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3 **Introduced parasites in food-webs: new species, shifting structures?**

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14

15 **Abstract**

16 Introduction of free-living species also result in co-introduction of their parasites. Since  
17 recent advances have shown that native parasites dramatically alter food web structure, I  
18 evaluate here how introduced parasites might reorganise food webs. Empirical evidence  
19 suggests that introduced parasites alter food webs qualitatively through topological changes  
20 and quantitatively through shifts in trophic relationships arising from modified host  
21 phenotypic traits. I argue that predicting the extent of food web reorganisation is, however,  
22 difficult due to underlying ecological and evolutionary processes that could provide  
23 contrasting food web outcomes, including enemy release, biotic resistance and parasite  
24 spillover and spillback. Nevertheless, I suggest these food web reorganisations represent a  
25 further aspect of human-mediated global change resulting in irreversible consequences across  
26 multiple trophic levels.

27

28 **Introduced species and their parasites**

29 Introduced species have adverse consequences for native biodiversity and raise global  
30 concerns over biotic homogenization [1-3]. Introductions of free-living species can also result  
31 in the co-introduction of their parasites [3,4]. Although the introduction process might filter  
32 out many of these [5], the consequences in the receiving ecosystem of those parasites that are  
33 co-introduced vary according to a number of factors including the complexity of their  
34 lifecycle, their ability to spillover to native species, and the resistance and tolerance of these  
35 new hosts to infection [5-7]. Although high mortality rates might be incurred, these tend to be  
36 a consequence of the emergence of an infectious disease [8-10] or be symptomatic of  
37 additional underlying stresses, such as poor environmental conditions [11]. Sub-lethal host  
38 consequences can include pathological, physiological and/or behavioural changes, with likely  
39 adverse consequences for growth, survival and fitness [7,11].

40 In considering the consequences of infection by non-native parasites, information from  
41 native parasites can be very revealing. Native parasites can profoundly shape the dynamics of  
42 their host populations and communities, alter competition strength and influence trophic  
43 relationships, and are important drivers of biodiversity [12-16]. Although their inclusion in  
44 food web studies has tended to be overlooked [17,18], recent studies suggest this has led to  
45 dramatic underestimates of food web connectivity and complexity [19,20]. This is because  
46 these studies on ‘infected food webs’ have revealed parasites alter food web structure and  
47 stability through, for example, substantially increasing connectivity, nestedness and linkage  
48 density [18-29]. As the consequences of infection by native parasites [13-15,24] are relatively  
49 similar to those of introduced parasites [7,11,24,30,31] and given the dramatic changes in  
50 structure and complexity that occur when native parasites are included in food webs [18-29],  
51 this raises the question of how introduced parasites might influence food web structures.  
52 Here, I explore this question through: (i) identifying how introductions of free living species  
53 and their parasites could influence food web topology; (ii) examining how parasite infections  
54 might influence introduction outcomes and food web topology; (iii) examining the processes  
55 and implications of parasite spillback and spillover between native and introduced species;  
56 and (iv) determining how parasite lifecycles and host species’ characteristics influence food  
57 web structure. Case studies highlight relevant examples and opportunities for further research  
58 (Boxes 1-3). The influences of introduced parasites on food web structure are considered  
59 through qualitative changes, such as topology [21,27], and through more quantitative  
60 perspectives, such as the magnitude of shifts in the intra- and inter-specific trophic  
61 interactions that result from host phenotypic modifications and might disrupt patterns of  
62 energy flow [6-8,24]. For simplicity and as pathogens are also parasitic by nature, parasites  
63 are defined here as organisms that feed on a single host individual per life history stage [32].

64

## 65 **Introduced species influence food web topology**

66 The introduction of a free-living species into a food web should increase food web diversity  
67 and cause some topological reorganisation through the formation of a new node that  
68 establishes new links [33]. Although the co-introduction of their parasitic fauna (both micro-  
69 and macro-parasites) should provide further new nodes and links [4], introduced species often  
70 bring a relatively low number of parasites into the recipient food web (Table 1). This is  
71 because they tend to lose their parasites during the introduction process [34] through such  
72 factors as only a small sub-set of propagules being introduced from the native range that  
73 might be uninfected or comprise uninfected life-stages; the parasite having a complex  
74 lifecycle that requires multiple hosts with some of these missing in the receiving food web;  
75 and strong selective pressures, founder events and population bottlenecks in both parasites  
76 and hosts that lead to their early extirpation [5,7,35]. Nevertheless, some parasites will be co-  
77 introduced [36], with Torchin *et al.* [5] suggesting that where an introduced species in their  
78 native range might have a mean of 16 parasites, three will remain in their introduced range.  
79 Introduced species do, however, gain an additional four native parasites through parasite  
80 acquisition during the introduction process [5,6]. Thus, while the number of new nodes  
81 resulting from co-introduced parasites might be low those introduced will still result in some  
82 shifts in food web topology (Table 1).

