate (i.e. curve asymptote)—and the shape of functional responses can reveal characteristics of consumer-resource interactions that are important for community dynamics and composition.

Invading predators with high ecological impact on their prey populations often have elevated functional responses compared to ecologically similar native species (Dick et al., 2017). Using comparative functional responses as an empirical screening method is thus rapidly gaining popularity among invasion biologists (Alexander, Dick, Weyl, Robinson, & Richardson, 2014; Barrios-O'Neill, Dick, Ricciardi, MacIsaac, & Emmerson, 2014; Dick et al., 2013; Rosewarne et al., 2016; Xu et al., 2016). The method typically infers invasion success and/or potential impacts from a limited number of prey species (frequently just one). However, biological invasions tend to lead to replacement of niche specialists by generalists (Clavel, Julliard, & Devictor, 2010), and numerous studies have identified a positive association between dietary generalism and invasion success (Arbaciauskas, Lesutiene, & Gasiunaite, 2013; Bessa-Gomes et al., 2003; Clavel et al., 2010; Jeschke & Strayer, 2006; Romanuk et al., 2009; but see Cassey, Blackburn, Sol, Duncan, & Lockwood, 2004; Jackson, Grey, Miller, Britton, & Donohue, 2016). Thus, the inefficient use of one

particular resident prey species does not necessarily preclude invasion success or impact upon ecological networks with realistic complexity. In other cases, a resident organism may be an inferior predator on a particular prey species, and falsely appear a weaker overall interactor, compared to an introduced predator solely as a result of differing specialisation, despite apparent ecological similarity (Dunoyer, Dijoux, Bollache, & Lagrue, 2014; Rosenfeld, 2002). Investigating functional responses with multiple prey, thereby taking into account the potential role of generalism and specialism, can buffer against such biases and at the same time improve the much needed representation of whole-ecosystem impacts of novel organisms (Ehrenfeld, 2011; Penk et al., 2015; Simberloff, 2011). Furthermore, novel organisms can themselves be controlled by resident predators (MacNeil, Dick, Alexander, Dodd, & Ricciardi, 2013; Pintor & Byers, 2015; Romanuk et al., 2009). Not accounting for top-down control experienced by introduced species, as has been typically the case in functional response-based screening methods, risks over-estimating their consumptive impacts and invasion success (but see Alexander, Raven, & Robinson, 2015; Barrios-O'Neill, Dick, Emmerson, et al., 2014).

Both top-down and bottom-up trophic interactions can thus directly affect the survival, fitness and ecological impacts of novel organisms. The complexity of these trophic links, including diet breadth and number of enemies, is an important determinant of invasion success (Romanuk et al., 2009). However, the logistics of incorporating multiple prey and predators into comparative functional responses may be demanding and frequently prohibitive.

We propose a conceptual framework for identifying and selecting a prioritized subset of trophic links to empirically assess the capacity for invasion success and ecological impacts of novel organisms (Figure 1). We provide a worked example of the application of the framework for an intermediate consumer, the marbled crayfish (*Procambarus fallax* forma *virginalis*) in German low-land lakes (Figure S1). This includes selection of both predators and prey, and can therefore instruct assessment of organisms of any trophic position. In addition, the marbled crayfish does not have any known native populations, and thus it is exemplary of quite complex assessment scenarios. For clarity, our arguments relate to predation, which includes true predation, herbivory, parasitism and parasitoidism. However, detritivory can also be an important dietary subsidy of generalist consumers (Jackson et al., 2016; Wise, Moldenhauer, & Halaj, 2006) and should be carried through the assessment if it contributes to the diet of the novel ("focal") organism. Although we focus on consumption, our framework can be applied to autotrophic energy acquisition, and extended to non-trophic and indirect interactions. Whereas the non-empirical steps of our framework are readily applicable to any type of interaction, non-trophic interactions may require different empirical methods.

