Freie Universität Berlin

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

Author(s): Penk, M., Saul, W.-C., Dick, J. T. A., Donohue, I., Alexander, M. E., Linzmaier, S., & Jeschke, J. M.

Document type: Postprint

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

1 **A trophic interaction framework for identifying the invasive**

2 **capacity of novel organisms**

3

4 Running title: An assessment framework for novel organisms

5 Word count: 6999

6

7 Marcin Penk*[1,2], Wolf-Christian Saul[2,3,4], Jaimie T.A. Dick[5], Ian Donohue[1], Mhairi E.

8 Alexander[6], Stefan Linzmaier[2,3,4] and Jonathan M. Jeschke[2,3,4]

9

10 [1]School of Natural Sciences, Trinity College Dublin, College Green, Dublin 2, Ireland

11 [2]Department of Biology, Chemistry, Pharmacy, Institute of Biology, Freie Universität Berlin,

12 Königin-Luise-Str. 1-3, 14195 Berlin, Germany

13 [3]Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB), Müggelseedamm 310,

14 12587 Berlin, Germany

15 [4]Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), Altensteinstr. 34,

16 14195 Berlin, Germany

17 [5]Institute for Global Food Security, School of Biological Sciences, Queen's University

18 Belfast, MBC, 97 Lisburn Road, Belfast BT9 7BL, Northern Ireland, UK

19 [6]Institute for Biomedical and Environmental Health Research (IBEHR), School of Science

20 and Sport, University of the West of Scotland, Paisley PA1 2BE, Scotland, UK

21

22 Corresponding author: penkm@tcd.ie

23 **Summary**

24 1. The likelihood and impacts of invasions by novel organisms (e.g. non-native species,

25   genetically-modified organisms) on the composition and functioning of receiving

26   biological communities hinges on their capacity to exploit resources and/or avoid

27   predation relative to resident counterparts. While assessment of invasion risk based on the

28   comparison of functional responses (per-capita consumption rate as a function of resource

29   density) of novel species with native analogues has been gaining popularity, it may be

30   undermined if alternative prey and potential predators are not represented realistically.

31 2. Here, we propose a conceptual framework that enables rigorous identification of trophic

32   traits conducive to invasion success by novel organisms – irrespective of their trophic

33   position – and their likely ecological impacts, given their arrival and establishment. We

34   focus on consumption here, but our framework can also be used for autotrophic energy

35   acquisition, and extended to non-trophic and indirect interactions.

36 3. The framework enables a structured and prioritised selection of subsets of trophic links for

37   invasion risk assessment. It is based on foraging theory and advances in comparative

38   functional responses in invasion ecology. It can even be used in the absence of a resident

39   comparator organism and when resources or predators are only partly known.

40 4. Our approach enhances the predictive power of species screening, and thus advances

41   prevention and management of invasions under a common framework for all types of

42   novel organisms.

43

44 **Key-words:** alien species, dietary generalism, ecological novelty, GMO, invasion success,

45 functional responses, predator-prey trophic interactions, risk assessment

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 prioritising 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, synthesised 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 (Mitchell *et al.* 2006; Downing *et al.* 2012; Mayer *et al.* 2013; 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 (Terborgh & Estes 2010; O'Connor *et al.* 2013) and food limitations for competitors (Strayer & Malcom 2007). Introduced predators can therefore affect resident prey populations significantly (Hays & Conant 2007;

71 Strayer 2009; Downing *et al.* 2012), with efficient exploitation of resources being conducive

72 to high population growth, likely invasion success, and potentially considerable ecological

73 impacts. Resource density is a key determinant of the feeding rate, and this relationship is

74 characterised by 'functional response' curves (Holling 1959). For instance, decreasing prey

75 density can reduce predator encounter rates with prey and thus offer a density-dependent prey

76 refuge in a predator-prey system with a sigmoidal (i.e. Type III) functional response, but not

77 with alternative functional response shapes where high proportions of prey are killed at low

78 prey densities (Type I, II or their variants; Holling 1959; Jeschke, Kopp & Tollrian 2004;

79 Jeschke & Tollrian 2005). Thus, the height – in particular the maximum feeding rate (i.e.

80 curve asymptote) – and the shape of functional responses can reveal characteristics of

81 consumer-resource interactions that are important for community dynamics and composition.

82   Invading predators with high ecological impact on their prey populations often have

83 elevated functional responses compared to ecologically similar native species (Dick *et al.*

84 2017). Using comparative functional responses as an empirical screening method is thus

85 rapidly gaining popularity among invasion biologists (Dick *et al.* 2013; Alexander *et al.*

86 2014; Barrios-O'Neill *et al.* 2014a; Rosewarne *et al.* 2016; Xu *et al.* 2016). The method

87 typically infers invasion success and/or potential impacts from a limited number of prey

88 species (frequently just one). However, biological invasions tend to lead to replacement of

89 niche specialists by generalists (Clavel, Julliard & Devictor 2010), and numerous studies

90 have identified a positive association between dietary generalism and invasion success

91 (Bessa-Gomes *et al.* 2003; Jeschke & Strayer 2006; Romanuk *et al.* 2009; Clavel, Julliard &

92 Devictor 2010; Arbaciauskas, Lesutiene & Gasiunaite 2013, but see Cassey *et al.* 2004 and

93 Jackson *et al.* 2016). Thus, the inefficient use of one particular resident prey species does not

94 necessarily preclude invasion success or impact upon ecological networks with realistic

95 complexity. In other cases, a resident organism may be an inferior predator on a particular

96   prey species, and falsely appear a weaker overall interactor, compared to an introduced

97   predator solely as a result of differing specialisation, despite apparent ecological similarity

98   (Rosenfeld 2002; Dunoyer *et al.* 2014). Investigating functional responses with multiple prey,

99   thereby taking into account the potential role of generalism and specialism, can buffer against

100   such biases and at the same time improve the much needed representation of whole-

101   ecosystem impacts of novel organisms (Ehrenfeld 2011; Simberloff 2011; Penk, Irvine &

102   Donohue 2015). Furthermore, novel organisms can themselves be controlled by resident

103   predators (Romanuk *et al.* 2009; MacNeil *et al.* 2013; Pintor & Byers 2015). Not accounting

104   for top-down control experienced by introduced species, as has been typically the case in

105   functional response-based screening methods, risks over-estimating their consumptive

106   impacts and invasion success (but see Barrios-O'Neill *et al.* 2014b; Alexander, Raven &

107   Robinson 2015).

108   Both top-down and bottom-up trophic interactions can thus directly affect the

109   survival, fitness and ecological impacts of novel organisms. The complexity of these trophic

110   links, including diet breadth and number of enemies, is an important determinant of invasion

111   success (Romanuk *et al.* 2009). However, the logistics of incorporating multiple prey and

112   predators into comparative functional responses may be demanding and frequently

113   prohibitive.

114   We propose a conceptual framework for identifying and selecting a prioritised subset

115   of trophic links to empirically identify the capacity for invasion success and ecological

116   impacts of novel organisms (Fig. 1). We provide a worked example of the application of the

117   framework for an intermediate consumer, the marbled crayfish (*Procambarus fallax* forma

118   *virginalis*) in German low-land lakes (Fig. S1). This includes selection of both predators and

119   prey, and can therefore instruct assessment of organisms of any trophic position. In addition,

120   the marbled crayfish does not have any known native populations, and thus it is exemplary of

121 quite complex assessment scenarios. For clarity, our arguments relate to predation, which

122 includes true predation, herbivory, parasitism and parasitoidism. However, detritivory can

123 also be an important dietary subsidy of generalist consumers (Wise, Moldenhauer & Halaj

124 2006; Jackson *et al.* 2016) and should be carried through the assessment if it contributes to

125 the diet of the novel ('focal') organism. Although we focus on consumption, our framework

126 can be applied to autotrophic energy acquisition, and extended to non-trophic and indirect

127 interactions. Whereas the non-empirical steps of our framework are readily applicable to any

128 type of interaction, non-trophic interactions may require different empirical methods.