83

84 Parasites with complex lifecycles that have infective, free-living lifestages can also be  
85 introduced in the absence of their non-native host species. For example, the nematode  
86 parasite *Anguillicoloides crassus* is native to the Japanese eel *Anguilla japonicus* but as a  
87 consequence of movements in the global aquaculture trade has spilled-over into the European  
88 eel *Anguilla anguilla* and is now widely distributed in their range [36,37]. The initial  
89 introduction of *A. crassus* into rivers in the UK was through water discharges from

90 aquaculture transport lorries that released only their eggs and juveniles into adjoining water  
91 courses [38]. These infective free-living lifestages then completed their lifecycle through  
92 infecting native crustacean intermediate hosts, with subsequent transmission to fish paratenic  
93 hosts and *A. anguilla* [38]. For food web topology, this would also have provided a number  
94 of new nodes and multiple new links across a range of trophic levels.

95

### 96 **Parasites influence introduction outcomes that affect food web topology**

97 The outcome of the introduction of a free-living species will strongly influence how their co-  
98 introduced parasites will subsequently affect food web topology. The establishment and  
99 subsequent invasion of the free-living species might be enhanced through enemy-release or  
100 inhibited by biotic resistance.

101

102 The enemy release hypothesis (ERH) relates to the parasite loss experienced by introduced  
103 species that was outlined in the previous section and predicts that the loss of their natural  
104 ‘enemies’ enhances their ability to establish and invade [24,39,40]. Indeed, with introduced  
105 species escaping at least 75 % of their parasites from their native range [32], there are likely  
106 to be substantial benefits in terms of their fitness and survival [5]. Despite the ERH having  
107 been used to help explain the invasion success of species as diverse as slugs [41], mosquitoes  
108 [42] and frogs [43], evidence is not unequivocal. This is because whilst introduced species  
109 can experience enemy release, they might also incur significantly higher levels of prevalence  
110 than in their native range and this could be detrimental to their fitness, impinge on their  
111 ability to invade and diminish their functional role in the receiving ecosystem [5,7]. Further,  
112 Colautti *et al.* [40] suggested many studies over-estimate the role of ERH in successful  
113 invasions as few experimentally test the differential effects of enemy release versus  
114 alternative factors.

115 By contrast, biotic resistance inhibits the survival, establishment and invasion of  
116 introduced species through, for example, the presence of native predators, strong competitors  
117 and/or parasites that impede their survival and reproduction (Table 1) [44]. For example,  
118 whilst introduced bivalves in the North Sea, such as *Crassostrea gigas* and *Ensis americanus*  
119 were believed to be free of parasites, providing competitive advantages over native bivalves,  
120 up to 80 % were found to be infected with native trematode parasites that were providing  
121 some natural biotic resistance against their colonisation [45].

122

123 The contrasting outcomes of enemy release and biotic resistance for introduced species  
124 and their parasites are important in determining the consequences for food web structure.  
125 Should invasive populations of free-living species develop, they can reach higher densities  
126 than both populations in their native range and functionally-similar native free-living species  
127 in the receiving ecosystem [7]. This might result in the displacement of native species,  
128 particularly those that exploit similar resources [41]. This is important as the parasite  
129 diversity of the invasive species can be substantially reduced compared to the displaced  
130 native species [32]. For example, Torchin *et al.* [46] revealed a native snail with 10 native  
131 trematode parasites in an aquatic food web was displaced by a functionally similar invasive  
132 snail with only one trematode; similar findings are apparent in Northern Ireland for the  
133 parasites of native and invasive amphipods [47]. Thus, the increased number of nodes and  
134 links in the food web formed by the invader and its parasites in food web topology might fail  
135 to compensate those lost through displacement. Similarly, Lafferty *et al.* [21] revealed snails  
136 in a coastal salt marsh were infected with up to 17 host-specific parasites, thus any population  
137 displacement by an invasive snail would be likely to result in substantial losses in food web  
138 nodes and links, and decreased robustness through increased secondary extinctions.

139

140 **Implications of parasite ‘spillback’ and ‘spillover’ for food web structure**

141 The shifts in food web topology resulting from co-introduced parasites will be strongly  
142 influenced by three processes: (i) enemy release; (ii) parasite introduction and spillover; and  
143 (iii) parasite acquisition and spillback (Table 1) [6]. The role of enemy release in determining  
144 the actual number of parasites co-introduced into the food web has already been outlined [5].  
145 Following their introduction, these parasites might now ‘spillover’ to native species, i.e. they  
146 ‘host-switch’ to native species [6,7] and so would represent a new consumer in the ecosystem  
147 that increases the number of food web links (Fig. 1). The most substantial shifts in food web  
148 topology are likely to result from those spilled-over parasites with complex lifecycles that are  
149 trophically transmitted and have intermediate hosts, as their lifestages will form a series of  
150 new nodes and links across multiple trophic levels (Fig. 1) [48].

