

1 **Parasites and Biological Invasions: Predicting ecological alterations at levels from**  
2 **individual hosts to whole networks**

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47 **Abstract**

48 The network approach is increasingly used by food-web ecologists and ecological  
49 parasitologists and has shed light on how parasite – host assemblages are organized, as well as  
50 on the role of parasites on the structure and stability of food webs. With accelerating rates of  
51 non-native parasites being introduced around the world, there is an increasing need to predict  
52 their ecological impacts and the network approach can be helpful in this regard. There is  
53 inherent complexity in parasite invasions as parasites are highly diverse in terms of taxa and  
54 life strategies. Furthermore, they may depend on their co-introduced host to successfully  
55 overcome some crucial steps in the invasion process. Free-living introduced species often  
56 experience enemy release during invasion, which reduces the number of introduced parasites.  
57 However, introduced parasites that successfully establish may alter the structure of the  
58 recipient network through various mechanisms including parasite spill-over and spill-back,  
59 and manipulative and non-manipulative phenotypic alterations. Despite limited literature on  
60 biological invasions in infectious food webs, some outstanding methodological issues and the  
61 considerable knowledge gaps that remain, the network approach provides valuable insights on  
62 some challenging questions, such as the link between structure and invasibility by parasites.  
63 Additional empirical data and theoretical investigations are needed to go further and the  
64 predictive power of the network approach will be improved by incorporating weighted  
65 methods that are based on trophic data collected using quantitative methods, such as stable  
66 isotope analyses.

67

68 **Keywords:**

69 Connectance; Introduced parasites; Enemy release; Food web; Quantitative networks;  
70 Stability; Stable isotopes; Topology

71 **1. Introduction**

72 Characteristics of food web structure can be expressed through features including species  
73 richness, functional diversity and topology, with the latter enabling calculation of network  
74 properties such as connectivity and chain length (Rooney and McCann, 2012). These  
75 characteristics and properties all contribute to building understandings of food web stability  
76 and complexity (Lafferty and Kuris, 2009). Predictive food web networks are often based on  
77 probabilistic rules that dictate that the diet choices of species are largely restricted to items in  
78 lower trophic positions as bound by predator-prey body sizes (Svånback et al., 2015).

79         Despite having body sizes much smaller than their hosts, parasite infections often have  
80 significant consequences for host biology; these are often nutritional due to the parasite  
81 feeding on or within the host (Barber et al., 2000). Parasite behaviour and development may  
82 also be associated with host pathological, physiological and/ or behavioural changes, with  
83 likely adverse consequences for their growth, survival and fitness (Johnson et al., 2008;  
84 Britton et al., 2011; Johnson and Hoverman, 2012). Consequently, parasites can profoundly  
85 shape the dynamics of their host populations and communities, alter intra- and inter-specific  
86 competition, influence trophic relationships and are important drivers of biodiversity through  
87 their contribution of large numbers of species and causal links between density dependent  
88 transmission and host specificity that increases biodiversity (Lafferty et al., 2006; Luque and  
89 Poulin, 2007; Hatcher et al., 2006, 2012a, 2014; Hatcher and Dunn, 2011; Dunn et al. 2012).

90         Trophic networks that have been developed using the general rules of predator-prey  
91 body sizes (Warren and Lawton, 1987; Emmerson and Raffaelli, 2004) have traditionally  
92 tended to overlook the inclusion of parasites (Beckermann and Petchey, 2009). In doing so,  
93 they may underestimate food web connectivity and complexity (Marcogliese and Cone, 1997;  
94 Thompson et al., 2005). This is because insights provided by ‘infectious food webs’ (i.e. food  
95 webs with both predators and parasites) in aquatic ecosystems have revealed that parasites

96 uniquely alter food web structure and stability through, for example, substantially increasing  
97 connectivity, nestedness and linkage density (Lafferty et al., 2006, 2008; Byers, 2008;  
98 Amundsen et al., 2009). The inclusion of parasites in trophic networks has enabled them to  
99 become considered as crucial components of ecosystems. They often dominate food web links  
100 (Lafferty et al., 2006), comprise substantial amounts of biomass (Kuris et al., 2008) and  
101 influence major aspects of ecological community structure (Wood et al., 2007).

102

103 The continuing acceleration of rates of international trade, travel and transport has resulted in  
104 a progressive mixing of biota from across the world via introductions of non-native species  
105 into many new regions (Hulme et al., 2009; Pyšek et al., 2010). Whilst the introduction  
106 process can filter out many parasites that would otherwise move with their non-native hosts, it  
107 enables others to be released, providing the opportunity for their ‘host-switching’ to native  
108 species (Torchin et al., 2003; Blakeslee et al., 2012; Sheath et al., 2015). The lack of co-  
109 evolution between the introduced parasite and their potential new hosts suggests that  
110 transmission may occur due to low resistance arising from poor immune responses and anti-  
111 predator behaviours (Taraschewski et al., 2006), although resistance will also depend on a  
112 wide range of environmental and biological factors (Blanchet et al., 2010; Penczykowski et  
113 al., 2011). Host responses to infection will vary according to factors including the complexity  
114 of the parasite’s life cycle and host resilience (e.g. their ability of hosts to adapt to infection  
115 via alterations in life history traits and their immune response that influences the severity of  
116 the infection) (Blanchet et al., 2010; Hawley et al., 2010) and high mortality rates might be  
117 incurred (Frick et al., 2010). Sub-lethal consequences for hosts include shifts in energetics and  
118 behaviour that may result in reduced host activity, growth, condition and fitness (Barber et al.,  
119 2000; Johnson and Hoverman, 2012).

120 From the perspective of the trophic network, the inclusion of an introduced parasite  
121 increases the number of connections (Britton, 2013). However, the extent of the network  
122 alteration is likely to be influenced by issues including the complexity of the parasite  
123 lifecycle. These life cycles can be relatively simple, where transmission is host to host. They  
124 can also be complex, especially when the final host is a fish or bird at a high trophic position  
125 and the parasite is of low trophic position (Jansen and Bakke, 1991; Macnab and Barber,  
126 2011). To overcome this discrepancy in their respective trophic positions, the parasite must  
127 navigate through a series of intermediate hosts before reaching their final host in which they  
128 sexually mature (Britton et al., 2009; Macnab and Barber, 2011). The parasite thus overcomes  
129 the ‘trophic vacuum’ between their low trophic position and the high trophic position of their  
130 final hosts (Parker et al., 2015), creating a series of new connections in the food web that  
131 connects species in low trophic positions with those at the top.

132

133 Given these different perspectives of trophic networks, parasites, and introduced species and  
134 their parasites, the aim of this review is to outline how alterations in the properties of trophic  
135 networks from introductions of free-living species and their parasites can be predicted. It  
136 initially provides an overview of parasite strategies and network analysis (Section 2), before  
137 discussing the effect of including parasites in trophic networks (Section 3), the establishment  
138 process of introduced parasites with a case study of enemy release (Section 4), and the  
139 processes that determine the extent of network alterations by established parasites (Section 5).  
140 These aspects are then all integrated in Section 6 that reviews how the consequences of  
141 biological invasions can be predicted using network analyses, and how food web structure can  
142 determine invasibility by parasites. Section 7 provides perspectives on analysing the influence  
143 of parasites on food web structure through comparing more quantitative approaches with the  
144 qualitative approaches outlined in previous sections. Final conclusions are then drawn in

145 Section 8. Throughout the review, when the term ‘parasite’ is used, it refers primarily to  
146 ‘macroparasites’, an artificial group of metazoan parasites, composed mainly of members of  
147 the Platyhelminthes (flatworms, including monogenean and digenean trematodes and  
148 cestodes), Nematelminthes (roundworms and allies, including nematodes and  
149 acanthocephalans) and Arthropods (true lice and parasitic copepods) (Barber et al., 2000).  
150 The terms ‘infectious food web’ or ‘whole food web’ are used to describe a trophic network  
151 that includes both free-living species and their parasites. Although all parasite taxa and  
152 strategies are concerned with biological invasions, many examples are from aquatic food  
153 webs, a reflection of the current literature.

154

## 155 **2. Overview of parasites and network analyses**

156

### 157 **2.1 The diversity of parasite strategies**

158 Whilst micro-predation suggests that the boundary between predation and parasitism can be  
159 blurred, it is generally accepted that parasitism differs from predation in the durability of the  
160 attack (brief for predators and durable for parasites) and the number of victims per life-stage  
161 (one host for parasites and more than one prey for predators). Within parasitism, life-history  
162 dichotomies have been proposed to categorize different parasite strategies, such as castrators,  
163 trophic transmission and intensity-dependent pathology (e.g. Anderson and May, 1979; May  
164 and Anderson, 1979; Kuris and Lafferty, 2000; Lafferty and Kuris, 2002; Poulin, 2011; Table  
165 1). These strategies are life-stage specific rather than species specific. They can thus differ  
166 across the life cycle of a parasite, such as between larval and adult stages (Poulin, 2011).

167 As parasite strategies do not have a single evolutionary origin then they have  
168 representative species from many phyla, especially in directly transmitted parasites (Poulin,  
169 2011). However, some strategies are dominated by particular phyla, such as micro-parasites

170 that tend to be mostly protozoans, bacteria or viruses, and trophically transmitted parasites  
171 that include many helminth species. Consequently, different parasite phyla potentially result  
172 in contrasting outcomes for food web structure. Of the parasite strategies outlined in Table 1,  
173 the dichotomies that arguably will have greatest influences on trophic networks are whether  
174 the parasite exploits a single host/ has multiple host species during its lifecycle and whether  
175 the parasite exploits a free-living species or another parasite, especially in relation to free-  
176 living species and multi-parasitism. Both of these will strongly influence the number of links  
177 in the network and its connectivity.

178

## 179 **2.2 Network analysis as a tool for ecological parasitologists**

180 A network is simply any collection of discrete entities potentially interacting as a system,  
181 which are usually represented by a set of nodes connected with directed or undirected edges  
182 (links) (Proulx et al., 2005). Network analysis consists in characterising, through various  
183 mathematical and statistical tools, the structure of such relational data and their emerging  
184 properties. It originates from graph theory, a branch of applied mathematics, and was quickly  
185 adopted by social scientists and psychologists to study human social organisation, and later by  
186 biologists to better understand metabolic pathways, gene and protein regulatory networks or  
187 neural networks, and by ecologists to investigate biotic interactions (Scott, 2000). For  
188 ecologists, nodes are usually distinct species (but it can be aggregates of species, life-stages of  
189 species, non-taxonomic groups or individuals) and links represent antagonistic (predation or  
190 parasitism) or mutualistic interactions. Biotic interactions are the backbone of ecological  
191 communities and the underlying ideas of global interdependence between species behind the  
192 concept of food webs were already mentioned by Darwin (Darwin, 1859) and Elton (Elton,  
193 1927) (Pocock et al., 2016). Nevertheless, a big step was taken when food-web theory  
194 borrowed concepts and tools from network theory.

195 In its basic version, an ecological network can take the form of a species-by-species  
196 matrix of interactions, where columns represent consumers (predators, parasites, pollinators)  
197 and rows represent resources (prey, hosts, plants). At the intersections of each row and  
198 column (i.e. the cells of the matrix), binary entries indicate whether a link exists between the  
199 two species (1: yes, 0: no) (Fig. 1a). Such a matrix leads to a bipartite interaction network  
200 (Fig. 1b), where links between members of the same group (i.e. between consumers or  
201 between resources) are not allowed. Bipartite networks can be particularly relevant for  
202 mutualistic and parasite - host interactions. When there is no group distinction between  
203 members (i.e. all links allowed), they all appear in both columns and rows of the matrix (Fig.  
204 1c). This results in a full interaction network (Fig. 1d), which is particularly relevant for  
205 predator - prey and parasite - host interactions, and especially when it comes to mixing both  
206 types of interactions in the same network (see below). The matrix is then used to calculate  
207 network statistics (metrics) like connectance, nestedness and modularity (Fig. 1e and 1f).  
208 They describe the structural attributes (topology) of the ecological network (Table 2). It is  
209 possible to consider species abundance and interaction frequency through quantitative  
210 approaches (Fig. 1g) with weighted metrics (Bersier et al., 2002). A range of computational  
211 approaches exists to visualise the network, the choice of a particular method depending on the  
212 structural attribute to be highlighted (Pocock et al., 2016).