129

130 **Mapping potential interaction partners in the target community**

131 Unless interaction with a particular resident organism is an *a priori* focus of assessment, an

132 initial step of comprehensively mapping a potential network of direct consumptive

133 interactions of the focal organism in the receiving ('target') community should enable

134 minimisation of selection biases that may impede realistic assessment of the impact of the

135 novel organism. This can be achieved by first listing all partners in direct consumptive

136 interactions of the focal organism in its established range. This is then followed by matching

137 all resident organisms in the target community that conform to the archetypes of these

138 interaction partners and are likely to at least partly share spatio-temporal distribution patterns

139 with the focal organism (Fig. 1). We define an archetype as organisms that have a similar set

140 of morphological and behavioural traits that can condition a given type of interaction (Cox &

141 Lima 2006; Winemiller *et al.* 2015), for example, feeding or defence strategy.

142   Observed trophic interactions in a given environment may not fully represent the

143 feeding preferences of an organism (Futuyma & Moreno 1988; Devictor *et al.* 2010), and

144 trophic interaction strength with a particular prey may depend on its availability in

145 comparison to other prey rather than on the true preference of the consumer (Jaworski *et al.*

146   2013; Davis *et al.* 2015; Hanmer et al. 2017), as well as on environmental drivers. Thus,

147   interaction partners of the focal organism as well as interaction strengths may vary among

148   communities that differ in species composition and densities. If the focal organism is already

149   established in the target environment, site-specific data about interaction partners should be

150   given precedence above data from other areas. Otherwise, information from multiple

151   communities within the distribution range of the focal species may improve control for

152   context-dependencies. Assigning preference attributes based on how frequent and dominant

153   interaction partners are throughout the established range (e.g. Kissling *et al.* 2014) can then

154   help prioritise the selection of interaction partners for assessment. Considering ontogenetic

155   stages of the focal organism with contrasting interaction partners (e.g. size class, identity or

156   trophic guild of prey or enemies) could further improve predictions because limitation at any

157   single stage preceding reproduction could constrict population dynamics (Werner & Gilliam

158   1984; Rudolf & Lafferty 2011).

159   For focal organisms that do not yet occur in nature, such as genetically modified,

160   resurrected, synthetic, hybridised or selectively bred organisms, interaction partners of

161   phylogenetically or functionally closest ('quasi-focal') organisms may provide reasonable

162   approximation. For example, the marbled crayfish, introduced recently to German

163   freshwaters (Chucholl, Morawetz & Groß 2012), originated in the aquarium trade and does

164   not have any known native populations (Vogt *et al.* 2015). However, it is morphologically

165   and functionally similar to the spiny-cheek crayfish (*Orconectes limosus*), a well-established

166   earlier invader in Germany which can be considered a quasi-focal organism. The spiny-cheek

167   crayfish is an omnivore that feeds on benthic invertebrates and macrophytes, and itself falls

168   prey to fish, waterfowl and mustelids. Interaction partners of the spiny-cheek crayfish are

169   thus good candidate prey and predators of the marbled crayfish (Fig. S1).

170

Screening for a prioritised 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 – invasion success, impact, or both (Fig. 1). The colonisation of areas beyond the point of introduction, synonymous with invasion success (Blackburn *et al.* 2011), is likely if an organism is able to utilise 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 prioritised 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 (Lockwood, Hoopes & Marchetti 2007; Penk, Irvine & Donohue 2015; Jackson *et al.* 2016). Further, interactions with keystone species or ecosystem engineers (Jones, Lawton & Shachak 1994; Power *et al.* 1996; Angelini *et al.* 2015), 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 (Fig. 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

196 ecosystem engineers, and those of conservation importance; Fig. 1), will depend on the

197 purpose of the assessment, trophic level and niche breadth of the focal organism, food web

198 complexity in the target ecosystem, management priorities and logistic constraints. For

199 example, monophagous and oligophagous predators, including parasites and parasitoids, have

200 inherently limited numbers of prey, while mesopredators typically have fewer predators than

201 basal prey (Turney & Buddle 2016). Figure 2 shows exemplary hypothetical module

202 structures for interaction settings between focal and resident organisms, indicating the

203 diversity of interactions that need to be considered. Some of the interactor group categories

204 will frequently overlap, and some may not be present in the target community. If the focal

205 organism is already established, experimental trials or field data can be used to ascertain and

206 prioritise interaction partners in the target community before engaging in full assessment.

207   Empirical examples of structured choices of prey in functional response studies of

208 invasive species are rare (but see Dick *et al.* 2013; Barrios-O'Neill *et al.* 2016; Xu *et al.*

209 2016). In our worked example of the marbled crayfish (Fig. S1), the mussel *Dreissena* spp.

210 has high abundance in the target community and is an ecosystem engineer. Dreissenids and

211 other animal prey with poor escape response are key and preferred contributors to crayfish

212 energy budgets (Momot 1995). The snails *Radix* spp. and *Bithynia tentaculata* are other

213 important primary consumers in the target community that are readily consumed by crayfish

214 (Olsen *et al.* 1991; Nyström, Brönmark & Granéli 1999). Testing predation on these three

215 mollusc taxa could thus inform the assessment of both invasion success and ecological

216 impacts of the marbled crayfish (Figs. S1 and S2). The quasi-focal organism (spiny-cheek

217 crayfish) is a major prey of perch (*Perca fluviatilis*), which is a relatively abundant fish

218 species in German low-land lakes and often holds key positions in food webs (Persson,

219 Bystrom & Wahlstrom 2000). Predation by perch is likely restricted to immature or post-

220 moult crayfish because of gape size limitation and the formidable defences of mature

221 crayfish. Nonetheless, this predatory fish could depress crayfish population dynamics, and

222 thus it is a potentially important interactor (Figs. S1 and S2).

223

224 **Empirically testing trophic interactions for the prioritised interaction subset**

225 Introduction of an organism that is of a predator or prey archetype already present in the

226 resident community implies that resident prey or predators, respectively, are likely already

227 familiar with such an archetype (Saul & Jeschke 2015). Because of such experience, it can be

228 assumed that a novel organism can impact resident prey populations more strongly than their

229 currently experienced predation pressure if its predatory traits toward a particular prey

230 archetype are superior relative to its resident analogues. Similarly, a novel organism risks

231 high impact from resident predators if its defences are weaker than those of its resident

232 analogues, thus promoting prey switching. Therefore, comparing the trophic interaction

233 strengths of the focal organism with its prey or predators, with those of an ecologically

234 similar resident, where such exists, provides a useful benchmark for gauging the magnitude

235 of interaction strength (van Kleunen *et al.* 2010; Dick *et al.* 2014). By definition, no two

236 species are identical (Ordonez 2014), but resident organisms that are of the same predator or

237 prey archetype (Cox & Lima 2006; Winemiller *et al.* 2015) can offer a useful approximation

238 of a reference baseline if any relevant functional differences between otherwise analogous

239 species are acknowledged. In our worked example, the marbled crayfish co-occurs with other

240 omnivorous crayfish (Chucholl, Morawetz & Groß 2012) of a similar predator and prey

241 archetype that can be used as comparators (Fig. S1).

242 On the other hand, a novel organism that does not have any resident comparator is

243 likely to have characteristics largely unfamiliar to resident prey and predators and thus the

244 potential to bypass their defences and offences (Saul & Jeschke 2015). In such a case, the

245 absolute, rather than comparative interaction strength of the focal novel organism with its

246 prey and predators can be of primary interest, and offtake rate of prey in relation to its

247 reproductive rate can be used to predict impact on prey populations (MacNeil *et al.* 2013;

248 Fig. 1). Qualitative pilot experiments can inform which degree of functional similarity can be

249 assumed as a baseline.