2 | MAPPING POTENTIAL INTERACTION PARTNERS IN THE TARGET COMMUNITY

Unless interaction with a particular resident organism is an *a priori* focus of assessment, an initial step of comprehensively mapping a

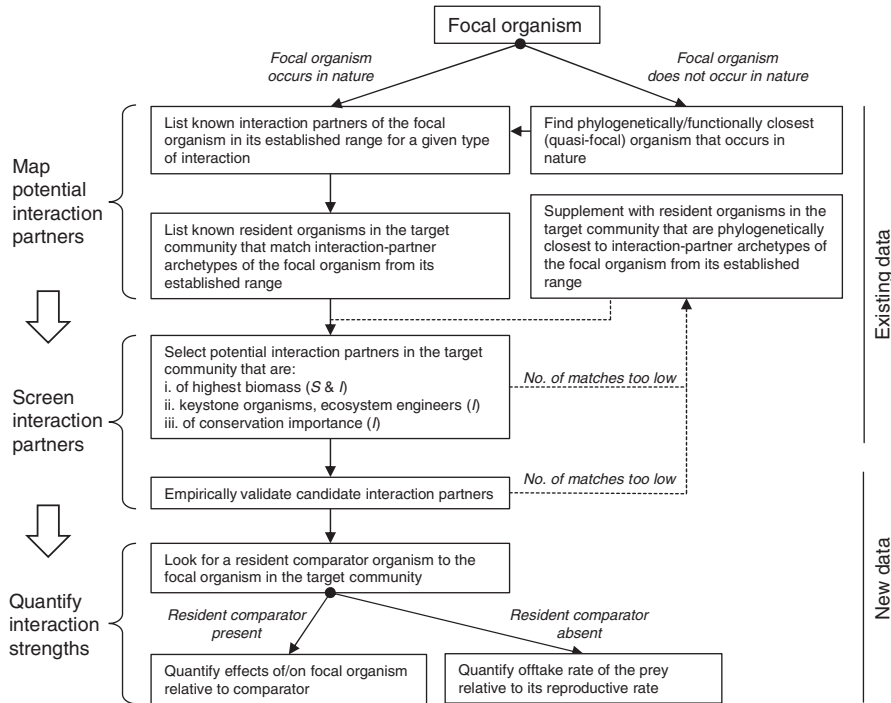


FIGURE 1 Framework for quantifying interaction strength of a focal organism with multiple resident organisms in the target community for a given type of interaction. Nodes and broken links indicate alternative and supplementary paths, respectively. *S* and *I* indicate interaction-partner categories relevant for the assessment of invasion success and ecological impacts, respectively

potential network of direct consumptive interactions of the focal organism in the receiving (“target”) community should enable minimisation of selection biases that may impede realistic assessment of the impact of the novel organism. This can be achieved by first listing all partners in direct consumptive interactions of the focal organism in its established range. This is then followed by matching all resident organisms in the target community that conform to the archetypes of these interaction partners and are likely to at least partly share spatio-temporal distribution patterns with the focal organism (Figure 1). We define an archetype as organisms that have a similar set of morphological and behavioural traits that can condition a given type of interaction (Cox & Lima, 2006; Winemiller, Fitzgerald, Bower, & Pianka, 2015), for example, feeding or defence strategy.

Observed trophic interactions in a given environment may not fully represent the feeding preferences of an organism (Devictor et al., 2010; Futuyma & Moreno, 1988), and trophic interaction strength with a particular prey may depend on its availability in comparison to other prey rather than on the true preference of the consumer (Davis et al., 2015; Hanmer, White, & Pawlik, 2017; Jaworski, Bompard, Genies, Amiens-Desneux, & Desneux, 2013), as well as on environmental drivers. Thus, interaction partners of the focal organism as well as interaction strengths may vary among communities that differ in species composition and densities. If the focal organism is already established in the target environment, site-specific data about interaction partners should be given precedence above data from other areas. Otherwise, information from multiple communities within the distribution range of the focal species may improve control for context-dependencies. Assigning preference attributes based on how frequent and dominant interaction partners are throughout the established range (e.g. Kissling et al., 2014) can then help prioritize the selection of interaction partners for assessment. Considering ontogenetic stages of the focal

organism with contrasting interaction partners (e.g. size class, identity or trophic guild of prey or enemies) could further improve predictions because limitation at any single stage preceding reproduction could constrict population dynamics (Rudolf & Lafferty, 2011; Werner & Gilliam, 1984).