213

214 Linking the structural attributes of networks with ecosystem-level properties, such as  
215 functionality (efficiency of energy transfer), stability (persistence of species through time),  
216 resilience (time needed to recover following perturbation) or robustness (resistance to species  
217 removal) is one of the most challenging and exciting issues in the study of ecological  
218 networks. For instance, compartmentalisation is supposed to limit the spread of disturbances  
219 though the whole network, whilst nestedness could limit the risk of secondary extinctions (see

220 Tylianakis et al., 2010 and references therein). The role of connectance is more complex and  
221 falls into the old diversity - stability debate (see Rooney and McCann, 2012). On the one  
222 hand, high connectance means increased generalism. This should stabilize the rate of  
223 ecosystem processes through time and promote robustness by providing a buffer in the  
224 responses of predators to fluctuating prey abundances (Dunne et al., 2002; Tylianakis et al.,  
225 2010). On the other hand, species diversity is supposed to confer stability and decreases with  
226 connectance. It follows that highly connected networks should be less stable. In such  
227 networks, apparent competition (indirect interaction in which two victim species negatively  
228 affect each other by enhancing the equilibrium density of a shared natural enemy, Holt, 1977)  
229 should be greater and its negative impact could result in a lower stability in terms of total  
230 biomass (Thébault and Fontaine, 2010). More than species diversity, it is the way diversity is  
231 distributed that could be important (Rooney and McCann, 2012). A pattern of interaction  
232 strengths with a few strong links for a majority of weak interactions has been shown to be  
233 powerfully stabilizing (McCann, 1998). Such skewed distribution could confer stability to  
234 highly diverse and connected networks.

235

236 Network analysis has been applied extensively to predator - prey interactions before being  
237 used to study mutually beneficial interactions, such as those between plants and pollinators or  
238 seed dispersers, and is just beginning to be used by ecological parasitologists. Typical parasite  
239 – host networks are bipartite and the first relationship between metrics that emerged was a  
240 rapid decrease in connectance with increasing species richness (or network size) (Mouillot et  
241 al., 2008; Poulin, 2010). Such a relationship is expected for antagonistic interactions, where  
242 there is a greater level of specialisation (coevolution) between partners. As a result of the  
243 constant arm race between parasites and hosts, parasites show some degree of specificity,  
244 which results in not all of the links being realized (Poulin, 2010). This decreases connectance,

245 especially in species-rich communities. Two other main structural patterns emerge from  
246 parasite – host networks: nestedness and, most importantly, modularity, which are partly  
247 driven by the intimacy of interactions (Fontaine et al., 2011) and are both extremes of the  
248 same continuum (Fig. 1e and 1f). Nevertheless, nestedness and modularity are not mutually  
249 exclusive, as interactions within a module may be nested (Lewinsohn et al., 2006).  
250 Differences in nestedness and modularity among parasite – host networks are beginning to be  
251 understood and may be explained by constraints linked to phylogeny (Krasnov et al., 2012;  
252 Lima et al., 2012; Brito et al., 2014; Bellay et al., 2011, 2013, 2015; Braga et al., 2014, 2015),  
253 geography (Braga et al., 2014, 2015), species abundances (Vasquez et al., 2005), host traits  
254 such as body size (Campiao et al., 2015), foraging strategy or habitat use (Brito et al., 2014),  
255 or parasite strategies (Graham et al., 2009; Lima et al., 2012; Bellay et al., 2013, 2015) (Table  
256 3).

257

258 In addition to the detection and understanding of structural patterns in parasite – host  
259 assemblages, network analysis has been used by ecological parasitologists to investigate the  
260 effects of climate change (Maunsell et al., 2015; Morris et al., 2015), land use (Albrecht et al.,  
261 2007; Tylianakis et al., 2007), habitat fragmentation (Murakami et al., 2008; Gagic et al.,  
262 2011; Kaartinen and Roslin, 2011; Valladares et al., 2012), nutrient enrichment (Fonseca et  
263 al., 2005), and biological invasions (Timms et al., 2012; Amundsen et al., 2013).  
264 Epidemiological networks, i.e. unipartite networks that connect hosts sharing at least one  
265 parasite species, can be derived from bipartite parasite – host networks to explore dynamics of  
266 parasite transmission among host populations (Pilosof et al., 2015).

267

### 268 **3. Infectious food webs: including parasites in trophic networks**

269

### 270 **3.1 From bipartite interaction networks to whole food webs**

271 Members of bipartite networks may be under control of other species that are not depicted in  
272 the network (Fontaine et al., 2011). For instance, flower visitors in a mutualistic network  
273 experience a wide range of predators that are likely to influence visitation patterns. Similarly,  
274 parasitoids can be the victims of secondary parasitoids (hyperparasitoids). Therefore, it can be  
275 difficult to fully understand the dynamics of interacting species. To account for this, a third  
276 group of species with no within-group links can be added to the classical bipartite network so  
277 as to generate a tripartite interaction network, for instance a plant – pollinator – predator  
278 network (Marrero et al., 2013), a plant – herbivore – parasitoid network, or a herbivore –  
279 parasitoid – hyperparasitoid network (Lohaus et al., 2013). However, network analysis in  
280 tripartite networks is rather limited and comes down to analysing the two stacked, bipartite  
281 networks separately.

282

283 Given the ubiquity of parasitism as a consumer strategy, food-web ecologists, who  
284 traditionally focus their attention on predator – prey interactions, were called to accommodate  
285 parasites into their network analyses (Cohen et al., 1993; Marcogliese and Cone, 1997;  
286 Marcogliese, 2003; Fontaine et al., 2011). This can be achieved by adding parasites to the list  
287 of entities that appear in both columns (consumers) and rows (resources) of the predation  
288 matrix (Fig. 2). The resulting ‘whole food web’ or ‘infectious food web’ is then a powerful  
289 tool to provide new insights on the ecological significance of parasites through their effect on  
290 food web structure and stability (see below), and on the fundamental principles of trophic  
291 organization in ecosystems.

292 In addition to the predator – prey links of traditional food webs, parasite inclusion  
293 introduces new types of links (Fig. 2a). Parasite – host links are those involved in almost all  
294 parasite strategies, whereby parasites feed on the free-living species they exploit as hosts.

295 Predator – parasite links occur when free-living species prey upon parasites either directly  
296 when parasites are at a free-living, non-feeding life stage, or indirectly when parasites are  
297 ingested along with the prey they exploit (concomitant predation) (Johnson et al., 2010;  
298 Thieltges et al., 2008, 2013). Trophically-transmitted parasites use concomitant predation to  
299 reach the next host. Finally, parasite – parasite links describe hyperparasitism (frequent  
300 among parasitoids) or predation among parasites (larval trematodes commonly engage in  
301 intraguild predation within their snail intermediate host; Sousa, 1992). It follows that the  
302 whole interaction matrix can be divided into four submatrices corresponding to the four types  
303 of links (Lafferty et al., 2006, Fig. 2b and 2c). Network statistics can be calculated either from  
304 the whole matrix or from a particular submatrix.

305

306 Including parasites in food webs raises some methodological issues. For instance, differences  
307 in how the links are described can substantially alter the way connectance is calculated  
308 because, of all the possible links that are added with parasites, some might appear illogical.  
309 Concerning the nodes, the complexity of the life cycle of some parasites raises the question of  
310 node resolution (Fig. 2b and 2c). Indeed, many parasites undergo extreme ontogenetic niche  
311 shifts during development to such an extreme degree that nodes could be viewed as life stages  
312 and not as trophic species, as it is often the case in traditional food webs (Preston et al., 2014).

313

### 314 **3.2 Impact of parasite inclusion on network metrics and properties**

315 We examined one terrestrial and ten aquatic food webs including both predation and  
316 parasitism (Table 4, aquatics webs are reviewed in Jephcott et al., 2016). Of the ten aquatic  
317 webs, eight are estuarine and only one is from the Southern Hemisphere, which limits  
318 extrapolation of results. The most widely reported finding is that parasite inclusion alters  
319 several key statistics calculated from the interaction matrix, with an increase in species

320 richness, chain length, linkage density, nestedness and connectance (Huxham et al., 1995;  
321 Memmott et al., 2000; Thompson et al., 2005; Lafferty et al., 2006; Hernandez and Sukhdeo,  
322 2008; Amundsen et al., 2009, 2013; Kuang and Zhang, 2011). However, the effect of parasite  
323 inclusion on nestedness and connectance, which should influence stability, has proved to be  
324 sensitive to the way nodes are defined (Fig. 2b and 2c). Preston et al. (2014) investigated  
325 three versions of a freshwater pond food web (Quick Pond in the San Francisco Bay Area of  
326 California, Preston et al., 2012) with varying levels of node resolution. Consistent with  
327 previous findings, nestedness and connectance increased after parasite inclusion when  
328 parasites were included as taxonomic species (a single node per parasite species), whereas the  
329 opposite occurred when nodes were disaggregated into parasite life stages. This is because in  
330 the highly resolved food web, the number of observed links did not increase in proportion  
331 with the number of possible links added by the parasite life stages (Preston et al., 2014). This  
332 question over node resolution has yet to be resolved.

333         The ecological significance of parasite-induced changes in food-web metrics generates  
334 a lot of interest but is far from being resolved. The relationship between structure and stability  
335 being complex, the role of increased connectance following parasite inclusion is not clear. It  
336 might be that parasites stabilise food webs because they are engaged in weak interactions with  
337 their hosts. Their inclusion in food webs therefore adds weak interactions and increases the  
338 heterogeneity of interaction strengths (few strong links for a majority of weak links), a pattern  
339 assumed to promote stability (McCann et al., 1998). Conversely, parasites make food webs  
340 more susceptible to secondary extinctions, especially where the parasites have complex  
341 lifecycles, as the removal of a single free-living would induce the loss of its parasites  
342 (Lafferty and Kuris, 2009; Chen et al., 2011). Several studies have highlighted that parasite-  
343 induced changes in food-web metrics could be the generic effects of adding complexity and  
344 diversity to the matrix through new nodes and links (Marcogliese, 2003; Lafferty et al., 2008;

345 Sukhdeo, 2010, 2012). This raises the argument as to what extent are the topological roles of  
346 parasites unique compared to those of free-living species? Of the links that involve parasites  
347 (Fig. 2a), it has been shown that concomitant links (between predators and the parasites of  
348 their prey) are those that have the greatest effect on network structure (Dunne et al., 2013;  
349 Cirtwill and Stouffer, 2015; see also Thielges et al., 2013). Concomitant predation might thus  
350 be what makes parasites unique (but see Jacobs et al., 2015). Parasites also differ from  
351 predators in that their trophic niches tend to be broader and have more gaps (Dunne et al.,  
352 2013). This may result from the complex life cycles of many parasites, with the successive  
353 exploitation of very different hosts in terms of body size or phylogeny (Section 3). Generative  
354 network models, such as the probabilistic niche model, provide powerful and new tools to  
355 better understand the roles of parasites in food webs and the relative importance of predation,  
356 parasitism and concomitant predation (see Jacobs et al., 2015).

357        Besides changing network metrics, including parasites also changes the frequency  
358 distribution of network motifs among food webs (Dunne et al., 2013; Cirtwill and Stouffer,  
359 2015). Again, the role of concomitant predation was highlighted but the ecological  
360 significance of the over- or under-representation of network motifs following parasite  
361 inclusion remains to be explored.