250

251 **Inference to real ecosystems**

252 *In situ* measurements and manipulations provide realistic settings, but tend to allow poor

253 control of confounding factors (but see Barrios-O'Neill *et al.* 2014a). Also, they cannot be

254 carried out if the focal organism is not (yet) present in the target environment. Laboratory

255 experiments, on the other hand, typically simplify biotic and abiotic contexts, and the applied

256 relevance of their results depends on the degree to which experimental settings facilitate

257 natural offensive and defensive behaviour. For example, sheltering or camouflage may alter

258 the shape of density-dependent predation, in that individual organisms devoid of their typical

259 protective settings during experiments are more exposed to predation (Whittingham &

260 Markland 2002; Horppila *et al.* 2003; Alexander, Dick & O'Connor 2013; Barrios-O'Neill *et*

261 *al.* 2015). Both ambient temperatures and environmental hypoxia can also affect activity

262 level, and moderate predator-prey interactions (Englund *et al.* 2011; Laverty *et al.* 2015; Penk

263 *et al.* 2016). Laboratory-derived functional responses typically isolate an individual predator

264 and single prey species (e.g. Dick *et al.* 2013; Barrios-O'Neill *et al.* 2014a; Xu *et al.* 2016,

265 but see Alexander, Dick & O'Connor 2013; Medoc, Spataro & Arditi 2013; Wasserman *et al.*

266 2016), and thus rarely account for prey switching or interference among predators which

267 could affect the outcome of an interaction (Amarasekare 2002; Tschanz, Bersier & Bacher

268 2007; van Leeuwen *et al.* 2013). The degree of spatio-temporal overlap of habitat use by the

269 focal organism and its interaction partners is another important consideration (Polis,

270 Anderson & Holt 1997). For example, a potentially strong interactor may have only a small

271 time window for realising such interactions if it rarely encounters particular prey and predator

272 species. Whereas detailed propositions for ameliorating these problems are beyond the scope

273 of this manuscript, we emphasise that lack of their consideration can undermine inference.

274 On the other hand, the need to quantify absolute interaction strengths accurately is

275 circumvented in comparative studies, which focus on consumption rates relative to a native

276 analogue rather than on absolute values, with an underlying assumption that both

277 comparators would be influenced similarly by experimental artefacts (Dick *et al.* 2014).

278 Indeed, comparative functional responses derived from simple laboratory experiments can be

279 highly successful in explaining real-ecosystem ecological impacts of invaders across

280 taxonomic and trophic groups (Dick *et al.* 2017). Context-dependencies may thus be

281 particularly influential in making inference from studies on a novel organism that does not

282 have a resident comparator because they rely on quantification of absolute interaction

283 strengths.

284 Our framework specifically focuses on biological interactions, but the importance of

285 intrinsic characteristics of the novel organism also has to be considered. For example,

286 prognoses of population and community dynamics require at least some information on the

287 reproductive rates of the focal organism and its interaction partners. The reproductive rate of

288 a consumer determines the degree to which it can capitalise numerically on its ability to

289 exploit prey and cumulatively increase its impact on prey populations, whereas the

290 reproductive rate of prey determines their capacity to persist under given predation pressure

291 (Twardochleb, Novak & Moore 2012). Both of these factors are key drivers of community

292 dynamics.

293 Any model necessitates a trade-off between generality, realism and precision (Levins

294 1966). It is impossible to achieve all of these simultaneously to full extent, and the decision

295 as to how to optimise this trade-off depends upon the focal system. We therefore present a

296 basic framework here, which needs to be adjusted and extended on a case-by-case basis to

297 make it useful for the particular focal system in question. For example, for many systems it

298 will be useful to incorporate non-consumptive or indirect interactions, or impacts on

299 ecosystem services into the basic framework.

300

301 **Non-consumptive and indirect interactions**

302 Consumptive interactions are the key focus of our framework (Fig. 1). However, non-

303 consumptive and indirect (trait-mediated) interactions, for example through interference,

304 facilitation and inhibition, can have important implications for community dynamics and in

305 some cases even take prominence over direct impacts (Suraci *et al.* 2016). Indirect

306 interactions occur when one species alters the effects that another species has on a third,

307 potentially confounding predicted impacts of a novel organism that are derived from two-

308 species studies (White, Wilson & Clarke 2006). For instance, changes to the foraging

309 behaviour of a resident intermediate consumer as a result of the presence of a novel higher-

310 order predator may alter the strength of interactions with a basal prey resource, releasing it

311 from predation pressure (Townsend 1996). Alternatively, the presence of a resident higher-

312 order predator may result in an exacerbated effect of a non-resident intermediate species

313 towards its prey in comparison to a resident consumer, again influencing impact of the focal

314 organism (Barrios-O'Neill *et al.* 2014b). Quantification of beneficial and disadvantageous

315 outcomes of such interactions, in particular regulation of feeding and mortality rates, could be

316 readily integrated in the empirical steps of our framework.

317

318 **Conclusions**

319 Key theoretical progress on functional responses in invasion ecology has come from

320 retrospective empirical attempts to explain invasion success and impacts of established

321 invaders (Hooff & Bollens 2004; Radford, Dickinson & Lord 2007; Bollache *et al.* 2008;

322 Dick *et al.* 2013). Such attempts typically focus on isolated interactions in which the invader

323 is clearly efficient and superior over a native comparator. However, biological invasions are

324 highly dependent on biological contexts (Donohue *et al.* 2013; Ricciardi *et al.* 2013; Saul,

325 Jeschke & Heger 2013), and robust prospective applications require a more comprehensive

326 assessment network with multiple interaction partners, including predators of the focal

327 organism. Applications of functional responses in biocontrol frequently fail to explain impact

328 on individual prey organisms (Lester & Harmsen 2002; Fernández-Arhex & Corley 2003).

329 The inclusion of predators and alternative prey, together with more realistic representation of

330 key abiotic conditions and explicit discussion of the relevance of results to natural

331 ecosystems can improve explanatory and predictive power of impact assessments. We

332 focused here on predation in a broad sense, but the same assessment protocol and analogous

333 empirical methods can be used for detritivorous and autotrophic energy acquisition (Radford,

334 Dickinson & Lord 2007; McNickle & Brown 2014).

335   Risk assessment based on performance in comparable environments, where such

336 information exists, is less laborious than collecting new data. However, interaction partners in

337 new and existing ranges should be compared in a structured way to minimise bias. The steps

338 of our framework that are based on existing data can be used to inform such comparisons

339 (Fig. 1). Furthermore, novel organisms can be introduced to dissimilar communities or

340 abiotic conditions in comparison to their existing ranges, or they can be absent in nature.

341 Such scenarios preclude comparisons based on performance elsewhere and necessitate

342 collection of new data (Fig. 1). In the face of limiting resources, a compromise between

343 experimental complexity and accuracy of risk assessments needs to be reached on a case-by-

344 case basis. Notably, relevant empirical data can be collected *in situ* (Angerbjorn, Tannerfeldt

345 & Erlinge 1999, Goss-Custard *et al.* 2006; Moustahfid *et al.* 2010, Barrios-O'Neill *et al.*

346 2014a), permitting empirical testing of organisms that do not lend themselves well to

347 laboratory conditions, or should not be interfered with on ethical grounds. In any case, the

348 broader interaction network in the focal ecosystem should be at least theoretically considered,

349 even if just to critically scrutinise the assessment outcomes. The non-empirical steps of our

350 framework can inform such exercises regardless of the scale or complexity of the system in

351 question.

352

359

360 **Data Accessibility**

361 This manuscript does not include any data.

362

363 **Author contributions statement**

364 MP, WCS and JMJ conceived key ideas; MP led the writing of the manuscript; all authors

365 contributed critically to the drafts.

366

367 **References**

368 Alexander, M.E., Dick, J.T.A. & O'Connor, N.E. (2013) Trait-mediated indirect interactions

369 in a marine intertidal system as quantified by functional responses. *Oikos,* **122**, 1521–1531.