For focal organisms that do not yet occur in nature, such as genetically modified, resurrected, synthetic, hybridized or selectively bred organisms, interaction partners of phylogenetically or functionally closest (“quasi-focal”) organisms may provide reasonable approximation. For example, the marbled crayfish, introduced recently to German freshwaters (Chucholl, Morawetz, & Groß, 2012), originated in the aquarium trade and does not have any known native populations (Vogt et al., 2015). However, it is morphologically and functionally similar to the spiny-cheek crayfish (*Orconectes limosus*), a well-established earlier invader in Germany which can be considered a quasi-focal organism. The spiny-cheek crayfish is an omnivore that feeds on benthic invertebrates and macrophytes, and itself falls prey to fish, waterfowl and mustelids. Interaction partners of the spiny-cheek crayfish are thus good candidate prey and predators of the marbled crayfish (Figure S1).

3 | SCREENING FOR A PRIORITIZED SUBSET OF THE MAPPED INTERACTION NETWORK

Should assessment be restricted to a subset of potential interaction partners, then criteria for selecting them depend on the goal of the assessment—invading success, impact, or both (Figure 1). The colonization of areas beyond the point of introduction, synonymous with invasion success (Blackburn et al., 2011), is likely if an organism is able to utilize abundant resources, and/or if it can avoid high extrinsic

mortality. Thus, we recommend focusing on potential resources with the highest biomass in the target ecosystem when selecting a prioritized subset of all identified potential interactions for the assessment of the likelihood of invasion. However, attention should also be paid to potential predators that are expected to have the highest predation pressure on the focal organism. Notably, high predation on the focal organism could come from consumers with high individual predation rates, or those that are not necessarily individually voracious but occur in high abundance (Dick et al., 2017).

Interactions of the focal organism with dominant predators and prey have the potential to affect major energy conduits within ecological networks and are thus conducive to strong ecosystem-level impacts, such as altered diversity, structure and functioning of target communities (Jackson et al., 2016; Lockwood, Hoopes, & Marchetti, 2007; Penk et al., 2015). Further, interactions with keystone species or ecosystem engineers (Angelini et al., 2015; Jones, Lawton, & Shachak, 1994; Power et al., 1996), which are not necessarily very abundant, could amplify the indirect impact of invaders and convey ecosystem-level impacts. They should also be considered. It is also important to consider interactions with individual predator and prey organisms of conservation importance, regardless of whether such interactions have the potential to affect the whole community (Figure 1).

In general, we advise selecting multiple prey and predator species of the focal organism for empirical assessment. However, their number and distribution among the interactor groups discussed above (i.e. those of highest biomass, keystone organisms and ecosystem engineers, and those of conservation importance; Figure 1), will depend on the purpose of the assessment, trophic level and niche breadth of the focal organism, food web complexity in the target ecosystem, management priorities and logistic constraints. For example, monophagous and oligophagous predators, including parasites and parasitoids, have

inherently limited numbers of prey, while mesopredators typically have fewer predators than basal prey (Turney & Buddle, 2016). Figure 2 shows exemplary hypothetical module structures for interaction settings between focal and resident organisms, indicating the diversity of interactions that need to be considered. Some of the interactor group categories will frequently overlap, and some may not be present in the target community. If the focal organism is already established, experimental trials or field data can be used to ascertain and prioritize interaction partners in the target community before engaging in full assessment.