362

363 Network theory also gives insights on how parasites, especially those with complex life cycle  
364 and trophic transmission, establish in host communities. For instance, it has been shown that  
365 parasites are more likely to colonize host species that are central in the food web, i.e. those  
366 that are highly connected and contained within modules of tightly interacting species (Chen et  
367 al., 2008; Anderson and Sukhdeo, 2011). This is because predators with wide diet ranges are  
368 more likely to eat prey serving as intermediate hosts, whilst prey with many predators may  
369 represent efficient transmission pathways. Consistently, Locke et al. (2014), who searched for

370 the factors that best predict the diversity of both larval and adult stages of the trophically  
371 transmitted parasites of 25 fish species from the Bothnian Bay, Finland, found that adult  
372 parasite diversity increased with prey diversity (i.e. diet range, generality) and larval diversity  
373 increased with predator diversity (i.e. vulnerability). Finally, highly connected species within  
374 core modules are less susceptible to extinction compared to less connected species, and thus  
375 may represent stable units for the persistence and evolution of complex life cycle parasites  
376 (Anderson and Sukhdeo, 2011).

377

378 In summary, the analysis of how parasites alter network properties has emerged as a major  
379 research theme in the last decade and has provided insights into how food web connectivity,  
380 stability and robustness alter when parasites are included. Although there remains a series of  
381 questions that have yet to be fully resolved in these networks, the studies completed to date  
382 suggest that network analysis will provide a strong tool for predicting how introductions of  
383 free-living species and their parasites will alter food web structure. However, before this is  
384 discussed, the processes that influence the establishment and trophic consequences of  
385 introduced non-native parasites are reviewed. This is because these processes have important  
386 implications for the number of introduced parasites that establish and thus the extent of the  
387 network alterations.

388

#### 389 **4. Parasites as alien species**

390

##### 391 **4.1 The establishment of introduced parasites**

392 Similar to introduced free-living species, for a non-native parasite to become invasive in a  
393 new range it has to overcome the barriers of transport, establishment and dispersal (Fig. 3;  
394 Lymbery et al., 2014). Co-introduced parasites are those introduced with their free-living host

395 (Fig. 3a). They are described as established when maintain self-sustaining populations in the  
396 new area through survival, reproduction and dispersal in their co-introduced hosts (Fig. 3b).  
397 Invasion includes a switch from exotic to native hosts (Fig. 3c). For parasites that have been  
398 introduced without their free-living host (Fig. 3d), such as free-living infective stages within  
399 ballast water (Goedknecht et al., 2015), establishment and invasion are confounded as they  
400 have to establish self-sustaining populations on or in native hosts to persist (Fig. 3e). In  
401 reality, there tends to be little distinction made between established, co-introduced and  
402 introduced parasites, given that parasites which are introduced but do not establish are  
403 unlikely to ever be recorded (Lymbery et al., 2014).

404         Of 98 co-introduced parasites recorded by Lymbery et al. (2014) at a global scale, 49  
405 % were helminths, 17 % were arthropods and 14 % were protozoans. Fish were by far the  
406 most common non-native hosts, with many freshwater species, and reflects the vulnerability  
407 of aquatic ecosystems to species introductions due to their high connectivity and the increase  
408 in global shipping and aquaculture activities (Goedknecht et al., 2015). For instance, many  
409 organisms, including bacteria, viruses and other free-living infective stages of metazoan  
410 parasites, are moved out of their natural range with ballast water. Given the high rate of  
411 introductions of fish hosting non-native parasites then, intuitively, structural alterations to  
412 freshwater food webs might be most likely to occur from introduced fish parasites, although  
413 this will be dependent upon the lifecycles of those parasites. For example, where these  
414 parasites have complex life cycles, they potentially form multiple new connections in the food  
415 web via filling the trophic vacuum, especially where they switch hosts to native species,  
416 altering trophic links within the food web. Where the parasites have direct lifecycles,  
417 however, their effects on food web structure might be limited.

418

419 **4.2 Enemy release: how many parasites from how many hosts?**

420 When a free-living species is introduced into a new range then it might be expected that its  
421 parasite fauna will be co-introduced (Fig. 3a, 4). It would then follow that these parasites  
422 would be included in the new trophic network, either in the overall matrix or in a sub-matrix  
423 with other parasites, depending on the approach being used (Section 3.1). However, the  
424 introduction process often filters out many of the parasites that would otherwise have been  
425 introduced (Blakeslee, 2012). Estimates are that only two new parasite species are introduced  
426 with every introduced free-living species (Torchin et al., 2003). The underlying hypothesis of  
427 this is the ‘Enemy release hypothesis’ and is an integral component of studies that consider  
428 how non-native parasites might influence native species, trophic networks and ecosystems. It  
429 predicts that the parasite loss experienced by introduced free-living species enhances their  
430 ability to establish and invade (Keane and Crawley, 2002; Mitchell and Power, 2003; Hatcher  
431 and Dunn, 2011). Torchin and Mitchell (2004) suggested that introduced species escape at  
432 least 75 % of their parasites from their native range and thus will gain substantial benefits  
433 regarding their fitness and survival in the invasive range (Torchin et al., 2003). It has been  
434 used as the basis to explain the invasion success of a diverse range of species, including non-  
435 native slugs (Ross et al., 2010), mosquitoes (Aliabadi and Juliano, 2002) and frogs (Marr et  
436 al., 2008).

437         Specific examples of enemy release include the invasive European green crab  
438 *Carcinus maenas* that has significantly reduced parasite diversity and prevalence in its  
439 invasive range compared with its natural range, with their greater population biomasses in the  
440 invasive range attributed to this (Torchin et al., 2001). Several amphipod species that have  
441 invaded British waters host a lower diversity, prevalence and burden of parasites than the  
442 native amphipod *Gammarus duebeni celticus* (MacNeil et al., 2003; Prenter et al., 2004). Of  
443 the five parasite species have been detected, three are shared by both the native and invasive  
444 amphipod species, but two are restricted to *G. duebeni celticus* (Dunn and Dick, 1998;

445 MacNeil et al., 2003). Torchin et al. (2005) found a similar pattern in mud-snail communities  
446 in North America; whilst the native snail *Cerithidea californica* was host to 10 trematode  
447 species, the invader *Batillaria cumingi* was host to only one. These specific examples are  
448 supported by meta-analyses of native and invasive animals and plants which have revealed a  
449 higher-than-average parasite diversity in native populations; for example of 473 plant species  
450 naturalized to the United States from Europe had, on average, 84 % fewer fungal pathogens  
451 and 24 % fewer virus species than native fauna (Mitchell and Power, 2003), whilst introduced  
452 fishes in the England and Wales had, on average, less than 9 % of the number of macro-  
453 parasites they had in their native range (Sheath et al., 2015).

454

455 The processes underlying ‘enemy release’ are therefore important when building trophic  
456 networks that incorporate introduced species. Enemy release suggests that the probability of  
457 the free-living species developing an established population is enhanced by the loss of  
458 substantial proportions of their natural parasite fauna, thus providing a new node. However, it  
459 also suggests that only a small proportion of non-native parasites will be co-introduced with  
460 free-living hosts, limiting the number of new parasite nodes and thus limiting the potential for  
461 the introduction to substantially alter the network properties. The potential for connectivity to  
462 then increase is also diminished when the introduced parasites that do establish are those with  
463 direct lifecycles that involve a single host species (Sheath et al., 2015).

464

#### 465 **4.3 Enemy release: a case study with invasive cichlids spp.**

466 Whilst enemy release in introduced free-living species is a well-established process (Section  
467 4.2), the actual pattern of parasite loss in invasive species tends to be highly variable, even  
468 among closely related host species or populations (e.g. Benejam et al., 2009; Blakeslee et al.,  
469 2012). This variation is likely driven by numerous factors related to invasion history, or to the

470 biological characteristics of the host and/ or parasite (Lafferty et al., 2010; MacLeod et al.,  
471 2010). As regional parasite species richness is strongly predicted by the richness of the  
472 available host species (Kamiya et al., 2014), then this pattern might also occur in a biological  
473 invasion context, i.e. the greater the number of introduced free-living species, the greater the  
474 number of parasites that can be both introduced and acquired by a given free-living species.  
475 The rapid formation of a community of non-native host species within an invaded territory is  
476 therefore expected to be associated with a simultaneous rapid formation of a parasite  
477 community. The transfer rate of parasites is thus expected to depend on the transfer rate of  
478 their hosts and so, therefore, the richest non-native host communities should be associated to  
479 the richest parasite communities. This prediction could have a central influence of the  
480 contemporary emergence and the evolution of host-parasite networks.

481         This suggests that the regional species richness of introduced parasites can be  
482 predicted from the richness of their potential introduced host species and, conversely, that the  
483 number of parasite species found in a region can be indicative of the pattern of free-living  
484 species introduction at the community scale in this region (in the case of a community of free-  
485 living species sharing the same pool of parasites). This was tested here using the taxonomic  
486 data of Firmat et al. (in press) concerning invasive cichlid fishes (commonly and thereafter  
487 called ‘tilapia’) that, whilst native to Africa, have been moved around the world for  
488 aquaculture purposes. They are now harmful invaders in several tropical and subtropical  
489 regions of the World (Canonico et al., 2005), providing replicated ‘natural experiments’ of  
490 species range expansion. The parasites used were Ancyrocephalidae, the super diverse species  
491 group of monogenean gill parasites harboring a low level of host specificity (Mendlova and  
492 Simkova, 2014; Van Steenberge et al., 2015). These gill parasites have simple life cycle, a  
493 low level of host specificity (e.g. Jimenez-Garcia et al., 2001) and their taxonomy, with more  
494 than 120 described species, is well established (Pariselle and Euzet, 2009). These traits thus

495 enable evaluation of the variation in parasite species richness to be tested against tilapia  
496 invasions.

497 For investigating the relationship between free-living versus parasite species richness  
498 in a biological invasion context, the data used here were based on literature and epidemiology  
499 survey data of Firmat et al. (in press) that provided a total of 14 case studies. Each case study  
500 represented a locality outside of Africa where a list of data on parasite species richness and  
501 the number of host species was available (*cf.* Appendix A, Firmat et al., in press). The number  
502 of introduced host species per regional case study was extracted from Fishbase (Froese and  
503 Pauly, 2011) and complemented with the comprehensive register on tilapias from the Food  
504 and Agriculture Organization (2004).

505 Before these data were analyzed, the species richness of hosts ( $R_h$ ) and parasites ( $R_p$ )  
506 were both  $\log(R+1)$  transformed, with an ordinary least-squares regression then performed on  
507  $\log(R_p + 1)$  vs.  $\log(R_h + 1)$ . Although log transformation for count data is generally not  
508 recommended (O'Hara and Kotze, 2010), here it allowed a biologically meaningful and  
509 simple modelling of the influence of host species richness on parasite species richness. This  
510 was because: (i) the slope of this log-log regression provided a direct estimate of the relative  
511 (i.e. proportional) increase in parasite richness induced by an increase in host richness in the  
512 system; and (ii) the procedure allowed fixing of the intercept to zero, a biologically  
513 meaningful value as no parasites are expected to be detected in the absence of host (i.e. when  
514  $R_h = 0$ ,  $\log(R_h + 1) = 0$  and  $R_p$  should be null, then a zero intercept corresponds to  $\log(R_p + 1)$   
515  $= 0$ ).

516 Variation in the reported parasite richness among the case studies ranged from 0 to 12  
517 species (mean  $\pm$  SD:  $3.86 \pm 2.82$ ). Figure 5 revealed that the number of parasites increased  
518 markedly with the number of hosts established during the twentieth century. The variance in  
519 host species richness explains 91 % of the variance in parasite richness across invaded

520 regions. The regression slope ( $b$ ) was 0.86 (95 % confidence interval: 0.70 - 1.03), indicating  
521 that for a 10 % increase in host species richness, parasite species richness increases by 8.6 %.  
522 Thus, each new introduced host species is expected to add almost one new parasite species to  
523 the food web. In other words, this suggests that the number of host species introductions in a  
524 new territory drives the number of introduced parasite species and then, potentially, the level  
525 of the enemy release phenomenon. Due to the low level of host specificity of monogenean  
526 parasites in this system, the potential number of ‘enemies’ of a given introduced free-living  
527 species will be increased by the number of other introduced free-living species. At the host  
528 species level, the potential number of parasites is broadly determined by the number of  
529 introduced hosts, i.e. the non-native host community richness, a driver of the number of co-  
530 introduced parasites.