370

371 Alexander, M.E., Dick, J.T.A., Weyl, O.L.F., Robinson, T.B. & Richardson, D.M. (2014)

372 Existing and emerging high impact invasive species are characterized by higher functional

373 responses than natives. *Biology Letters,* **10**, doi: 10.1098/rsbl.2013.0946.

374

375 Alexander, M.E., Raven, H.J. & Robinson, T.B. (2015) Foraging decisions of a native whelk,

376 *Trochia cingulata* Linnaeus, and the effects of invasive mussels on prey choice. *Journal of*

377 *Experimental Marine Biology and Ecology,* **470**, 26–33.

378

379 Amarasekare, P. (2002) Interference competition and species coexistence. *Proceedings of the*

380 *Royal Society B: Biological Sciences,* **269**, 2541–2550.

381

382 Angelini, C., van der Heide, T., Griffin, J.N., Morton, J.P., Derksen-Hooijberg, M., Lamers,

383 L.P.M., Smolders, A.J.P. & Silliman, B.R. (2015) Foundation species' overlap enhances

384 biodiversity and multifunctionality from the patch to landscape scale in southeastern United

385 States salt marshes. *Proceedings of the Royal Society of London B: Biological Sciences,* **282**,

386 doi: 10.1098/rspb.2015.0421.

387

388 Angerbjorn, A., Tannerfeldt, M. & Erlinge, S. (1999) Predator-prey relationships: Arctic

389 foxes and lemmings. *Journal of Animal Ecology*, **68**, 34–49.

390

391 Arbaciauskas, K., Lesutiene, J. & Gasiunaite, Z.R. (2013) Feeding strategies and elemental

392 composition in Ponto-Caspian peracaridans from contrasting environments: can

393 stoichiometric plasticity promote invasion success? *Freshwater Biology,* **58**, 1052–1068.

394

395 Barrios-O'Neill, D., Dick, J.T.A., Ricciardi, A., MacIsaac, H.J. & Emmerson, M.C. (2014a)

396   Deep impact: in situ functional responses reveal context-dependent interactions between

397   vertically migrating invasive and native mesopredators and shared prey. *Freshwater Biology*,

398   **59**, 2194–2203.

399

400   Barrios-O'Neill, D., Dick, J.T.A., Emmerson, M.C., Ricciardi, A., MacIsaac, H.J., Alexander,

401   M.E. & Bovy, H.C. (2014b) Fortune favours the bold: a higher predator reduces the impact of

402   a native but not an invasive intermediate predator. *Journal of Animal Ecology,* **83**, 693–701.

403

404   Barrios-O'Neill, D., Dick, J.T.A., Emmerson, M.C., Ricciardi, A. & MacIsaac, H.J. (2015)

405   Predator-free space, functional responses and biological invasions. *Functional Ecology,* **29**,

406   377–384.

407

408   Barrios-O'Neill, D., Kelly, R., Dick, J.T.A., Ricciardi, A., MacIsaac, H.J. & Emmerson, M.C.

409   (2016) On the context-dependent scaling of consumer feeding rates. *Ecology Letters*, **19**,

410   668–678.

411

412   Bessa-Gomes, C., Danek-Gontard, M., Cassey, P., Moller, A.P., Legendre, S. & Clobert, J.

413   (2003) Mating behaviour influences extinction risk: insights from demographic modelling

414   and comparative analysis of avian extinction risk. *Annales Zoologici Fennici,* **40**, 231–245.

415

416   Blackburn, T.M., Pyšek, P., Bacher, S., Carlton, J.T., Duncan, R.P., Jarošík, V., Wilson,

417   J.R.U. & Richardson, D.M. (2011) A proposed unified framework for biological invasions.

418   *Trends in Ecology and Evolution,* **26**, 333–339.

419

420   Bollache, L., Dick, J.T.A., Farnsworth, K.D. & Montgomery, W.I. (2008) Comparison of the

421   functional responses of invasive and native amphipods. *Biology Letters,* **4**, 166–169.

422

423   Cassey, P., Blackburn, T.M., Sol, D., Duncan, R.P. & Lockwood, J.L. (2004) Global patterns

424   of introduction effort and establishment success in birds. *Proceedings of the Royal Society B:*

425   *Biological Sciences,* **271**, S405–S408.

426

427   Chucholl, C., Morawetz, K. & Groß, H. (2012) The clones are coming – strong increase in

428   marmorkrebs [*Procambarus fallax* (Hagen, 1870) f. *virginalis*] records from Europe. *Aquatic*

429   *Invasions*, **7**, 511–519.

430

431   Clavel, J., Julliard, R. & Devictor, V. (2010) Worldwide decline of specialist species: toward

432   a global functional homogenization? *Frontiers in Ecology and the Environment,* **9**, 222–228.

433

434   Cox, J.G. & Lima, S.L. (2006) Naiveté and an aquatic-terrestrial dichotomy in the effects of

435   introduced predators. *Trends in Ecology and Evolution*, **21**, 674–680.

436

437   Davis, N.E., Forsyth, D.M., Triggs, B., Pascoe, C., Benshemesh, J., Robley, A., Lawrence, J.,

438   Ritchie, E.G., Nimmo, D.G. & Lumsden, L.F. (2015) Interspecific and geographic variation

439   in the diets of sympatric carnivores: dingoes/wild dogs and red foxes in south-eastern

440   Australia. *PLoS ONE,* **10**, e0120975.

441

442   Devictor, V., Clavel, J., Julliard, R., Lavergne, S., Mouillot, D., Thuiller, W., Venail, P.,

443   Villéger, S. & Mouquet, N. (2010) Defining and measuring ecological specialization. *Journal*

444   *of Applied Ecology,* **47**, 15–25.

445

446   Dick, J.T.A., Gallagher, K., Avlijas, S., Clarke, H.C., Lewis, S.E., Leung, S., Minchin, D.,

447   Caffrey, J., Alexander, M.E., Maguire, C., Harrod, C., Reid, N., Haddaway, N.R.,

448   Farnsworth, K.D., Penk, M. & Ricciardi, A. (2013) Ecological impacts of an invasive

449   predator explained and predicted by comparative functional responses. *Biological Invasions,*

450   **15**, 837–846.

451

452   Dick, J.T.A., Alexander, M.E., Jeschke, J.M., Ricciardi, A., MacIsaac, H.J., Robinson, T.B.,

453   Kumschick, S., Weyl, O.L.F., Dunn, A.M., Hatcher, M.J., Paterson, R.A., Farnsworth, K.D.

454   & Richardson, D.M. (2014) Advancing impact prediction and hypothesis testing in invasion

455   ecology using a comparative functional response approach. *Biological Invasions,* **16**, 735–

456   753.

457

458   Dick, J.T.A., Laverty, C., Lennon, J.J., Barrios-O'Neill, D., Mensink, P.J., Britton, J.R.,

459   Medoc, V., Boets, P., Alexander, M.E., Taylor, N.G., Dunn, A.M., Hatcher, M.J., Rosewarne,

460   P.J., Crookes, S., MacIsaac, H.J., Xu, M., Ricciardi, A., Wasserman, R.J., Ellender, B.R.,

461   Weyl, O.L.F., Lucy, F.E., Banks, P.B., Dodd, J.A., MacNeil, C., Penk, M.R., Aldridge, D.C.

462   & Caffrey, J.M. (2017). Invader Relative Impact Potential: a new metric to understand and

463   predict the ecological impacts of existing, emerging and future invasive alien species. *Journal*

464   *of Applied Ecology*, doi: 10.1111/1365-2664.12849.

465

466   Donohue, I., Petchey, O.L., Montoya, J.M., Jackson, A.L., McNally, L., Viana, M., Healy,

467   K., Lurgi, M., O'Connor, N.E. & Emmerson, M.C. (2013) On the dimensionality of

468   ecological stability. *Ecology Letters*, **16**, 421–429.