Empirical examples of structured choices of prey in functional response studies of invasive species are rare (but see Barrios-O'Neill et al., 2016; Dick et al., 2013; Xu et al., 2016). In our worked example of the marbled crayfish (Figure S1), the mussel *Dreissena* spp. has high abundance in the target community and is an ecosystem engineer. Dreissenids and other animal prey with poor escape response are key and preferred contributors to crayfish energy budgets (Momot, 1995). The snails *Radix* spp. and *Bithynia tentaculata* are other important primary consumers in the target community that are readily consumed by crayfish (Nyström, Brönmark, & Granéli, 1999; Olsen, Lodge, Capelli, & Houlihan, 1991). Testing predation on these three mollusc taxa could thus inform the assessment of both invasion success and ecological impacts of the marbled crayfish (Figures S1 and S2). The quasi-focal organism (spiny-cheek crayfish) is a major prey of perch (*Perca fluviatilis*), which is a relatively abundant fish species in German low-land lakes and often holds key positions in food webs (Persson, Bystrom, & Wahlstrom, 2000). Predation by perch is likely restricted to immature or post-moult crayfish because of gape size limitation and the formidable defences of mature crayfish. Nonetheless, this predatory fish could depress crayfish population dynamics, and thus it is a potentially important interactor (Figures S1 and S2).

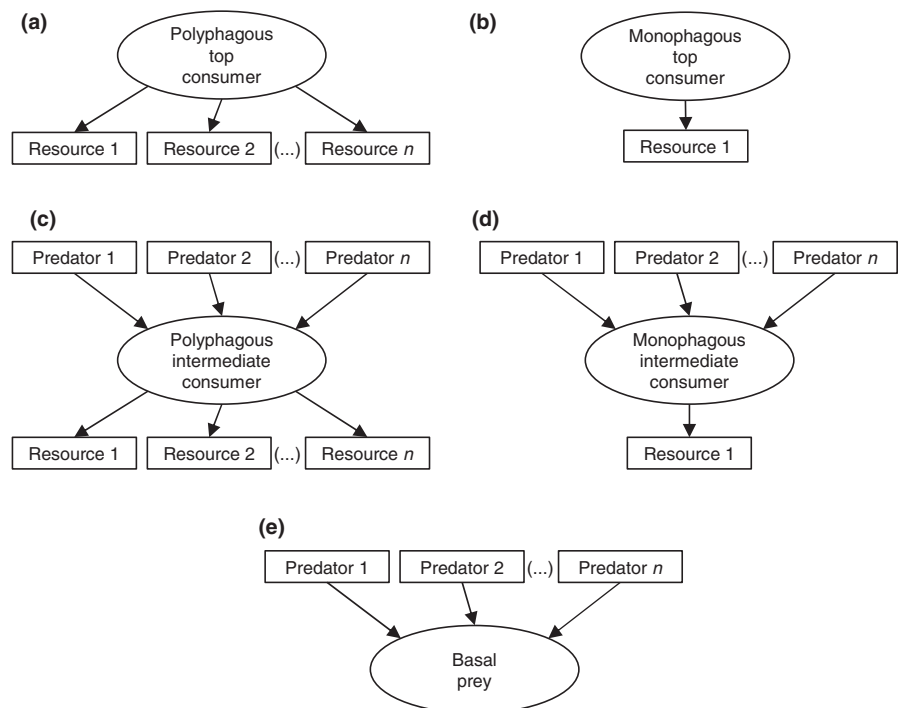


FIGURE 2 Hypothetical interaction module structures for testing trophic interactions of a focal organism (oval shapes) representing top (a, b), intermediate (c, d) and basal (e) trophic positions, and two extrema on the diet-breadth continuum (polyphagous [a, c] and monophagous [b, d])