531         Taking the extreme case of the Grande Terre Island (New Caledonia, South West  
532 Pacific), only one introduction event was reported and no gill parasites were detected (Firmat  
533 et al., in press). This exemplifies that where free-living species introduction are rare, this is  
534 then reflected in the parasite fauna. Conversely, the regions of highest parasite richness were  
535 those that had been highly exposed to the trading of live tilapias during recent decades (e.g.  
536 Madagascar, Mexico, China), indicating the initial parasite loss of enemy release can be partly  
537 compensated by the repeated introductions of new host species and therefore of new parasites.  
538 This raises questions over the effects of multiple parasitic infections on host fitness. In these  
539 examples, an increased cost of multi-species infection might be expected given that  
540 Ancyrocephalid parasites species appear to occupy different microhabitats on the tilapia gills  
541 (Madanire-Moyo et al., 2011), potentially leading to higher energetic costs of infection.

542

## 543 **5. How exotic parasites alter networks: parasite-host interactions and consequences**

544

## 545 **5.1 Parasite spill-over**

546 Where non-native parasites are co-introduced into a new range, despite enemy release, then  
547 their introduced free-living hosts can then act as a ‘reservoir’ of potential transmission to  
548 native species. This source of infection and subsequent transmission to native hosts is referred  
549 to as parasite ‘spill-over’ (Britton, 2013; Thompson, 2013) (Fig. 4). This spill-over can also  
550 occur when an introduced parasite is able to infect native hosts. An example from European  
551 freshwaters is the nematode parasite *Anguillicoloides crassus* (Kirk, 2003). Native to the  
552 Japanese eel *Anguilla japonicas*, it was introduced into Europe via their movements in the  
553 global aquaculture trade. It has since spilled-over into the European eel *Anguilla anguilla* and  
554 is now widely distributed in their range (Kirk, 2003). Infections of *A. anguilla* are then caused  
555 by both consumption of both intermediate hosts (copepods) but also of paratenic hosts, i.e. via  
556 post-cyclic transmission (Pegg et al., 2015a). Thus, from a network perspective, the spill-over  
557 of a co-introduced non-native parasite into the native community increases the number of new  
558 links in the network from the same number of nodes, increasing connectance and, potentially,  
559 linkage density. Where an introduced parasite infects final hosts via two mechanisms, such as  
560 in *A. crassus*, then increased connectance should also result.

561

## 562 **5.2 Parasite acquisition and spill-back processes**

563 The process of parasite ‘spill-back’ can occur following the introduction of a free-living  
564 species. This is where the introduced species becomes infected with native parasites and then  
565 act as ‘reservoirs’ of infection for the subsequent spillback of these parasites to their native  
566 hosts (Kelly et al., 2009; Fig. 4). For example, in Australia, the invasive Cane toad *Bufo*  
567 *marinus* played an important spillback role in the emergence of two myxosporean parasites of  
568 native frogs, the Green and golden bell frog *Litoria aurea* and the Southern bell frog *Litoria*  
569 *raniformis*, facilitating parasite dispersal and transmission, and the consequent population

570 declines of the frogs (Hartigan et al., 2011). The invasive crayfish *Pacifastacus leniusculus*  
571 displays both spill-over and spill-back. For spill-over, it is an asymptomatic host for the  
572 introduced fungus *Aphanomyces astaci* (crayfish plague) that is subsequently transmitted to  
573 white-clawed crayfish *Austropotamobius pallipes* (Kelly et al., 2009). For spillback, it hosts  
574 the native microsporidian *Thelohania contejeani* where it acts as a reservoir of infection for *A.*  
575 *pallipes* which then tends to also cause mortality (Dunn et al., 2009).

576         Given that enemy release is a process common to many introduced free-living species,  
577 then their parasite fauna in their new range are often dominated by native parasites acquired  
578 in their new locality (Torchin et al., 2003, Kelly et al., 2009; Sheath et al., 2015; Fig. 4). This  
579 is the case for many exotic fish species that have been translocated globally as parasite-free  
580 eggs or juveniles, such as rainbow trout *Oncorhynchus mykiss* (Ortubay et al., 1994) and  
581 brown trout *Salmo trutta* (Hine et al., 2000). Thus, the threats of parasitism from non-native  
582 species often includes altered native host-parasite dynamics (Tompkins et al., 2011), which  
583 potentially results in either the spill-back (Daszak et al., 2000, Kelly et al., 2009), or dilution  
584 of, infections by native parasites (Telfer et al., 2005, Thieltges et al., 2009). Both can have  
585 considerable influences on food web topology (Fig. 4).

586         The extent of parasite acquisition by introduced free-living species is variable  
587 according to a number of factors that affects their exposure and vulnerability to infection.  
588 Paterson et al. (2012) suggested five factors that strongly determined these outcomes for fish:  
589 total body length, time since introduction, phylogenetic relatedness to the native fish fauna,  
590 trophic level and native fish species richness. Kelly et al. (2009) suggested that parasite spill-  
591 back occurred when an introduced free-living species was a competent host for a native  
592 parasite, with the presence of this additional host then increasing disease impacts in native  
593 species as they act as a reservoir. In their review of animal-parasite literature, they revealed  
594 that native parasites accounted for 67 % of the parasite fauna of introduced free-living species

595 from across a range of taxonomic groups, indicating their competence for hosting native  
596 parasites and their potential for creating novel network links.

597

598 In considering spill-over and spill-back processes for infectious food webs, their key  
599 influence on network properties appears to be increasing connectance by providing a greater  
600 number of realised links for the same number of nodes. However, given that parasite  
601 infections can result in population declines and, in cases of disease emergence, population  
602 extirpations, the longer term consequences of these processes might differ with, for example,  
603 potentially deleterious effects on the nodes and links resulting from these transmission  
604 processes.

605

### 606 **5.3 Parasite life-cycles and the trophic vacuum**

607 Some parasites have evolved complex lifecycles in which they are trophically transferred up  
608 food chains in order for them to overcome the issues of their low trophic position versus the  
609 high trophic position of their final host. Recent studies have termed this difference in parasite  
610 and host trophic position as the ‘trophic vacuum’, given that most adult helminth parasites  
611 sexually reproduce in vertebrates that have high positions in food chains, with their free-living  
612 propagules unable to be transmitted directly to these hosts. This trophic vacuum is thus filled  
613 by one or more intermediate hosts (Benesh et al., 2014; Parker et al., 2015). This raises a  
614 number of questions over why the parasite then does not grow and develop further in the  
615 intermediate hosts, and instead shows suppressions of growth and reproduction until  
616 transmission to the final host, a process that can involve being transmitted through multiple  
617 intermediate hosts (Parker et al., 2015). It has been suggested that it relates to selection  
618 pressures associated with the increased longevity and higher growth that is possible by the  
619 parasite in the final host (due to their relatively large body size of these hosts) versus

620 intermediate hosts (that are often copepods or gammarid species). The selection pressure is  
621 thus for larger parasite body size and higher fecundity at sexual maturity that is only possible  
622 in the relatively large final host (Parker et al., 2015).

623

624 Within an infectious food web, these complex lifecycles can form chains that link species of  
625 very low trophic position with those much higher in the network, potentially leading to  
626 increased connectance and linkage density. For an introduced parasite with a complex  
627 lifecycle, it also suggests that their likelihood of establishment is probably going to be  
628 diminished versus a parasite with a direct lifecycle unless appropriate native species are  
629 present that can act as intermediate hosts. Accordingly, of the 98 examples of parasite co-  
630 introductions recorded by Lymbery et al. (2014), 64% had a direct lifecycle and 36% had a  
631 complex lifecycle. However, should these complex parasites establish then there is potential  
632 for a greater shift in network properties.

633

#### 634 **5.4 Parasite impacts on hosts: manipulative and non-manipulative alterations**

635 Host manipulation is the alteration of the host phenotype in a way that promotes the  
636 reproductive success of the parasite. It is found among various parasite strategies including  
637 parasitoids, vector-transmitted parasites and trophically-transmitted parasites (Poulin and  
638 Maure, 2015). It helps trophically-transmitted parasites to fill the trophic vacuum and usually  
639 involves the behavioural manipulation of the intermediate host that increases the likelihood of  
640 that host being predated by the next host in the lifecycle (Loot et al., 2001; Britton et al.,  
641 2009). Amphipods provide strong examples of intermediate hosts that are manipulated by  
642 their parasites to facilitate their predation by a fish or bird final host (Britton and Andreou,  
643 2016). Infections by the trematode parasite *Microphallus papillorobustus* divides populations  
644 of *Gammarus insensibilis* into two groups: an infected group of individuals that inhabit the

645 surface of salt marshes and an uninfected group of individuals that remains near the bottom  
646 (Ponton et al., 2005). This shift in habitat use promotes predation of *G. insensibilis* by bird  
647 final hosts (Britton and Andreou, 2016). Infected *Gammarus roeseli* with *Polymorphus*  
648 *minutus* exhibit reverse geotaxis, elevating their time spent at the water surface (Bauer et al.,  
649 2005; Médoc et al., 2006). In conjunction with reduced activity, this increases their predation  
650 risk by bird final hosts (Jacquin et al., 2014). This also decreases their predation risk by three-  
651 spined sticklebacks *Gasterosteus aculeatus*, a non-host for *P. minutus* (Médoc et al., 2009),  
652 highlighting that the effects of parasite manipulation on network properties might be more  
653 complex than simply strengthening the links involved in trophic transmission (Médoc and  
654 Beisel, 2009, 2011).

655 Parasite manipulation has also been detected in fish intermediate hosts. The cestode  
656 parasite *Ligula intestinalis* is generally recognised as modifying the behaviour of its  
657 intermediate fish hosts (Loot et al., 2001; Britton and Andreou, 2016). Where fish are  
658 infected, they are increasingly encountered in the littoral zone, increasing their predation risk  
659 to the final bird host (Loot et al., 2001; Britton et al., 2009). In doing so, the infected fish  
660 potentially exploit different food resources to their uninfected conspecifics (Adamek et al.,  
661 1996), thus directly and indirectly creating a series of novel links within the food web.  
662 Another, and spectacular, example of link creation by parasites is the host manipulation by  
663 nematomorphs, whereby infected crickets are manipulated to commit suicide by jumping into  
664 water, where the adult parasites reproduce (Thomas et al., 2002). This makes a new and  
665 valuable food source for fish and modifies the food web (Sato et al., 2012).

666

667 Thus, the manipulation of new hosts by an introduced parasite with a complex lifecycle has  
668 the potential to alter the links within the network, especially where weighted approaches are

669 being used. The example of the nematomorphs also highlights the potential for manipulation  
670 to connect food webs across ecosystem boundaries.

671

672 Parasite infections can also modify the host phenotype through consequences that are not  
673 associated with manipulation, such as impaired traits and altered behaviours that result from  
674 pathological or physiological impacts (Knudsen et al., 2004) which can then affect other  
675 behaviours, such as foraging and prey selectivity (Pegg et al., 2015b). As example is the  
676 common carp *Cyprinus carpio* when infected, as the final host, with *Bothriocephalus*  
677 *acheilognathi*, a non-native intestinal cestode parasite. Infections impair the foraging ability  
678 of hosts through reducing, for example, their consumption rates (Britton et al., 2011, 2012).  
679 Infected individuals then increasingly specialise on feeding on less motile food sources that  
680 divides their population trophic niche into infected and uninfected sub-groups (Pegg et al.,  
681 2015b; Britton and Andreou, 2016), increasing connectance. This also raises the question as  
682 to whether *C. carpio* should be included in the network as a single node or as two nodes split  
683 between uninfected and infected sub-groups.