469

470   Downing, A.S., van Nes, E.H., Janse, J.H., Witte, F., Cornelissen, I.J.M., Scheffer, M. &

471   Mooij, W.M. (2012) Collapse and reorganization of a food web of Mwanza Gulf, Lake

472   Victoria. *Ecological Applications,* **22**, 229–239.

473

474   Dunoyer, L., Dijoux, L., Bollache, L. & Lagrue, C. (2013) Effects of crayfish on leaf litter

475   breakdown and shredder prey: are native and introduced species functionally redundant?

476   *Biological Invasions,* **16**, 1545–1555.

477

478   Ehrenfeld, J.G. (2011) Ecosystem consequences of biological invasions. *Annual Reviews of*

479   *Ecology, Evolution, and Systematics,* **41**, 59–80.

480

481   Englund, G., Öhlund, G., Hein, C.L. & Diehl, S. (2011) Temperature dependence of the

482   functional response. *Ecology Letters,* **14**, 914–921.

483

484   Fernández-Arhex, V. & Corley, J.C. (2003) The functional response of parasitoids and its

485   implications for biological control. *Biocontrol Science and Technology,* **13**, 403–413.

486

487   Futuyma, D.J. & Moreno, G. (1988) The evolution of ecological specialization. *Annual*

488   *Review of Ecology and Systematics,* **19**, 207–233.

489

490   Goss-Custard, J.D., West, A.D., Yates, M.G., Caldow, R.W., Stillman, R.A., Bardsley, L.,

491   Castilla, J., Castro, M., Dierschke, V., Durell, S.E., Eichhorn, G., Ens, B.J., Exo, K.M.,

492   Udayangani-Fernando, P., Ferns, P.N., Hockey, P.A., Gill, J.A., Johnstone, I., Kalejta-

493   Summers, B., Masero, J.A., Moreira, F., Nagarajan, R.V., Owens, I.P., Pacheco, C., Perez-

494   Hurtado, A., Rogers, D., Scheiffarth, G., Sitters, H., Sutherland, W.J., Triplet, P., Worrall,

495   D.H., Zharikov, Y., Zwarts, L. & Pettifor, R.A. (2006) Intake rates and the functional

496   response in shorebirds (Charadriiformes) eating macro-invertebrates. *Biological Reviews*, **81**,

497   501–529.

498

499   Hanmer, J., White, J.W. & Pawlik, J.R. (2017) Application of diet theory reveals context-

500   dependent foraging preferences in an herbivorous coral reef fish. *Oecologia*, **184**, 127–137.

501

502   Hays, W.S.T. & Conant, S. (2007) Biology and impacts of pacific island invasive species: 1.

503   a worldwide review of effects of the small Indian mongoose, *Herpestes javanicus* (Carnivora:

504   Herpestidae). *Pacific Science,* **61**, 3–16.

505

506   Holling, C.S. (1959) The components of predation as revealed by a study of small-mammal

507   predation of the European pine sawfly. *The Canadian Entomologist,* **91,** 293–320.

508

509   Hooff, R., C. & Bollens, S., M. (2004) Functional response and potential predatory impact of

510   *Tortanus dextrilobatus*, a carnivorous copepod recently introduced to the San Francisco

511   Estuary. *Marine Ecology Progress Series,* **277**, 167–179.

512

513   Horppila, J., Liljendahl-Nurminen, A., Malinen, T., Salonen, M., Tuomaala, A., Uusitalo, L.

514   & Vinni, M. (2003) *Mysis relicta* in a eutrophic lake: consequences of obligatory habitat

515   shifts. *Limnology and Oceanography,* **48**, 1214–1222.

516

517   Jackson, M.C., Grey, J., Miller, K., Britton, J.R. & Donohue, I. (2016) Dietary niche

518   constriction when invaders meet natives: evidence from freshwater decapods. *Journal of*

519   *Animal Ecology,* **85**, 1098–1107.

520

521   Jaworski, C.C., Bompard, A., Genies, L., Amiens-Desneux, E. & Desneux, N. (2013)

522   Preference and prey switching in a generalist predator attacking local and invasive alien

523   pests. *PLoS ONE,* **8**, e82231.

524

525   Jeschke, J.M., Kopp, M. & Tollrian, R. (2004) Consumer-food systems: why type I

526   functional responses are exclusive to filter feeders. *Biological Reviews*, **79**, 337–349.

527

528   Jeschke, J.M & Tollrian, R. (2005) Effects of predator confusion on functional responses.

529   *Oikos*, **111**, 547–555.

530

531   Jeschke, J.M. & Strayer, D.L. (2006) Determinants of vertebrate invasion success in Europe

532   and North America. *Global Change Biology,* **12**, 1608–1619.

533

534   Jeschke, J.M., Keesing, F. & Ostfeld, R.S. (2013) Novel organisms: comparing invasive

535   species, GMOs, and emerging pathogens. *Ambio*, **42**, 541–548.

536

537   Jones, C.G., Lawton, J.H. & Shachak, M. (1994) Organisms as ecosystem engineers. *Oikos,*

538   **69**, 373–386.

539

540   Kissling, W.D., Dalby, L., Fløjgaard, C., Lenoir, J., Sandel, B., Sandom, C., Trøjelsgaard, K.

541   & Svenning, J.-C. (2014) Establishing macroecological trait datasets: digitalization,

542   extrapolation, and validation of diet preferences in terrestrial mammals worldwide. *Ecology*

543   *and Evolution,* **4**, 2913–2930.

544

545   Laverty, C., Dick, J.T.A., Alexander, M.E. & Lucy, F.E. (2015) Differential ecological

546   impacts of invader and native predatory freshwater amphipods under environmental change

547   are revealed by comparative functional responses. *Biological Invasions*, **17**, 1761–1770.

548

549   Lester, P.J. & Harmsen, R. (2002) Functional and numerical responses do not always indicate

550   the most effective predator for biological control: an analysis of two predators in a two-prey

551   system. *Journal of Applied Ecology,* **39**, 455–468.

552

553   Levins, R. (1966) The strategy of model building in population biology. *American Scientist,*

554   **54,** 421–431.

555

556   Lockwood, J.L., Hoopes, M.F. & Marchetti, M.P. (2007) *Invasion Ecology.* Blackwell

557   Publishing, Oxford.

558

559   MacNeil, C., Dick, J.T.A., Alexander, M., Dodd, J. & Ricciardi, A. (2013) Predators vs.

560   alien: differential biotic resistance to an invasive species by two resident predators. *NeoBiota*,

561   **19**, 1–19.

562

563   Mayer, C., M., Burlakova, L., E. , Eklöv, P., Fitzgerald, D., Karatayev, A., Y., Ludsin, S., A.,

564   Millard, S., Mills, E., L. , Ostapenya, A.P., Rudstam, L., G. , Zhu, B. & Zhukova, T., V.

565   (2013) Benthification of freshwater lakes. *Quagga and Zebra Mussels: Biology, Impacts, and*

566   *Control* (eds T.F. Nalepa & D.W. Schloesser), pp. 575–586. CRC Press, Boca Raton, FL.

567

568   McNickle, G.G. & Brown, J.S. (2014) When Michaelis and Menten met Holling: towards a

569   mechanistic theory of plant nutrient foraging behaviour. *AoB PLANTS,* **6**, doi:

570   10.1093/aobpla/plu066.

571

572   Medoc, V., Spataro, T. & Arditi, R. (2013) Prey: predator ratio dependence in the functional

573   response of a freshwater amphipod. *Freshwater Biology*, **58**, 858–865.

574

575   Mitchell, C.E., Agrawal, A.A., Bever, J.D., Gilbert, G.S., Hufbauer, R.A., Klironomos, J.N.,

576   Maron, J.L., Morris, W.F., Parker, I.M., Power, A.G., Seabloom, E.W., Torchin, M.E. &

577   Vázquez, D.P. (2006) Biotic interactions and plant invasions. *Ecology Letters*, **9**, 726–740.

578

579   Momot, W.T. (1995) Redefining the role of crayfish in aquatic ecosystems. *Reviews in*

580   *Fisheries Science*, **3**, 33–63.