4 | EMPIRICALLY TESTING TROPHIC INTERACTIONS FOR THE PRIORITIZED INTERACTION SUBSET

Introduction of an organism that is of a predator or prey archetype already present in the resident community implies that resident prey or predators, respectively, are likely already familiar with such an archetype (Saul & Jeschke, 2015). Because of such experience, it can be assumed that a novel organism can impact resident prey populations more strongly than their currently experienced predation pressure if its predatory traits toward a particular prey archetype are superior relative to its resident analogues. Similarly, a novel organism risks high impact from resident predators if its defences are weaker than those of its resident analogues, thus promoting prey switching. Therefore, comparing the trophic interaction strengths of the focal organism with its prey or predators, with those of an ecologically similar resident, where such exists, provides a useful benchmark for gauging the magnitude of interaction strength (Dick et al., 2014; van Kleunen, Dawson, Schlaepfer, Jeschke, & Fischer, 2010). By definition, no two species are identical (Ordonez, 2014), but resident organisms that are of the same predator or prey archetype (Cox & Lima, 2006; Winemiller et al., 2015) can offer a useful approximation of a reference baseline if any relevant functional differences between otherwise analogous species are acknowledged. In our worked example, the marbled crayfish co-occurs with other omnivorous crayfish (Chucholl et al., 2012) of a similar predator and prey archetype that can be used as comparators (Figure S1).

On the other hand, a novel organism that does not have any resident comparator is likely to have characteristics largely unfamiliar to resident prey and predators and thus the potential to bypass their defences and offences (Saul & Jeschke, 2015). In such a case, the absolute, rather than comparative interaction strength of the focal novel organism with its prey and predators can be of primary interest, and offtake rate of prey in relation to its reproductive rate can be used to predict impact on prey populations (MacNeil et al., 2013; Figure 1). Qualitative pilot experiments can inform which degree of functional similarity can be assumed as a baseline.

5 | INFERENCE TO REAL ECOSYSTEMS

In situ measurements and manipulations provide realistic settings, but tend to allow poor control of confounding factors (but see Barrios-O'Neill, Dick, Ricciardi, et al., 2014). Also, they cannot be carried out if the focal organism is not (yet) present in the target environment. Laboratory experiments, on the other hand, typically simplify biotic and abiotic contexts, and the applied relevance of their results depends on the degree to which experimental settings facilitate natural offensive and defensive behaviour. For example, sheltering or camouflage may alter the shape of density-dependent predation, in that individual organisms devoid of their typical protective settings during experiments are more exposed to predation (Alexander, Dick, & O'Connor, 2013; Barrios-O'Neill, Dick, Emmerson, Ricciardi,

& MacIsaac, 2015; Horppila et al., 2003; Whittingham & Markland, 2002). Both ambient temperatures and environmental hypoxia can also affect activity level, and moderate predator-prey interactions (Englund, Öhlund, Hein, & Diehl, 2011; Laverty, Dick, Alexander, & Lucy, 2015; Penk, Jeschke, Minchin, & Donohue, 2016). Laboratory-derived functional responses typically isolate an individual predator and single prey species (e.g. Barrios-O'Neill, Dick, Ricciardi, et al., 2014; Dick et al., 2013; Xu et al., 2016; but see Alexander et al., 2013; Medoc, Spataro, & Arditi, 2013; Wasserman et al., 2016), and thus rarely account for prey switching or interference among predators which could affect the outcome of an interaction (Amarasekare, 2002; Tschanz, Bersier, & Bacher, 2007; van Leeuwen, Brännström, Jansen, Dieckmann, & Rossberg, 2013). The degree of spatio-temporal overlap of habitat use by the focal organism and its interaction partners is another important consideration (Polis, Anderson, & Holt, 1997). For example, a potentially strong interactor may have only a small time window for realising such interactions if it rarely encounters particular prey and predator species. Detailed propositions for ameliorating these problems are beyond the scope of this manuscript, but we emphasize that lack of their consideration can undermine inference.

The need to quantify absolute interaction strengths accurately is largely circumvented in comparative studies, which focus on consumption rates relative to a native analogue rather than on absolute values, with an underlying assumption that both comparators would be influenced similarly by experimental artefacts (Dick et al., 2014). Indeed, comparative functional responses derived from simple laboratory experiments can be highly successful in explaining real-ecosystem ecological impacts of invaders across taxonomic and trophic groups (Dick et al., 2017). Context-dependencies may thus be particularly influential in making inference from studies on a novel organism that does not have a resident comparator because they rely on quantification of absolute interaction strengths.