684 Infections by parasites can also be important through their effects on host foraging  
685 time budgets and the associated selectivity in prey items. For example, when *Schistocephalus*  
686 *solidus* infect *G. aculeatus*, the foraging time of the fish increases and they invest less in anti-  
687 predator behaviours (Milinski, 1985). The fish also select smaller prey than their uninfected  
688 conspecifics (Milinski, 1984; Cunningham et al., 1994). This finding is, however, contrary to  
689 Ranta (1995), who suggested that larger items were taken by infected individuals compared  
690 with uninfected conspecifics, with this being a compensatory mechanism to overcome some  
691 of the energy costs caused by the parasite.

692

693 Consequently, irrespective of manipulation, parasite infections can markedly alter the host  
694 phenotype and this can have marked consequences for the trophic ecology of the host. These  
695 consequences can then modify the links within the food web, including through processes  
696 such as parasite-mediated competition.

697

## 698 **5.5 Parasite mediated competition and coexistence**

699 Parasite mediated competition can have important implications for the prey selectivity of  
700 parasitized individuals and thus the connections within the trophic network (Holt and  
701 Pickering, 1985; Holt and Dobson, 2006; Hatcher et al., 2006, 2012b,c). In essence, the  
702 infection by a focal parasite on a free-living species potentially alters the competitive ability  
703 of the host, resulting in either increased or reduced access to a shared resource (Dunn et al.,  
704 2012; Hatcher et al., 2006, 2012a). If reduced, then it might lead to that host having to exploit  
705 other resources to maintain their energetic requirements and thus could be a driver of the  
706 formation of new network links.

707 At an intraspecific level, the competitive ability of infective hosts may be reduced  
708 compared to their uninfected conspecifics, potentially leading to intra-specific niche  
709 partitioning (Hatcher et al., 2012a). For inter-specific competitive interactions, parasites can  
710 reverse competitive interactions where one host species out-competes another in the absence  
711 of a parasite; however, due to lower resistance to the parasite, they develop infections and  
712 subsequently the competitive interaction becomes more symmetrical (Hatcher et al., 2006).  
713 Apparent competition occurs when two host species that do not normally compete are  
714 infected by the same parasite species that creates a link between them and creates an indirect  
715 competitive interaction (Dunn et al., 2012; Hatcher et al., 2006, 2012a). This competition is  
716 generally driven by one host species being more resistant to the parasite and acting as a

717 reservoir that feedbacks greater parasite pressure on to the other host species (Hatcher et al.,  
718 2006).

719

720 Parasite mediated coexistence is where the infection by a parasite suppresses the interspecific  
721 competitive ability of its host sufficiently to enable the host species to coexist with an  
722 otherwise inferior competitor species. The effect can even be as extreme as to allow a species  
723 to colonise an area when it would otherwise be competitively excluded by the host species.  
724 For example, two Caribbean *Alonissidis* lizard species are only able to coexist when the malarial  
725 parasite (*Plasmodium azurophilum*) reduces the competitive ability of *Alonissidis gingivinus*  
726 (Schall, 1992). In this way, parasite mediated coexistence can be important in maintaining  
727 species richness and patterns of biodiversity. It will then, by extension, also be important in  
728 regulating trophic relationships and thus strongly influence the extent of the connections  
729 within the trophic network.

730

## 731 **6. Integrating biological invasions into infectious food webs**

732

### 733 **6.1 Linking network structure and invasibility by parasites**

734 Invasibility, along with invasiveness, are two major concepts in invasion ecology (Richardson  
735 and Pyšek, 2006). Invasiveness is the propensity of an introduced species to invade a recipient  
736 ecosystem, with its expected determinants including introduction history, species traits, and  
737 ecological and evolutionary processes (van Kleunen et al., 2010). It is beyond the scope of  
738 this Section to discuss this further. Invasibility is the susceptibility of the recipient ecosystem  
739 to the establishment and spread of introduced species (Lonsdale, 1999). Whilst the roles of  
740 species diversity and the patterns of resource use and competition in resistance to invasion are  
741 important in determining the outcomes of introductions (Kennedy et al., 2002), network

742 approaches potentially provide a new effective, integrative tool to search for structural  
743 features that determine invasibility. The relationship between food web structure and  
744 invasibility has been investigated almost exclusively regarding introduced free-living species.  
745 However, their main results can be used to address the case of co-introduced parasites, given  
746 that their success depends on that of their co-introduced host. Again, the structural features  
747 that are of most interest are connectance, nestedness and modularity. Here, the effects of  
748 connectance are primarily discussed, since patterns of nestedness and modularity are often the  
749 consequences of varying connectance values (Riede et al., 2010; Lurgi et al., 2014).

750

751 Connectance has been found to either constrain or promote invasion. A negative relationship  
752 between connectance and invasibility was first reported in the theoretical work by Romanuk  
753 et al. (2009) and later in the empirical study by Wei et al. (2015), who tested experimentally  
754 how the resource competition networks of resident bacterial communities affected invasion  
755 resistance to the plant pathogen *Ralstonia solanacearum*. In highly connected webs, all  
756 members efficiently exploit most resources. This results in increased competition and a  
757 crowded niche space, constraining invasion. Nevertheless, the effect of connectance on  
758 invasibility might depend on the trophic level of the invader (Baiser et al., 2010). This is  
759 because connectance seems to be positively linked to the fraction of intermediate species  
760 (Vermaat et al., 2009), which may constitute prey or predators for the invader depending on  
761 its position in the food web. It follows that invasion success is predicted to decrease with  
762 connectance for exotic herbivores due to a high number of potential predators, and to increase  
763 with connectance for exotic top predators due to a high number of potential resources (Baiser  
764 et al., 2010). More recently, and contrary to previous findings, the theoretical works by Lurgi  
765 et al. (2014) and Hui et al. (2016) illustrated how highly connected networks might be more  
766 vulnerable to invasions. This is because of the link between connectance and stability; highly

767 connected networks could encompass more reinforcing feedbacks between species, which  
768 makes them unstable and might create opportunity niches for invasion (Hui et al., 2016).  
769 Conversely, networks with low connectance are more stable in terms of total biomass even  
770 when individual species abundances fluctuate, and are thus more robust to biological  
771 invasions (Lurgi et al., 2014). Another explanation lies on species diversity. Higher levels of  
772 diversity are known to confer resistance to invasion and more connected food webs are often  
773 less diverse (Lurgi et al., 2014). This could explain the positive relationship between  
774 connectance and invasibility.

775

776 In addition to the successful establishment of their host, co-introduced parasites with a  
777 complex life cycle must overcome another critical step before establishing which is to find the  
778 next host(s) and the transmission pathway(s) needed to complete their cycle. Intuitively,  
779 highly diverse networks should provide more opportunities to find a suitable host, but they  
780 generally exhibit low connectance. As previously discussed, this might decrease invasibility  
781 by the co-introduced host. Similarly, it should be easier to find suitable transmission pathways  
782 in highly connected networks, which are also supposed to facilitate invasion by the co-  
783 introduced host, but where parasites might face the problem of finding a suitable host as these  
784 networks are often less diverse. Therefore, it is difficult to predict how the structure of the  
785 recipient food web may determine invasibility by co-introduced parasites as antagonistic  
786 effects can be confounded. A rough prediction could be that the invasion success of parasites  
787 with complex life-cycles decreases with the level of host specificity and the number of  
788 successive hosts involved in the cycle.

789

790 Spill-over to native hosts may allow co-introduced parasites to establish in the recipient food  
791 web even when its structure constrains invasibility by their co-introduced host. Infecting a

792 native host is the first step of the invasion process for non-native parasites that are introduced  
793 alone at a free-living infective stage. Once in the native hosts, non-native parasites (either  
794 introduced or co-introduced) have first to meet life-cycle requirements in terms of successive  
795 hosts and transmission pathways. As discussed above, this might depend on host specificity,  
796 the complexity of the cycle, and the compromise between diversity and connectance. Second,  
797 they have to cope with the recipient parasite – host network, as the native hosts they exploit  
798 are themselves likely to be already exploited by a range of native parasites. The role of the  
799 structure of recipient parasite – host networks on invasibility by parasites is a question that  
800 remains to be addressed. For instance, connectance in parasite – host networks decreases  
801 rapidly with increasing number of species (Poulin, 2010). It follows that it might be easier for  
802 exotic parasites to avoid competition with native parasites in large networks. Modularity  
803 might also play a role in invasibility by parasites in that highly compartmentalized networks  
804 are formed by clearly bounded modules, with few interactions between modules,  
805 corresponding to spatially or temporally partitioned niches and habitats that are potentially  
806 available. This suggests that invasive species experiencing strong ontogenetic niche shifts,  
807 such as some complex lifecycle parasites, are more likely to invade highly modular networks  
808 (Hui et al., 2016).

809

## 810 **6.2 Impact of exotic parasites on food-web structure**

811 As when it comes to infectious food webs, the introduction of new parasites first adds greater  
812 complexity via new nodes and links. Once past this generic effect and in the case of invasion,  
813 which implies spill-over to native hosts, long-term effects are more difficult to predict as they  
814 depend on parasite strategy, the levels of virulence, pathogenicity and specificity, the  
815 presence of natural enemies that confer biotic resistance (e.g. predators, other parasites and

816 hyperparasites), and the evolutionary responses of both hosts and parasites (see Table 1 in  
817 Britton, 2013).

818         A rough categorisation can be made regarding the level of pathogenicity (i.e. the  
819 extent to which infection reduces host fitness). Highly pathogenic parasites might cause the  
820 decline or even the exclusion of native hosts, sometimes followed by secondary extinctions.  
821 There is, however, no empirical work illustrating the structural effect of such parasites,  
822 although it can be argued that in the extreme cases of species exclusion, this results to  
823 network simplification through a reduction in the number of nodes and links. These parasites  
824 are sometimes referred as ‘emerging infectious diseases’, which are diseases that have  
825 appeared in a population for the first time and have significant social, economic and  
826 ecological costs (Hatcher et al., 2012b), or as ‘biological weapons’, because they facilitate  
827 invasion by their co-introduced host through their negative impacts on native hosts, which  
828 constitute natural enemies for invaders (Strauss et al., 2012). They include parasitoids, and  
829 particularly those used in classic biocontrol, microparasites like fungi, protozoans, bacteria  
830 and viruses, or macroparasites (see examples in Hatcher et al., 2012; Strauss et al., 2012;  
831 Dunn and Hatcher, 2015). The fungus that causes crayfish plague and discussed in Section 5.2  
832 is a good example. Another popular example is the parapoxvirus that spilled-over from grey  
833 squirrels to red squirrels in which it causes a deleterious disease (Tompkins et al., 2003). The  
834 releases of insect parasitoids to control agricultural pests provide good examples of the  
835 intentional introduction of pathogenic parasites. Spill-over to non-target species frequently  
836 occurs and may cause local extinctions and profoundly reorganize the networks (Hawkins and  
837 Marino, 1997; Boettner et al., 2000; Henneman and Memmott, 2001; Parry, 2009).

838         In contrast, invasive parasites of low pathogenicity can make invaded networks more  
839 complex through the creation and persistence of new nodes and links. This might be the case  
840 with many macro-parasites, like helminths with complex life-cycles, with the assumption that

841 the more complex the lifecycle, the greater the effect on network complexity. To our  
842 knowledge, the empirical work by Amundsen et al. (2013) is currently the only available  
843 study that compares the structure of an infectious food web pre- and post-invasion. The study  
844 evaluated how the introduction of two fish species, arctic charr *Salvelinus alpinus* and *G.*  
845 *aculeatus*, altered the pelagic network of Lake Takvatn, a subarctic lake in northern Norway.  
846 Arctic charr and stickleback facilitated the arrival of four new birds feeding almost exclusively  
847 on these two fish, and five new parasites, including one parasite that use the fish as an  
848 obligate host. Several of these parasites also infected native species in the food web during the  
849 completion of their life cycles. In comparing the pre- and post-invasion infectious food webs,  
850 the post-invasion web had greater complexity with more nodes (39 vs. 50 species), more links  
851 (282 vs. 440), and an increase in linkage density, mean trophic level, omnivory, vulnerability  
852 and nestedness. Only connectance slightly decreased, with this a common pattern when  
853 adding consumers with some degree of specificity, such as parasites. Most interestingly, 79 %  
854 of the 158 new-established links involved parasites with many predator – parasite links.  
855 Trophically-transmitted parasites were highly connected, thus highlighting the important  
856 contribution of this parasite strategy to the complexity of networks.