581

582   Moustahfid, H., Tyrrell, M.C., Link, J.S., Nye, J.A., Smith, B.E. & Gamble, R.J. (2010)

583   Functional feeding responses of piscivorous fishes from the northeast US continental shelf.

584   *Oecologia*, **163**, 1059–1067.

585

586   Nyström, P., Brönmark, C. & Granéli, W. (1999) Influence of an exotic and a native crayfish

587   species on a littoral benthic community. *Oikos*, **85**, 545–553.

588

589   O'Connor, N.E., Emmerson, M.C., Crowe, T.P. & Donohue, I. (2013) Distinguishing

590   between direct and indirect effects of predators in complex ecosystems. *Journal of Animal*

591   *Ecology*, **82**, 438–448.

592

593   Olsen, T.M., Lodge, D.M., Capelli, G.M. & Houlihan, R.J. (1991) Mechanisms of impact of

594   an introduced crayfish (*Orconectes rusticus*) on littoral congeners, snails, and macrophytes.

595   *Canadian Journal of Fisheries and Aquatic Sciences*, **48**, 1853–1861.

596

597 Ordonez, A. (2014) Functional and phylogenetic similarity of alien plants to co-occurring

598 natives. *Ecology,* **95**, 1191–1202.

599

600 Penk, M., Irvine, K. & Donohue, I. (2015) Ecosystem-level effects of a globally spreading

601 invertebrate invader are not moderated by a functionally similar native. *Journal of Animal*

602 *Ecology,* **84**, 1628–1636.

603

604 Penk, M.R., Jeschke, J.M., Minchin, D. & Donohue, I. (2016) Warming can enhance invasion

605 success through asymmetries in energetic performance. *Journal of Animal Ecology*, **85**, 419–

606 426.

607

608 Persson, L., Bystrom, P. & Wahlstrom, E. (2000) Cannibalism and competition in Eurasian

609 perch: population dynamics of an ontogenetic omnivore. *Ecology*, **81**, 1058–1071.

610

611 Pintor, L.M. & Byers, J.E. (2015) Do native predators benefit from non-native prey? *Ecology*

612 *Letters*. **18**, 1174–1180.

613

614 Polis, G.A., Anderson, W.B. & Holt, R.D. (1997) Towards an integration of landscape and

615 food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of*

616 *Ecology and Systematics,* **28**, 289–316.

617

618 Power, M.E., Tilman, D., Estes, J.A., Menge, B.A., Bond, W.J., Mills, L.S., Daily, G.,

619 Castilla, J.C., Lubchenco, J. & Paine, R.T. (1996) Challenges in the quest for keystones:

620 identifying keystone species is difficult—but essential to understanding how loss of species

621 will affect ecosystems. *Bioscience,* **46**, 609–620.

622

623 Radford, I.J., Dickinson, K.J.M. & Lord, J.M. (2007) Functional and performance

624 comparisons of invasive *Hieracium lepidulum* and co-occurring species in New Zealand.

625 *Austral Ecology,* **32**, 338–354.

626

627 Ricciardi, A., Hoopes, M.F., Marchetti, M.P. & Lockwood, J.L. (2013) Progress toward

628 understanding the ecological impacts of nonnative species. *Ecological Monographs,* **83**, 263–

629 282.

630

631 Romanuk, T.N., Zhou, Y., Brose, U., Berlow, E.L., Williams, R.J. & Martinez, N.D. (2009)

632 Predicting invasion success in complex ecological networks. *Philosophical Transactions of*

633 *the Royal Society of London B: Biological Sciences,* **364**, 1743–1754.

634

635 Rosenfeld, J.S. (2002) Functional redundancy in ecology and conservation. *Oikos,* **98**, 156–

636 162.

637

638 Rosewarne, P.J., Mortimer, R.J.G., Newton, R.J., Grocock, C., Wing, C.D. & Dunn, A.M.

639 (2016) Feeding behaviour, predatory functional responses and trophic interactions of the

640 invasive Chinese mitten crab (*Eriocheir sinensis*) and signal crayfish (*Pacifastacus*

641 *leniusculus*). *Freshwater Biology*, **61**, 426–443.

642

643 Rudolf, V.H.W. & Lafferty, K.D. (2011) Stage structure alters how complexity affects

644 stability of ecological networks. *Ecology Letters*, **14**, 75–79.

645

646 Saul, W.-C., Jeschke, J.M. & Heger, T. (2013) The role of eco-evolutionary experience

647   in invasion success. *NeoBiota,* **17**, 57–74.

648

649   Saul, W.-C. & Jeschke, J.M. (2015) Eco-evolutionary experience in novel species

650   interactions. *Ecology Letters,* **18**, 236–245.

651

652   Simberloff, D. (2011) How common are invasion-induced ecosystem impacts? *Biological*

653   *Invasions,* **13**, 1255–1268.

654

655   Simberloff, D., Martin, J.-L., Genovesi, P., Maris, V., Wardle, D.A., Aronson, J.,

656   Courchamp, F., Galil, B., García-Berthou, E., Pascal, M., Pyšek, P., Sousa, R., Tabacchi, E.

657   & Vilà, M. (2013) Impacts of biological invasions: what's what and the way forward. *Trends*

658   *in Ecology and Evolution,* **28**, 58–66.

659

660   Strayer, D.L. & Malcom, H.M. (2007) Effects of zebra mussels (*Dreissena polymorpha*) on

661   native bivalves: the beginning of the end or the end of the beginning? *Journal of the North*

662   *American Benthological Society,* **26**, 111–122.

663

664   Strayer, D.L. (2009) Twenty years of zebra mussels: lessons from the mollusk that made

665   headlines. *Frontiers in Ecology and the Environment,* **7**, 135–141.

666

667   Suraci, J.P., Clinchy, M., Dill, L.M., Roberts, D. & Zanette, L.Y. (2016) Fear of large

668   carnivores causes a trophic cascade. *Nature Communications*, **7**, 10698.

669

670   Terborgh, J. & Estes, J.A. (2010) *Trophic Cascades: Predators, Prey, and the Changing*

671   *Dynamics of Nature*. Island Press, Washington DC.

672

673 Townsend, C.R. (1996) Invasion biology and ecological impacts of brown trout *Salmo trutta*

674 in New Zealand. *Biological Conservation*, **78**, 13–22.

675

676 Tschanz, B., Bersier, L.-F. & Bacher, S. (2007) Functional responses: a question of

677 alternative prey and predator density. *Ecology,* **88**, 1300–1308.

678

679 Turney, S. & Buddle, C.M. (2016) Pyramids of species richness: the determinants and

680 distribution of species diversity across trophic levels. *Oikos*, **125**, 1224–1232.

681

682 Twardochleb, L.A., Novak, M. & Moore, J.W. (2012) Using the functional response of a

683 consumer to predict biotic resistance to invasive prey. *Ecological Applications*, **22**, 1162–

684 1171.

685

686 van Kleunen, M., Dawson, W., Schlaepfer, D., Jeschke, J.M. & Fischer, M. (2010) Are

687 invaders different? A conceptual framework of comparative approaches for assessing

688 determinants of invasiveness. *Ecology Letters,* **13**, 947–958.

689

690 van Leeuwen, E., Brännström, Å., Jansen, V.A.A., Dieckmann, U. & Rossberg, A.G. (2013)

691 A generalized functional response for predators that switch between multiple prey species.

692 *Journal of Theoretical Biology,* **328**, 89–98.

693

694 Vogt, G., Falckenhayn, C., Schrimpf, A., Schmid, K., Hanna, K., Panteleit, J., Helm, M.,

695 Schulz, R. & Lyko, F. (2015) The marbled crayfish as a paradigm for saltational speciation

696 by autopolyploidy and parthenogenesis in animals. *Biology Open*, **4**, 1583–1594.