Our framework specifically focuses on biological interactions, but the importance of intrinsic characteristics of the novel organism also has to be considered. For example, prognoses of population and community dynamics require at least some information on the reproductive rates of the focal organism and its interaction partners. The reproductive rate of a consumer determines the degree to which it can capitalize numerically on its ability to exploit prey and cumulatively increase its impact on prey populations, whereas the reproductive rate of prey determines their capacity to persist under given predation pressure (Twardochleb, Novak, & Moore, 2012). Both of these factors are key drivers of community dynamics.

Any model necessitates a trade-off between generality, realism and precision (Levins, 1966). It is impossible to achieve all of these simultaneously to full extent, and the decision as to how to optimize this trade-off depends upon the focal system. We therefore present a basic framework here, which needs to be adjusted and extended on a case-by-case basis to make it useful for the particular focal system in question. For example, for many systems it will be useful to incorporate non-consumptive or indirect interactions, or impacts on ecosystem services into the basic framework.

6 | NON-CONSUMPTIVE AND INDIRECT INTERACTIONS

Consumptive interactions are the key focus of our framework (Figure 1). However, non-consumptive and indirect (trait-mediated) interactions, for example through interference, facilitation and inhibition, can have important implications for community dynamics and in some cases even take prominence over direct impacts (Suraci, Clinchy, Dill, Roberts, & Zanette, 2016). Indirect interactions occur when one species alters the effects that another species has on a third, potentially confounding predicted impacts of a novel organism that are derived from two-species studies (White, Wilson, & Clarke, 2006). For instance, changes to the foraging behaviour of a resident intermediate consumer as a result of the presence of a novel higher-order predator may alter the strength of interactions with a basal prey resource, releasing it from predation pressure (Townsend, 1996). Alternatively, the presence of a resident higher-order predator may result in an exacerbated effect of a non-resident intermediate species towards its prey in comparison to a resident consumer, again influencing impact of the focal organism (Barrios-O'Neill, Dick, Emmerson, et al., 2014). Quantification of beneficial and disadvantageous outcomes of such interactions, in particular regulation of feeding and mortality rates, could be readily integrated in the empirical steps of our framework.

7 | CONCLUSIONS

Key theoretical progress on functional responses in invasion ecology has come from retrospective empirical attempts to explain invasion success and impacts of established invaders (Bollache, Dick, Farnsworth, & Montgomery, 2008; Dick et al., 2013; Hooff & Bollens, 2004; Radford, Dickinson, & Lord, 2007). Such attempts typically focus on isolated interactions in which the invader is clearly efficient and superior over a native comparator. However, biological invasions are highly dependent on biological contexts (Donohue et al., 2013; Ricciardi, Hoopes, Marchetti, & Lockwood, 2013; Saul et al., 2013), and robust prospective applications require a more comprehensive assessment network with multiple interaction partners, including predators of the focal organism. Applications of functional responses in biocontrol frequently fail to explain impact on individual prey organisms (Fernández-Arhex & Corley, 2003; Lester & Harmsen, 2002). The inclusion of predators and alternative prey, together with more realistic representation of key abiotic conditions and explicit discussion of the relevance of results to natural ecosystems can improve explanatory and predictive power of impact assessments. We focused here on predation in a broad sense, but the same assessment protocol and analogous empirical methods can be used for detritivorous and autotrophic energy acquisition (McNickle & Brown, 2014; Radford et al., 2007).