857 Amundsen et al. (2013) did not, however, address the question of modularity. As  
858 discussed in Section 6.1, highly compartmentalized networks might more easily accommodate  
859 complex-life cycle parasites than non-modular networks because the distinct modules  
860 correspond to partitioned niches and habitats. In return, the introduction of parasites with  
861 complex lifecycles should decrease modularity as they create links between modules. This  
862 effect should increase with the length of the cycle (i.e. the number of successive hosts) and  
863 the magnitude to the ontogenetic shifts. We are not aware of empirical works that could  
864 illustrate this effect.

865

866 Parasites of low pathogenicity are more likely to be co-introduced as the probability of their  
867 co-introduced hosts surviving the translocation process is expected to decrease with the  
868 pathogenicity of the parasites they carry (Blackburn et al., 2011; Strauss et al., 2012; Lymbery  
869 et al., 2014). Consequently, it might be expected that co-introduced parasites are more likely  
870 to make invaded networks more complex than to simplify them. However, the effects of co-  
871 introduced parasites can be confounded with the concomitant effects of their co-introduced  
872 hosts, which can drastically disturb the structure of the invaded network and at the same time  
873 threaten native parasites.

874

### 875 **6.3 How invader – induced changes in network structure affect parasites**

876 Invasive species (which refers only to free-living species in this Section) can modulate the  
877 dynamics of native parasites in many ways, either directly or indirectly (Table 5, see  
878 examples in Johnson et al., 2010 and Poulin et al., 2011). Here, we focus on the structural  
879 changes induced by biological invasions to discuss their potential effects on native parasites.

880 Few studies used the network approach to investigate how invaders affect native  
881 parasites, and it has been done mostly on parasitoids. Heleno et al. (2009) investigated how  
882 alien plants integrated into the native plant – herbivore – parasitoid tripartite network of the  
883 laurel forest in the Azores archipelago. They found no significant effect on network structure  
884 but a significant decrease in network size as plant and insect (both herbivores and parasitoids)  
885 richness decreased with plant invasion. Although insect abundance was not significantly  
886 affected by alien plants, insect biomass was significantly reduced because small insects on  
887 alien plants replaced large insects on native plants. Similarly, Carvalheiro et al. (2010)  
888 investigated how the invasive plant *Gaultheria shallon* integrated into the plant - herbivore –  
889 parasitoid network of a site dominated by *Calluna vulgaris* in the UK. They found a decrease  
890 in the abundance of all insects and a decrease in the richness of parasitoids, but these effects

891 were confined to trophic specialists, not generalists. In terms of network structure, because  
892 specialist species dominated the undisturbed food web, *G. shallon* invasion caused a reduction  
893 of the importance of their trophic links, leading to an increase in the evenness of species  
894 abundances and interaction frequencies (Carvalho et al., 2010). Timms et al. (2012) found  
895 that invasion by gypsy moth (*Lymantria dispar*), one of the most harmful invasive forest  
896 insects in North America, had no significant effect on the structure of the native parasitoid –  
897 herbivore network. There was only a little sharing of parasitoids with native hosts and gypsy  
898 moth was the target of a generalist parasitoid that increased its specialization on gypsy moth  
899 at high gypsy moth abundances.

900         There is not enough empirical and theoretical works to infer a general pattern for the  
901 effects of invaders on the structure of recipient parasite – host networks, and it is likely that it  
902 depends on the structure of the pre-invasion food web. The works by Heleno et al. (2009),  
903 Carvalho et al. (2010) and Timms et al. (2012) emphasize the benefit of using the network  
904 approach with information on diet breadth to understand and predict the responses of native  
905 species to invasion. It permits the detection of bottom-up cascade effects that can lead to  
906 further top-down effects, via apparent competition (Carvalho et al., 2010).

907

908 By definition, invasive species proliferate in recipient ecosystems and can dominate invaded  
909 communities in terms of abundance or biomass. It follows that invasive species can become  
910 profitable prey for native predators. For instance, in North America, many freshwater  
911 predators have shifted their diet to include the round goby (*Neogobius melanostomus*) and/or  
912 the zebra mussel (*Dreissena polymorpha*), two of the most problematic freshwater invaders  
913 (reviewed in Bulté et al., 2012). In addition, a broad diet with opportunistic feeding is  
914 expected to be one of the attributes of successful invaders (Ricciardi and Rasmussen, 1998).  
915 Invasive species can thus become generalist consumers in the invaded food web, creating

916 links with many native resources. Combining high generality with high vulnerability makes  
917 invasive species, and especially those at intermediate trophic levels, likely to occupy a central  
918 location in invaded food webs in that they are highly connected. Invasion might lead to food  
919 web contraction with increased connectivity around invasive species and reduced connectivity  
920 among native species, without marked change in overall connectance. Several studies  
921 documented the preferential use by parasites of free-living species that occupy central  
922 locations in food webs and represent hubs (Chen et al., 2008; Amundsen et al., 2009;  
923 Anderson and Sukhdeo, 2011). These species constitute stable ecological and evolutionary  
924 units for parasites and offer transmission opportunities. Following the colonization time  
925 hypothesis (Guégan and Kennedy, 1993), one might thus predict that invasive species should  
926 acquire local parasites over time, and should host a significant fraction of parasite diversity  
927 due to their central position. The work by Gendron et al. (2012) supports this prediction. As  
928 predicted by the enemy-release hypothesis, they showed that the round goby was less infected  
929 than native fish in the early phase of its establishment in the St. Lawrence River. However,  
930 this advantage over native species is expected to be of short duration as the parasite richness and  
931 abundance of the older population of round goby in Lake St. Clair has more than doubled  
932 within 15 years (Gendron et al. 2012).

933

## 934 **7. Qualitative versus quantitative approaches**

935 The application of network analyses to predict how introduced free-living species and their  
936 parasites alter network properties has revealed their high utility in demonstrating the extent of  
937 the changes that can be incurred in native systems. However, trophic networks that are built  
938 on binary matrices provide only a qualitative perspective of food web structure (Section 2.2).  
939 Whilst more quantitative approaches are possible that incorporate species abundance and  
940 interaction frequency using weighted metrics (e.g. Bersier et al., 2002), these are reliant on

941 either using robust empirical data on predator – prey relationships or using heuristic  
942 approaches where these data are unavailable (e.g. Amundsen et al., 2013). Thus, these  
943 network approaches are, arguably, unable to incorporate some of the more complex aspects of  
944 host-parasite trophic relationships that could result from processes such as parasite  
945 manipulation and infection-induced host phenotype alterations (Section 5). Thus, approaches  
946 that integrate the more qualitative network approaches discussed in this review with more  
947 quantitative approaches, such as stable isotope analyses, should provide greater insights into  
948 how parasites alter trophic relationships (Britton, 2013; Britton and Andreou, 2016). They  
949 should also help test how parasite loading affects trophic niche sizes and how infections  
950 modify energy flux (Britton and Andreou, 2016).

951         As the ratios of the stable isotopes of carbon ( $^{13}\text{C}$ :  $^{12}\text{C}$ ) and nitrogen ( $^{15}\text{N}$ :  $^{14}\text{N}$ ) vary  
952 predictably from resource to consumer (Fry, 2007), they enable reconstruction of the trophic  
953 structure and the analysis of the trophic niche sizes and the overall food web structure (Grey,  
954 2006). The carbon values ( $\delta^{13}\text{C}$ ) of a consumer species indicates their energy source, with  
955 enrichment of approximately 1 ‰ indicating the move up a trophic position; the stable  
956 nitrogen isotope ( $\delta^{15}\text{N}$ ) typically becomes enriched by 3 to 4 ‰ between prey and predator  
957 tissue and so is an indicator of consumer trophic position (Deniro and Epstein, 1981;  
958 Minagawa and Wada, 1984). The application of stable isotope techniques, using the  
959 predictable relationship between the isotopic composition of consumers and their diet, is then  
960 sufficiently powerful to detect long-term (e.g. 3 to 6 months) dietary differences between  
961 individuals of the same population (Fry, 2007), such as those that are parasitized with a  
962 specific parasite and those that are uninfected (Pegg et al., 2015b).

963         Examples of how parasites can affect the trophic niche of host populations are  
964 demonstrated in Figure 6 and 7. In all cases, the host populations were sampled using electric  
965 fishing and seine netting, with dorsal muscle samples taken from a random selection of up to

966 30 fish per host population. Concomitantly, macro-invertebrate samples were collected by  
967 kick- and sweep-netting. All samples were dried at 50°C for 48 hours before being sent to the  
968 Cornell Isotope Laboratory for analysis (Cornell University, New York, USA). The outputs  
969 were values of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  for each individual fish and their putative food resources. Where  
970  $\delta^{15}\text{N}$  has been converted to trophic position (TP), it used the formula  $[(\delta^{15}\text{N}_i - \delta^{15}\text{N}_{\text{baseline}}) /$   
971  $3.4] + 2$ , where  $\text{N}_{\text{baseline}}$  is the mean  $\delta^{15}\text{N}$  of the putative food resources (macro-invertebrates).  
972 Where  $\delta^{13}\text{C}$  was converted to  $\text{C}_{\text{corr}}$ , conversion was via  $(\delta^{13}\text{C}_i - \delta^{13}\text{C}_{\text{mean}}) / \text{CR}$ , where  $\delta^{13}\text{C}_{\text{corr}}$   
973 is the corrected carbon isotope ratio of the fish,  $\delta^{13}\text{C}_i$  is the uncorrected isotope ratio of the  
974 fish,  $\delta^{13}\text{C}_{\text{mean}}$  is the mean macro-invertebrate isotope ratio and CR is the invertebrate carbon  
975 range ( $\delta^{13}\text{C}_{\text{max}} - \delta^{13}\text{C}_{\text{min}}$ ). Irrespective of whether the stable isotope data were corrected or  
976 not, they were used to determine the trophic niche width of each population sub-group  
977 (infected/ uninfected with the focal parasite) using the metric ‘standard ellipse area’ ( $\text{SEAc}$ )  
978 (Jackson et al., 2011; Jackson et al., 2012). These ellipses are based on the distribution of  
979 individuals in isotopic space as an estimate of each species core trophic niche using the ‘siar’  
980 package (Jackson et al., 2011; Parnell et al., 2010) in the ‘R’ computing programme (R Core  
981 Development Team 2012). The subscript ‘c’ in ‘ $\text{SEAc}$ ’ indicates that a small sample size  
982 correction factor was used, as sample size tended to be below 20 per species per sub-group  
983 (Jackson et al., 2011).

984 Figure 6 shows the trophic niche sizes of sub-groups of minnow *Phoxinus phoxinus*  
985 and bullhead *Cottus gobio* that are infected/ uninfected with the focal parasite  
986 *Pomphorhynchus laevis* in the River Loddon, Southern England. This is an intestinal parasite  
987 that has a complex lifecycle involving *G. pulex* as the intermediate host. In both species, the  
988 infected fishes had a trophic niche that sat within the larger trophic niche of the uninfected  
989 fishes, suggesting that although both sub-groups were consuming similar prey items, the  
990 infected individuals were specialising on only a proportion of these items, resulting in

991 constriction of their niche. Figure 7 revealed the trophic niche sizes of the infected/ uninfected  
992 sub-groups of a roach *Rutilus rutilus* population infected with *L. intestinalis*, and a *G.*  
993 *aculeatus* population infected with *Schistocephalus solidus*. Both parasites have a complex  
994 lifecycle where the fish represent the second intermediate host, where the final host is a fish-  
995 eating bird. For both host-parasite systems, the trophic niche of the infected fishes had almost  
996 completely diverged from that of the uninfected fishes. Thus, across these examples, stable  
997 isotope analysis revealed that trophic consequences of infection for the host population were  
998 marked, with these insights difficult to predict from qualitative network approaches. These  
999 outputs could then be used as the basis of weighting the interaction frequencies between  
1000 infected population sub-groups and their prey.