697

698 Wasserman, R.J., Alexander, M.E., Dalu, T., Ellender, B.R., Kaiser, H. & Weyl, O.L.F.

699 (2016) Using functional responses to quantify interaction effects among predators.

700 *Functional Ecology*, doi: 10.1111/1365-2435.12682.

701

702 Werner, E.E. & Gilliam, J.F. (1984) The ontogenetic niche and species interactions in size-

703 structured populations. *Annual Review of Ecology and Systematics,* **15**, 393–425.

704

705 White, E.M., Wilson, J.C. & Clarke, A.R. (2006) Biotic indirect effect: a neglected concept in

706 invasion biology. *Diversity and Distributions,* **12**, 443–445.

707

708 Whittingham, M. & Markland, H. (2002) The influence of substrate on the functional

709 response of an avian granivore and its implications for farmland bird conservation.

710 *Oecologia,* **130**, 637–644.

711

712 Winemiller, K.O., Fitzgerald, D.B., Bower, L.M. & Pianka, E.R. (2015) Functional traits,

713 convergent evolution, and periodic tables of niches. *Ecology Letters,* **18**, 737–751.

714

715 Wise, D.H., Moldenhauer, D.M. & Halaj, J. (2006) Using stable isotopes to reveal shifts in

716 prey consumption by generalist predators. *Ecological Applications,* **16**, 865–876.

717

718 Xu, M., Mu, X., Dick, J.T.A., Fang, M., Gu, D., Luo, D., Zhang, J., Luo, J. & Hu, Y. (2016)

719 Comparative functional responses predict the invasiveness and ecological impacts of alien

720 herbivorous snails. *PLoS ONE,* **11**, e0147017.

721

Supporting Information

Fig. S1. Illustration of predator and prey selection using an example of the marbled crayfish.

Fig. S2. Illustration of an interaction module structure for testing, using an example of the

marbled crayfish.

Figure captions

Fig. 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.

Fig. 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
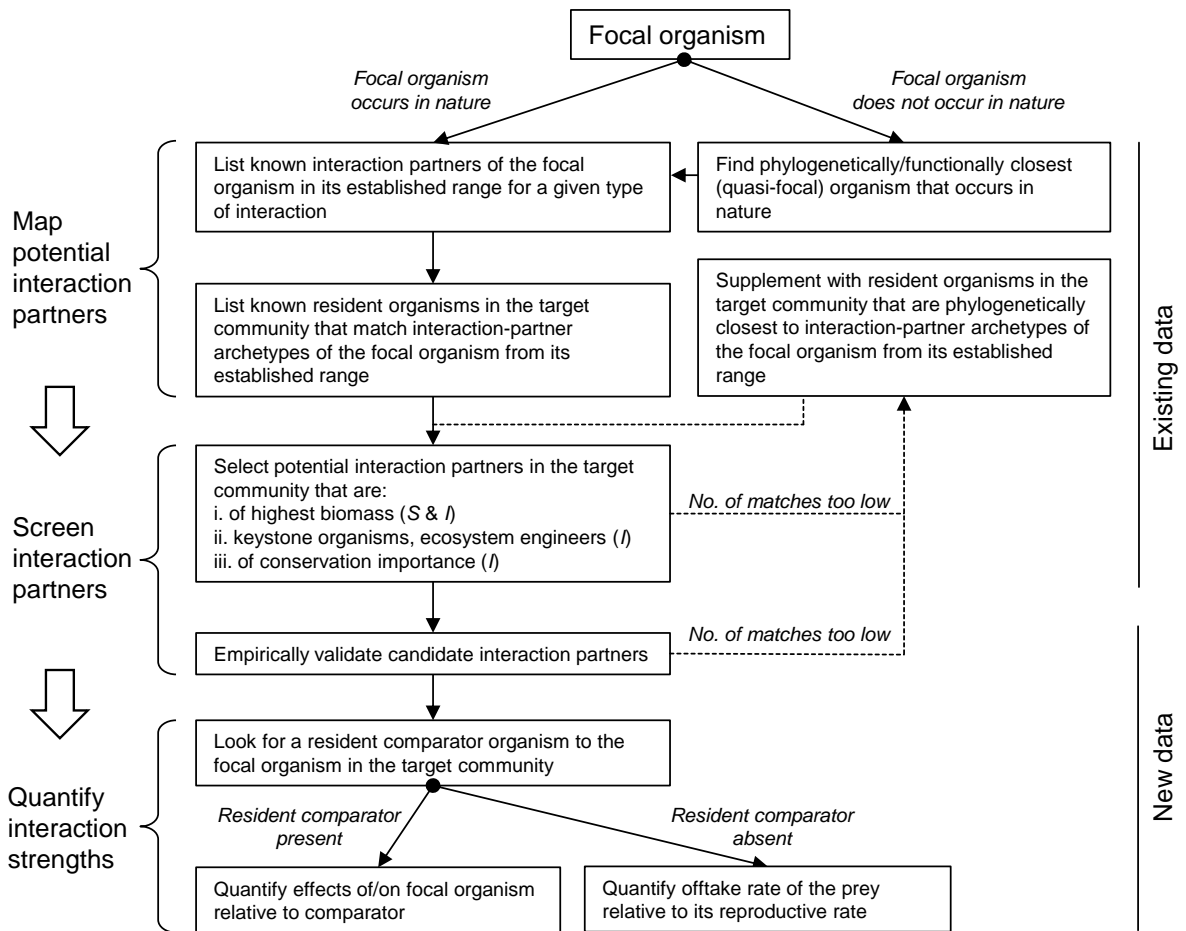
monophagous [b, d]).
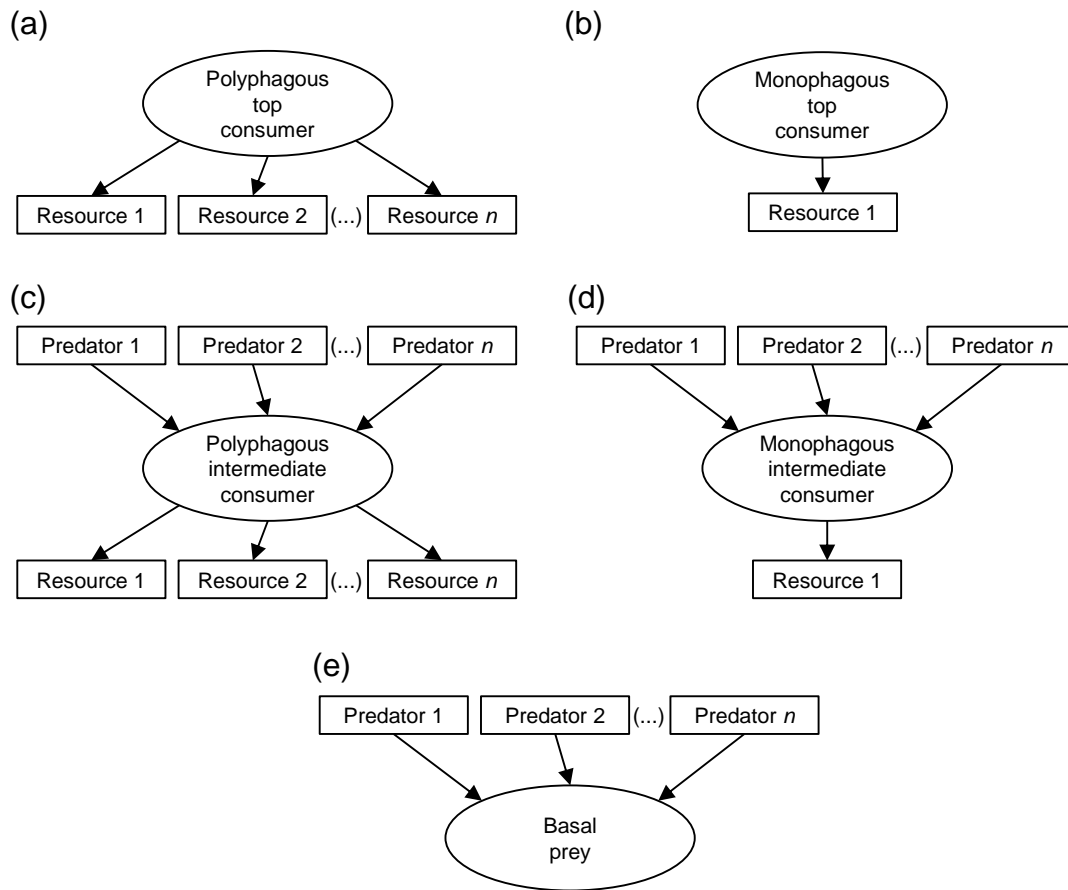
747