Risk assessment based on performance in comparable environments, where such information exists, is less laborious than collecting new data. However, interaction partners in new and existing ranges should be compared in a structured way to minimize bias. The steps

of our framework that are based on existing data can be used to inform such comparisons (Figure 1). Furthermore, novel organisms can be introduced to dissimilar communities or abiotic conditions in comparison to their existing ranges, or they can be absent in nature. Such scenarios preclude comparisons based on performance elsewhere and necessitate collection of new data (Figure 1). In the face of limiting resources, a compromise between experimental complexity and accuracy of risk assessments needs to be reached on a case-by-case basis. Notably, relevant empirical data can be collected in situ (Angerbjorn, Tannerfeldt, & Erlinge, 1999; Barrios-O'Neill, Dick, Ricciardi, et al., 2014; Goss-Custard et al., 2006; Moustahfid et al., 2010), permitting empirical testing of organisms that do not lend themselves well to laboratory conditions, or should not be interfered with on ethical grounds. In any case, the broader interaction network in the focal ecosystem should be at least theoretically considered, even if just to critically scrutinize the assessment outcomes. The non-empirical steps of our framework can inform such exercises regardless of the scale or complexity of the system in question.

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AUTHORS' CONTRIBUTIONS

M.P., W.C.S. and J.M.J. conceived key ideas; M.P. led the writing of the manuscript; all authors contributed critically to the drafts.

DATA ACCESSIBILITY

This manuscript does not include any data.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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Supporting Information

A trophic interaction framework for identifying the invasive capacity of novel organisms

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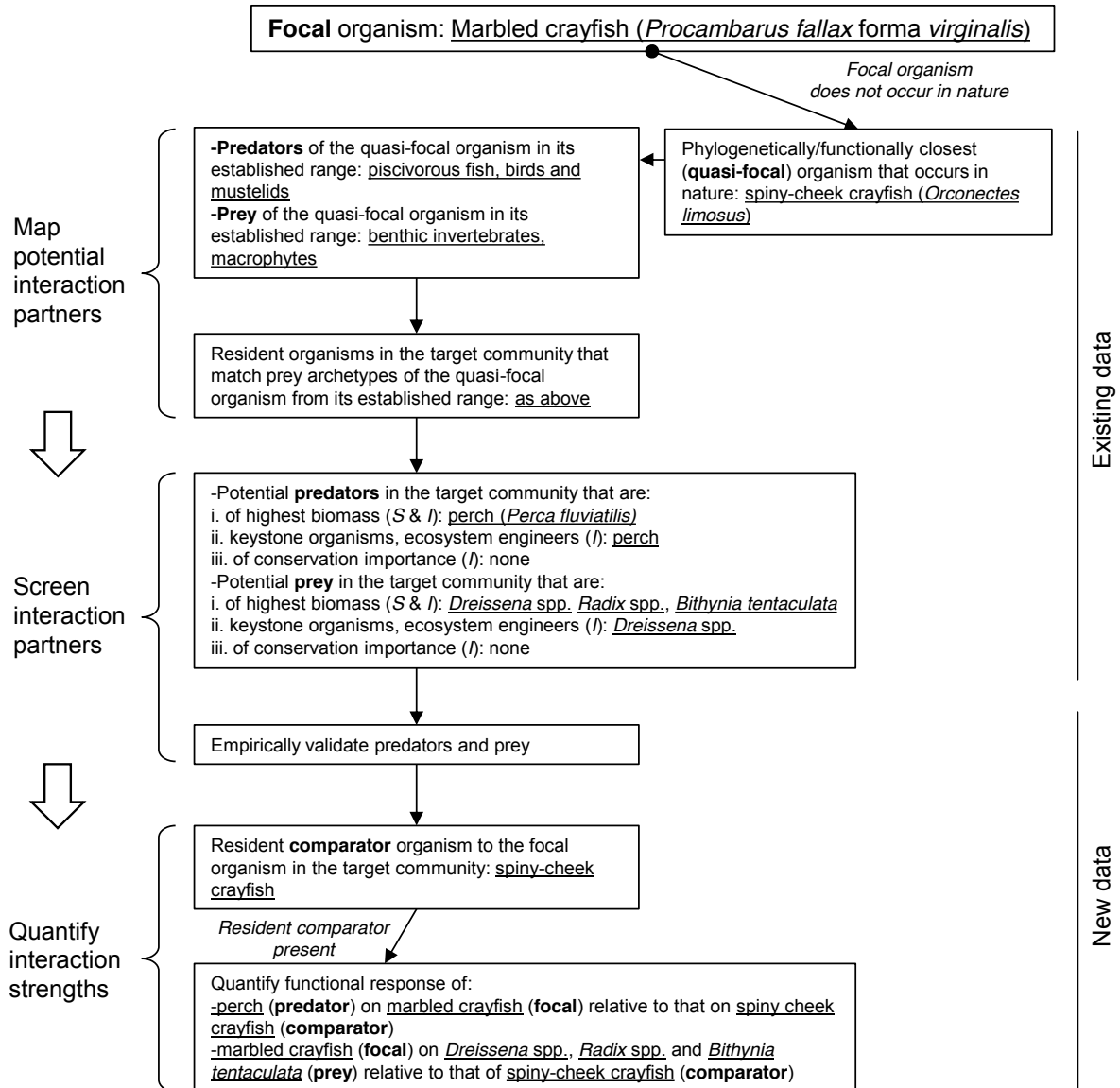