1001

## 1002 **8. Conclusions and forward look**

1003 Parasites can reach novel ecosystems with or without free-living species, and despite enemy  
1004 release, the rate of parasite introductions is accelerating around the world. Identifying the  
1005 structural features of recipient networks that constrain or promote the establishment success  
1006 of introduced parasites has proven to be complex as antagonistic effects might be confounded.  
1007 Particularly, the role of species diversity and connectance in invasibility by parasites has to be  
1008 explored further. Less ambiguously, it seems that modular networks could more easily  
1009 accommodate parasites experiencing strong ontogenetic shifts. Once established, the extent to  
1010 which exotic parasites alter food-web structure mostly depends on their life-strategies. For  
1011 instance, pathogenic parasites causing emerging infectious diseases or acting as biological  
1012 weapons for their co-introduced host are likely to make food webs more simple through the  
1013 removal of nodes and links, whereas complex-life cycle parasites with trophic transmission  
1014 are likely to make food webs more complex through the creation of new links. At the  
1015 individual and population levels, this involves various processes including parasite spill-over

1016 and spill-back, the modification of host phenotype and the mediation of biotic interactions.  
1017 However, the ecological significance of such increased complexity in networks, and  
1018 particularly whether it promotes or constrains stability, has to be further explored through  
1019 theoretical and experimental investigations. For this, some outstanding methodological issues  
1020 have to be resolved such as the problem of node resolution, or the question of how to deal  
1021 with the distinct sub-webs of a whole food web.

1022 In addition to the traditional predator – prey links, including parasites in food webs  
1023 adds new types of links that are often unequally documented. For instance, predator – parasite  
1024 links, whereby free-living species prey directly on parasites at a free-living stage or indirectly  
1025 through concomitant predation of their host, are not the most obvious and may be quite  
1026 difficult to detect and quantify. However, concomitant predation could be what makes the  
1027 topological role of parasites unique compared to free-living species, while predation on  
1028 parasites may confer biotic resistance to native networks. Additional data are needed on  
1029 predator – parasite links.

1030 The network approach improves our understanding of invasive species impacts as it  
1031 allows to track how they propagate throughout invaded communities through bottom-up and  
1032 top-down effects involving density-dependent regulation and apparent competition.  
1033 Nevertheless, some impacts may not be detected with a qualitative approach, which does not  
1034 account for the strength of interactions. This is particularly true for parasites, which establish  
1035 weak links with their hosts compared to predator – prey links. Accounting for this asymmetry  
1036 of interaction strength through empirical data, heuristic approaches or stable isotopes, is also  
1037 important when it comes to investigate the role of parasites in food-web stability. To go  
1038 further in this way, it has been proposed to combine the network approach with an energetic  
1039 approach (Sukhdeo, 2012). Under the energetic perspective, energy is the currency of  
1040 biological and can be used to characterize the role of parasites in food webs, for instance, by

1041 focusing on how host biomass and its stability constrains parasitism or how parasites drive  
1042 energy fluxes in the web. This can be done by measuring and scaling up the costs associated  
1043 with infection at the individual scale to the whole population based on parasite prevalence  
1044 (see Lettini and Sukhdeo, 2010 for an example).

1045 On the long run, free-living invaders are predicted to become important players in  
1046 parasite diversity. As stated by the ‘invasional meltdown hypothesis’ (Simberloff and Von  
1047 Holle, 1999) and illustrated in Amundsen et al. (2013), free-living invaders and the food-web  
1048 reconfigurations they induce should facilitate subsequent invasions by the species with which  
1049 they have co-evolved, including parasites, while their central location in the web should  
1050 facilitate the acquisition of local parasites.

1051

1052

1053

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1591 **Figures legends**

1592

1593 Figure 1: Examples of interaction matrices and networks. Letters indicate entities that  
1594 potentially interact (e.g. taxonomic species) and binary entries indicate the links (1: yes, 0:  
1595 no). (a) interaction matrix and (b) its visualization for a qualitative bipartite network where  
1596 the entities form two groups (a to h and i to l) with no within-group interaction allowed. (c)  
1597 interaction matrix and (d) its visualization for a qualitative network where all interactions are  
1598 allowed. Arrows indicate the direction of the interaction (e.g. from a resource to its  
1599 consumer). (e) nested bipartite network where specialist species interact with proper subsets  
1600 of the species that interact with more generalist ones. (f) modular bipartite network where  
1601 species are organized in modules and interact more within than among modules. (g)

1602 quantitative bipartite network where bars indicate species abundances and linkage width  
1603 indicates interaction frequency.

1604

1605 Figure 2: Example of an ecological network (a) where black nodes are free-living species  
1606 (FL1 to FL5) and grey nodes are parasites (P1, P2 and HP). Black arrows indicate predator -  
1607 prey links and grey arrows those that involve parasites: parasite - host links (curved arrows),  
1608 predator - parasite links (solid arrows) and parasite - parasite links (curved arrow between HP  
1609 and P2). P1 is a complex-life cycle with three developmental stages: (ds1) the free-living  
1610 stage infective to the intermediate host FL3, (ds2) the larval stage found FL3, and (ds3) the  
1611 adult reproducing in the definitive host FL5, a predator of FL3. P2 is a simple life-cycle  
1612 parasite exploiting FL2, and itself exploited by HP, a hyperparasite. Predator - parasite links  
1613 include direct predation on parasites at a free - living stage (e.g. between FL2 and ds1), and  
1614 concomitant predation, when parasites are consumed along with they host (e.g. between FL5  
1615 and ds2, FL4 and P2 with HP). The corresponding interaction matrix (b and c) include a  
1616 predator - prey subweb (upper left quadrant), a parasite - host subweb (upper right quadrant),  
1617 a predator - parasite subweb (lower left quadrant) and a parasite - parasite subweb (lower  
1618 right quadrant). Nodes can be defined as taxonomic species (b) or developmental stages (c),  
1619 here to account for the strong ontogenetic shifts experienced by P1.

1620

1621 Figure 3: Processes involved in the invasion by an exotic parasite that comes either along with  
1622 its exotic host as a co-introduced parasite or alone as an introduced parasite. For a co-  
1623 introduced parasite (a), establishment in the recipient ecosystems occurs in case of survival,  
1624 dispersal and reproduction in the exotic host (b), and invasion occurs when it spreads among  
1625 native hosts (c). For an introduced parasite (d), establishment and invasion are not

1626 distinguishable as its persistence in the recipient ecosystem depends on its ability to infect and  
1627 spread among native hosts (e).

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1629 Figure 4: Influence of enemy release, parasite spill-over, parasite spill-back and parasite  
1630 acquisition on the number of network connections in a food web invaded by introduced free-  
1631 living species, co-introduced parasites, and introduced parasites. Shaded boxes denote  
1632 processes, dashed lines denote interactions between the species via the different processes,  
1633 and solid lines denote the contributions of each category of parasite and free-living species to  
1634 the number of network connections and, ultimately, food web structure.

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1636 Figure 5: Effect of the number of cichlid hosts introduced in a world region on the observed  
1637 regional species richness of parasites ( $n = 14$ ). Each point represents one region of the World  
1638 out of hosts' native ranges (Africa) where Ancyrocephalid parasites were sampled. The grey  
1639 line represents the predictions of a log-log linear regression and the grey area its 95 %  
1640 confidence interval ( $R^2 = 0.91$ ).

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1642 Figure 6: Trophic niches of subgroups of infected (grey ellipse; individual data points grey  
1643 circles) and uninfected (black ellipse; individual data points black circles) for populations of  
1644 bullhead *Cottus gobio* (left) and minnow *Phoxinus phoxinus* (right) infected with  
1645 *Pomphorhynchus laevis* from the River Loddon, Southern England, sampled in June 2015  
1646 (unpublished data). Both infected sub-groups show strong patterns of niche constriction.  
1647 Differences in values on the X and Y axis are for the purposes of presentation and clarity  
1648 only.

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1650 Figure 7: Trophic niches of subgroups of infected (grey ellipse; individual data points grey  
1651 circles) and uninfected (black ellipse; individual data points black circles) for lentic  
1652 populations of roach *Rutilus rutilus* with the parasite *Ligula intestinalis* (left) and three spined  
1653 stickleback *Gasterosteus aculeatus* population infected with *Schistocephalus solidus* (right) in  
1654 England (unpublished data). Both infected sub-groups show strong patterns of niche  
1655 divergence from their uninfected conspecifics. Differences in values of the X and Y axis  
1656 between the plots are due to the fish being sampled from different waterbodies.  
1657

1659 Table 1. Parasite life-history dichotomies and their implications for parasite strategies

Life history dichotomy	Implication for parasite strategy
The parasite has an obligate association with the host/ has a physical association with the host	Parasites that live in or on their host and are physiologically dependent on it (e.g. nutrient acquisition) differ from behavioural parasites, such as brood parasites exploiting the parental care of their hosts, while klepto-parasites steal their food items.
The parasite exploits a single host/ has multiple host species during its life cycle	Parasites with a simple life cycle exploit only a single individual from one host species; transmission can be vertical (parent to offspring) and/or horizontal (between unrelated individuals). Parasites with complex life cycles undergo larval development in one or up to three successive intermediate hosts before reproducing in the definitive host.
Parasite infection affects host fitness/ does not affect host fitness	Parasitic castrators suppress host reproduction either directly, by feeding on gonads, or indirectly, by diverting energy away from gonad development or by secreting “castrating” hormones. Alternatively, fitness is affected by death before reproduction, such as where parasitoid larvae are laid in or on a single host, or sometimes penetrate it via direct contact or through ingestion, and consume host tissues to grow until emergence, which leads to host death.
Infection is lethal/ sub-lethal	In parasitoids, host death tends to be an inevitable outcome of their own development. By contrast, although parasitic castrators reduce host fitness to zero, they benefit from the long life of their host. Also, host death is required for trophically transmitted parasites whose transmission relies on the consumption of an infected intermediate host by a predatory host.
The pathology of parasite infection is intensity-dependent/ intensity-independent pathology	This separates micro-parasites from macro-parasites. Micro-parasites multiply directly within the host, whereas macro-parasites do not and whose impact is proportional to the number of separate individual parasites that infect the host.
The parasite exploits a free-living species/ exploits another parasite	A hyper-parasite is a parasite that is host to another parasite. By contrast, super-parasitism is where a parasite infects an already infected host individual (e.g. in insect parasitoids), and multi-parasitism is where an individual host is infected by more than one parasite species.
Parasitism is the only trophic strategy for the parasite/ the parasite has multiple trophic strategies, of which parasitism is one.	Obligate parasites are completely dependent on parasitism for their nutritional requirements. By contrast, facultative parasites only engage in parasitism under appropriate circumstances and are able to obtain resources through other means under different circumstances.

1661 Table 2: Summary of some metrics commonly used to characterize the structure of antagonist  
 1662 networks (predator - prey webs, parasite - host webs or whole food webs where both free-  
 1663 living species and parasites are included). For more details on the metrics, their quantitative  
 1664 versions and their calculation see Bersier et al., (2002), Bascompte et al., (2003); Olesen et  
 1665 al., (2007), Fortuna et al., (2010).