748   Fig. 1

749

750

751

752

753

754

755

756

757

758

759

(a)

Polyphagous top consumer

Resource 1   Resource 2   (...)   Resource *n*

(b)

Monophagous top consumer

Resource 1

(c)

Predator 1   Predator 2   (...)   Predator *n*

Polyphagous intermediate consumer

Resource 1   Resource 2   (...)   Resource *n*

(d)

Predator 1   Predator 2   (...)   Predator *n*

Monophagous intermediate consumer

Resource 1

(e)

Predator 1   Predator 2   (...)   Predator *n*

Basal prey

760

761   Fig. 2

762

763

764

765

766

767

768

769

770

771

772
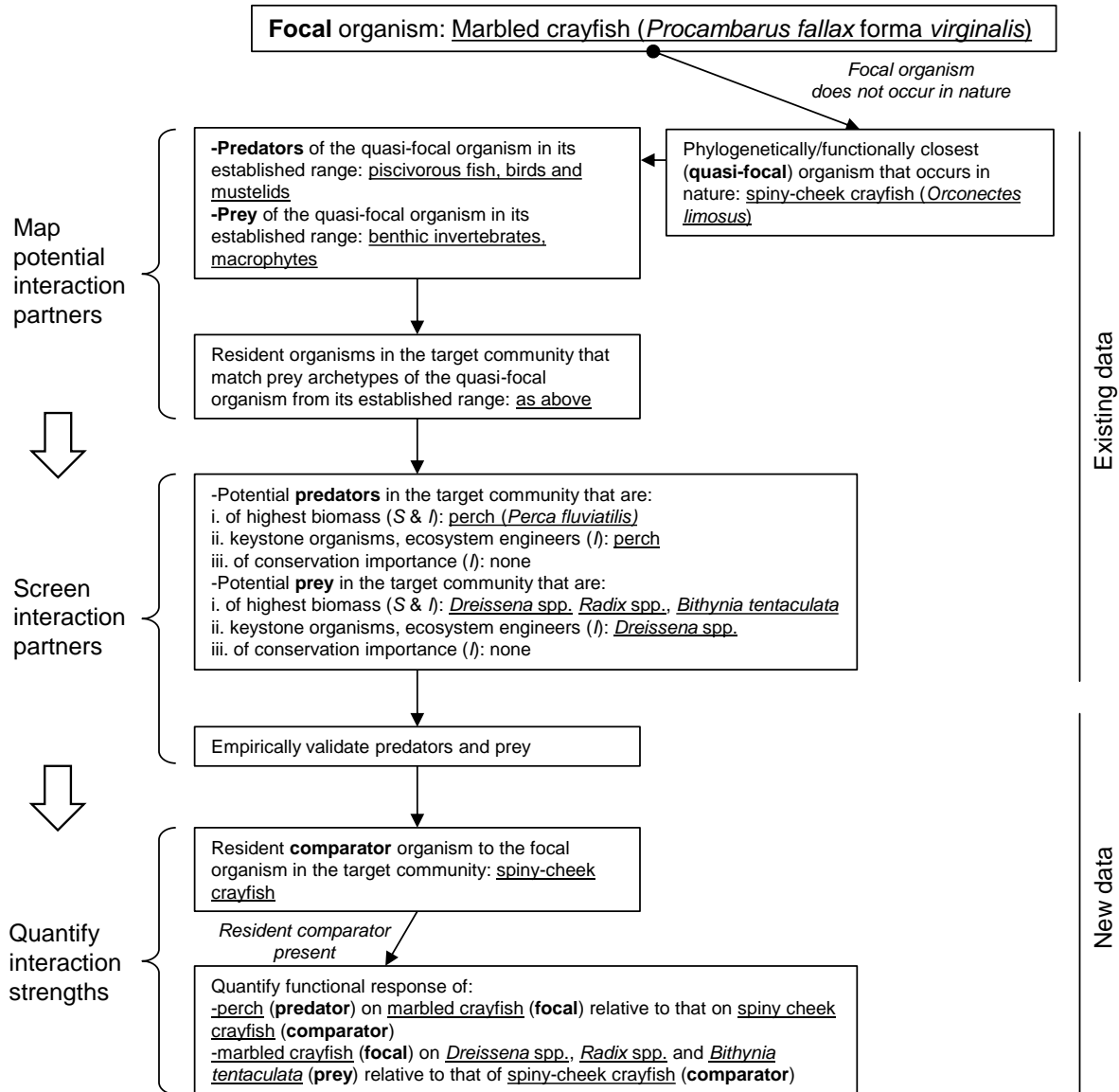
773

774 **Supporting Information**

775

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

777

778 Marcin Penk, Wolf-Christian Saul, Jaimie T.A. Dick, Ian Donohue, Mhairi E. Alexander,

779 Stefan Linzmaier and Jonathan M. Jeschke

780

781

782

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
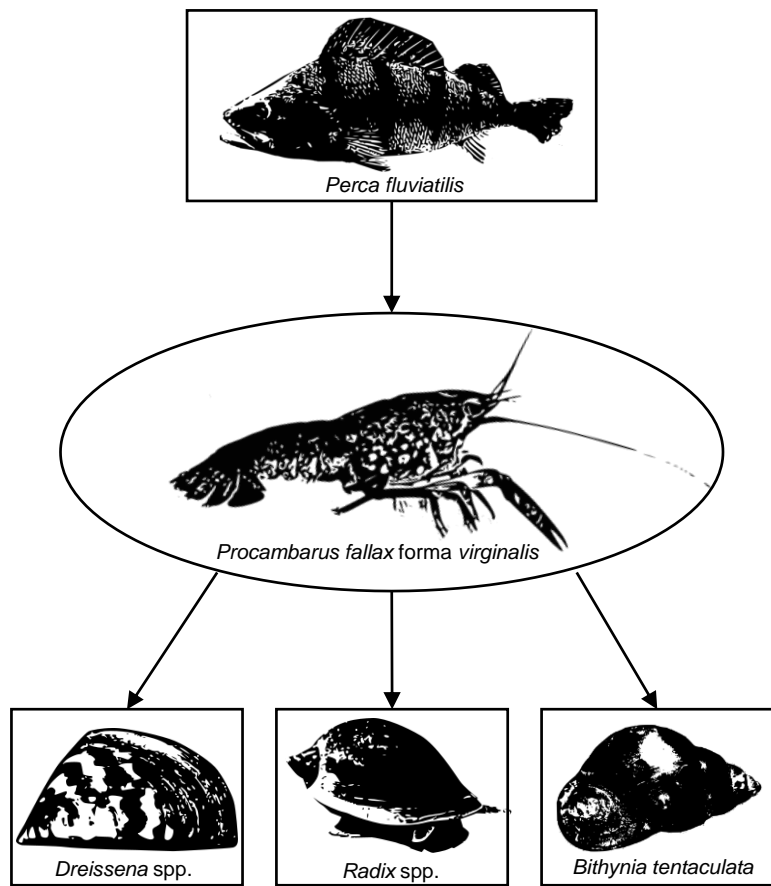
example.

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.

804

805