Fig. S1. Illustration of the framework for quantifying interaction strength of a focal organism with resident organisms in the target community, using an example of predator and prey selection for the marbled crayfish (*Procambarus fallax* forma *virginalis*) in a German low-land lake. *S* and *I* indicate prey categories relevant for the assessment of invasion success and ecological impacts, respectively. Quasi-focal organism is also the resident comparator in this example.

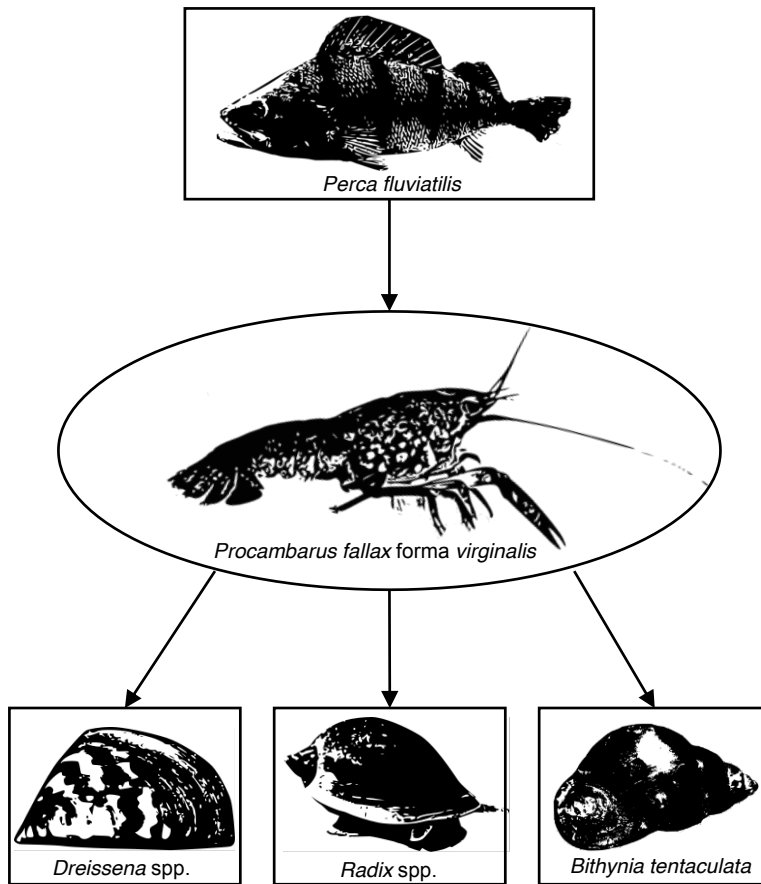


Fig. S2. Illustration of the interaction module structure for testing using an example of predator and prey (top and bottom boxes, respectively) selected for the marbled crayfish (central box) in a German low-land lake. Organisms are not to scale.