Metric	Definition
Richness	Number of nodes
Connectance	Proportion of possible links that are realized
Link density	Mean number of links per node
Generality	Mean number of prey or host per predator or parasite species
Vulnerability	Mean number of predator or parasite per prey or host species
Omnivory	Proportion of taxa that feed on more than one trophic level
Chain length	Total number of trophic levels
Nestedness	Non-random pattern of link distribution where specialist taxa interact with a proper subset of the group of taxa with which generalists interact
Modularity	Non-random pattern of link distribution where taxa form groups of highly-connected taxa (i.e. modules) with more links among themselves than with the taxa of other groups

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1678 Table 3: Factors that may explain differences in nestedness and modularity in parasite – host  
 1679 networks

Factor	How it may promote nestedness or modularity
Phylogeny	Phylogenetic continuity among hosts promotes parasite sharing and a nested pattern. Alternatively, phylogenetic gaps promote modularity with the detection of a phylogenetic signal within modules.
Spatial overlap	At a large scale, overlapping geographical ranges promote parasite sharing and therefore nestedness. At a smaller scale, host species using the same micro-habitats are more likely to belong to the same modules and to share the same parasites.
Species abundances	Abundant species tend to have more links than rare species. Asymmetry in species abundance may thus promote a nested pattern where abundant hosts harbour many parasites, with a high proportion of specialists, whereas rare hosts tend to be parasitized by generalists.
Host size	Large host species tend to harbour more parasites than small hosts. Asymmetry in host size may thus promote nestedness. Because asymmetry in host size
Foraging strategy	Host species having the same foraging strategy are more likely to belong to the same modules and to share the same parasites. Host species with a more diversified diet are more exposed to parasites than specialists. Asymmetry in diet diversity may thus promote nestedness.
Host - parasite specificity	A high degree of specialization promotes modularity whereas a lower specificity creates links between modules and therefore decreases modularity.
Life cycle complexity	Parasites with a complex life-cycle and experiencing strong ontogenetic shifts may connect distinct modules and decrease modularity.

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1691 Table 4: List of eleven model food webs that include both predators and parasites

Name	Location	References
Loch Leven	United Kingdom	Huxham et al. (1995)
Ythan Estuary	United Kingdom	Huxham et al. (1995)
Broom fauna at Silwood Park	United Kingdom	Memmott et al. (2000)
Otago Harbour	New Zealand	Thompson et al. (2005); Mouritsen et al. (2011)
Carpinteria Salt Marsh	USA, California	Lafferty et al. (2006); Kuris et al. (2008); Hechinger et al. (2011)
Estero de Punta Banda	Mexico	Kuris et al. (2008); Hechinger et al. (2011)
Bahía Falsa	Mexico	Kuris et al. (2008); Hechinger et al. (2011)
Muskingum Brook	USA, New Jersey	Hernandez and Sukhdeo (2008)
Lake Takvatn	Norway	Amundsen et al. (2009, 2013)
Flensburg Fjord	Germany/Denmark	Zander et al. (2011)
Sylt Tidal Basin	Germany/Denmark	Thieltges et al. (2011)

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1694 Table 5: how invasive species can modulate the dynamic of native parasites

	Positive effect on transmission	Negative effect on transmission
The invasive species serve as host (spillback)	Better transmission in the invasive species than in the natives	Better transmission in the native species than in the invasives
The invasive species do not serve as host	Decreased abundance of the natural enemies (predators, other parasites and hyperparasites) of the native parasites (e.g. through predation or competition) Increased abundance of the native hosts (e.g. through negative effects on their natural enemies) Trait-mediated indirect effects (e.g. behavioural changes in the native hosts that promote transmission)	Direct predation on the native parasites or their free-living infective stages Concomitant predation Decreased abundance of the native host (e.g. through predation or competition) Trait-mediated indirect effects (e.g. behavioural changes in the native hosts that constrain transmission)

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1696

1697 **Appendix A: Data for the case study of enemy release in invasive cichlids spp.**

1698

1699 The table below shows a literature survey combining the reported Ancyrocephalid gill  
 1700 parasites species richness and the number of introduced host species per territory.

1701 Taxonomic abbreviations for host and parasite genus: *O.*= *Oreochromis*, *T.*= *Tilapia*, *S.*=

1702 *Sarotherodon*, *C.*= *Cichlidogyrus*, *S.*= *Scutogyrus*. This table synthetizes available data on

1703 regional species richness of ancyrocephalid parasites in tilapia populations established out of

1704 Africa. The literature on gill monogenean parasite of invasive African cichlids was reviewed

1705 with the objective to make the survey as exhaustive as possible and with information for a

1706 representative set of territories (islands or countries). This includes published papers or

1707 reports obtained from ISI Web of Knowledge and Google Scholar (with the keywords

1708 *Cichlidogyrus* OR *Scutogyrus* OR ancyrocephalid\* OR monogen\* AND tilapia) as well as

1709 informally published literature (i.e. ‘grey publications’).

1710

1711

Territory	Reference	Host species analyzed	Established host species names (Food and Agriculture Organization, 2004; Froese and Pauly, 2011)	Monogenean species names	Number sampled hosts individual s analyzed	Number of African host species analyzed	Number of established host species (Food and Agriculture Organization, 2004; Froese and Pauly, 2011)	of Gill monogenean species richness
Mexico	(Jimenez-Garcia <i>et al.</i> , 2001; Flores Crespo and Flores Crespo, 2003)	<i>O. aureus</i> <i>O. mossambicus</i> <i>O. niloticus</i> <i>Cichlasoma fenestratum</i> <sup>n</sup>	<i>O. aureus</i> <i>O. mossambicus</i> <i>O. niloticus</i> <i>T. rendalli</i> <i>T. zillii</i>	<i>C. haplochromii</i> <i>C. dossoui</i> <i>S. longicornis</i> <i>C. sclerosus</i> <i>C. tilapiae</i>	403	4	5	5
Cuba	(Mendoza-Franco <i>et al.</i> , 2006)	<i>T. rendalli</i>	<i>O. aureus</i> <i>O. mossambicus</i> <i>O. niloticus</i> <i>T. rendalli</i>	<i>C. sclerosus</i> <i>C. tilapiae</i>	–	1	4	2

Panama	(Roche et al., 2010)	<i>O. niloticus</i>	<i>O. aureus</i>	<i>C. dossoui</i>	80	2	3	3
		<i>Vieja maculicauda</i> <sup>n</sup>	<i>O. mossambicus</i>	<i>C. sp1</i>				
			<i>O. niloticus</i>	<i>C. sp2</i>				
Brazil	(Jerônimo et al., 2011; Pantoja et al., 2012)	<i>O. niloticus</i>	<i>O. aureus</i>	<i>C. tilapiae</i>	240	1	4	5
			<i>O. mossambicus</i>	<i>C. sclerosus</i>				
			<i>O. niloticus</i>	<i>C. thurstonae</i>				
			<i>T. rendalli</i>	<i>C. halli</i>				
				<i>S. longicornis</i>				
Bangladesh	(Ferdousi and Chandra, 2002) <sup>1</sup>	<i>O. niloticus</i>	<i>O. niloticus</i>	<i>C. sclerosus</i>	–	2	2	4
		<i>O. mossambicus</i>	<i>O. mossambicus</i>	<i>C. thurstonae</i>				
				<i>C. tilapiae</i>				
				<i>S. longicornis</i>				
Madagascar	(Rakotofiringa, 1986) <sup>1</sup>	<i>O. niloticus</i>	<i>O. niloticus</i>	<i>C. anthracanthus</i>	–	8	8	12
		<i>O. mossambicus</i>	<i>O. mossambicus</i>	<i>C. tilapiae</i>				
		<i>O. macrochir</i>	<i>O. macrochir</i>	<i>C. sclerosus</i>				
		<i>T. rendalli</i>	<i>O. aureus</i>	<i>C. thurstonae</i>				
		<i>T. sparrmanii</i>	<i>O. spirulus</i>	<i>C. halli</i>				
		<i>T. zillii</i>	<i>T. rendalli</i>	<i>C. ergensi</i>				
		<i>T. shiranus</i>	<i>T. sparrmanii</i>	<i>S. longicornis</i>				
		<i>T. sp.</i>	<i>T. zillii</i>	<i>S. gravivaginus</i>				
		<i>T. « 3/4 »</i>		<i>C. dossoui</i>				
				<i>C. halinus</i>				
				<i>C. quaestio</i>				
				<i>C. sp.</i>				
Colombia	(Kritsky, 1974)	<i>O. mossambicus</i>	<i>O. mossambicus</i>	<i>C. sclerosus</i>	–	1	3	2
			<i>O. niloticus</i>	<i>C. tilapiae</i>				
			<i>T. rendalli</i>					
Viet Nam	(Arthur and Te, 2006)	<i>O. mossambicus</i>	<i>O. mossambicus</i>	<i>C. sclerosus</i>	–	3	4	3
		<i>O. niloticus</i>	<i>O. niloticus</i>	<i>C. tilapiae</i>				
		<i>T. sp.</i>	<i>O. aureus</i>	<i>C. sp.</i>				
			<i>T. sp.</i>					

Philippines	(Natividad et al., 1986)	<i>O. niloticus</i>	<i>O. niloticus</i>	<i>C. sclerosus</i>	175	1	6	4
			<i>O. aureus</i>	<i>C. tilapiae</i>				
			<i>O. mossambicus</i>	<i>C. tiberianus</i>				
			<i>O. spirulus</i>	<i>S. longicornis</i>				
			<i>O. sp.</i>					
			<i>T. zillii</i>					
Thailand	(Lerssutthichawal, 2008)	<i>O. niloticus</i>	<i>O. niloticus</i>	<i>S. longicornis</i>	–	1	5	5
		(including the red aquaculture morph)	<i>O. aureus</i>	<i>C. sclerosus</i>				
			<i>O. mossambicus</i>	<i>C. tilapiae</i>				
			<i>T. zillii</i>	<i>C. halli</i>				
			<i>T. rendalli</i>	<i>C. thurstonae</i>				
China	(Wu et al., 2006; Li et al., 2009)	<i>O. niloticus</i>	<i>O. niloticus</i>	<i>C. sclerosus</i>	–	2	6	5
		<i>O. aureus</i>	<i>O. aureus</i>	<i>C. haplochromii</i>				
			<i>O. mossambicus</i>	<i>C. thurstonae</i>				
			<i>S. galilaeus</i>	<i>C. levequei</i>				
			<i>S. melanotheron</i>	<i>S. longicornis</i>				
			<i>T. zillii</i>					
Japan	(Maneevitakusanti and Nagasawa, 2012)	<i>O. mossambicus</i>	<i>O. aureus</i>	<i>C. tilapiae</i>	212	3	9	3
		<i>O. niloticus</i>	<i>O. macrochir</i>	<i>C. sclerosus</i>				
		<i>T. zillii</i>	<i>O. mossambicus</i>	<i>C. halli</i>				
			<i>O. niloticus</i>					
			<i>O. urolepis hornorum</i>					
			<i>S. galilaeus</i>					
			<i>S. melanotheron</i>					
			<i>T. sparmanii</i>					
			<i>T. zillii</i>					
Australia	(Webb, 2003)	<i>O. mossambicus</i>	<i>O. aureus</i>	<i>C. tilapiae</i>	668	2	4	1
		<i>T. mariae</i>	<i>O. mossambicus</i>					
			<i>T. mariae</i>					
			<i>T. zillii</i>					
New Caledonia	Firmat et al. In press	<i>O. mossambicus</i>	<i>O. mossambicus</i>	-	62	1	2	0
			<i>S. occidentalis</i> <sup>2</sup>					

1713 **Footnotes:**

1714 <sup>1</sup> Parasite list revised from the current taxonomic standards (see Pariselle and Euzet, 2009)

1715 <sup>2</sup> In New Caldedonia, *Sarotherodon occidentalis*, is reported to have been introduced  
1716 simultaneously with *Oreochromis mossambicus* (Marquet et al., 2003). It would be the only  
1717 record of this species West African species out of Africa (Froese and Pauly, 2011) but it's  
1718 presence has not been confirmed by a three week field work aiming at sampling tilapia on the  
1719 Grande Terre Island (Firmat and Alibert, personal observation). We therefore have some  
1720 doubts on its real establishment in New Caledonia and we suspect a taxonomic error caused  
1721 by the strong sexual dimorphism in *O. mossambicus*.

1722 <sup>n</sup> Native (New World) cichlid species parasitized by introduced tilapia parasites.

1723

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