151

152 Parasite acquisition occurs when introduced free-living species become infected by native  
153 parasites; in the topological food web, new links are thus formed that might increase  
154 connectance and nestedness. The process might also have implications for the quantitative  
155 food web, as acquisition might result in parasite ‘spillback’ to the native species and disrupt  
156 trophic interactions [6]. This is dependent on whether the introduced host is competent [6,49].  
157 If it is, then its population can act as a ‘reservoir’ in which the parasite persists and  
158 reproduces, and from which its infective stages disperse and result in increased parasite  
159 prevalence in native hosts [6]. Conversely, if the introduced host species is not competent  
160 then it can act as an infection ‘sink’ that dilutes infection levels in native hosts [6,7]. Some  
161 introduced hosts actually incur higher infection levels than native hosts, as observed in  
162 introduced European starlings in the USA that acted as a reservoir for equine encephalitis  
163 virus [49]. Across these reservoir and sink scenarios, considerable alterations in the trophic  
164 interactions are thus likely between the native and introduced hosts and parasites as infection

165 modifies the phenotypic traits of infected individuals, causing shifts and reorganisation in the  
166 quantitative food web [50].

167

168 **Shifts in food web structure are affected by parasite lifecycles and host characteristics**

169 The parasite lifecycle, host phenotypic modifications and confounding infections by native  
170 parasites are additional factors that determine how introduced parasites might alter food web  
171 structure, particularly with regard to quantitative changes (Table 1). Modifications to the host  
172 phenotype will vary depending on the hosts and the parasite concerned, but generally include  
173 altered foraging behaviour, feeding rates, competitive relationships, and shifts in life history  
174 traits such as altered growth rates and reproductive traits [13]. These modifications to host  
175 phenotype might impact trophic interactions through shifts in intra- and inter-specific  
176 competition and trophic relationships, and potentially result in considerable alterations to  
177 energy flow through the food web.

178

179 *Direct and complex parasite lifecycles*

180 In the topological food web, an introduced parasite with a direct lifecycle and a single  
181 definitive host might result in only one new node and link, i.e. there would be little  
182 reorganisation. By contrast, the spillover to native hosts of an introduced parasite with a  
183 complex lifecycle involving trophic transmission could result in a number of new nodes and  
184 multiple new links that causes substantial reorganisation, with this supported by some  
185 empirical evidence from introduced parasites (Box 1) and supplementary examples from  
186 native parasites [12,20,24]. In the quantitative food web, parasite lifecycles are important  
187 regarding how the host phenotypes might be altered and shift trophic relationships. As native  
188 parasites with complex lifecycles often increase their likelihood of transmission by  
189 manipulating host anti-predator behaviours that increase the likelihood of predation and so



190 completion of the parasite lifecycle [13], then similar scenarios could be likely for spilled-  
191 over parasites in native hosts and acquired native parasites in introduced hosts.  
192 Notwithstanding, Lagrue *et al.* [51] found that while the acanthocephalan parasite  
193 *Pomphorhynchus laevis* manipulated the drifting behaviour of its native intermediate hosts  
194 (e.g. *Gammarus pulex*), this was not apparent in an introduced intermediate host (*Gammarus*  
195 *roeseli*).

196

### 197 *Influence of host characteristics on food web consequences*

198 Where an introduced parasite spills over into a native species, the potential shifts in food web  
199 structure depend on a range of factors relating to the host species, including their functional  
200 role(s), affected life stage, modified phenotypic trait(s), genetic diversity and parasite  
201 resistance and tolerance [32,52-54]. Resistance and tolerance of native hosts to the parasite  
202 might be low due to poor immune responses and anti-predator behaviours resulting from their  
203 lack of shared evolutionary history [55]. A spilled-over parasite that meets low resistance and  
204 tolerance in native hosts can lead to high mortality rates, i.e. there will be an epizootic that  
205 could have substantial implications for food web structure (Box 2). Note, however, that the  
206 level of parasite resistance and tolerance in naïve hosts will depend on a wide range of  
207 environmental and biological factors, including host genetic diversity [5,8]. Moreover, rapid  
208 evolutionary responses over two or three generations have been recorded in host populations  
209 following disease emergence that have provided enhanced immune responses to infection and  
210 so minimised the pathology [8] and consequently the impacts for food web structure.

211

212 The indigenous parasites of the native hosts can also represent confounding infections that  
213 add complexity in determining which parasites - native or introduced - are actually adapting  
214 the host phenotype [13]. This is compounded by native parasite infections also leading to

215 reciprocal effects between the host and parasite [56]. These effects include ‘vicious circles’ of  
216 infection whereby hosts become more vulnerable to subsequent infections [57], leading to  
217 further complexity in deciphering which parasites are modifying the host phenotype.

218

### 219 **Concluding remarks and research perspectives**

220 Consequences for the topological food web of an introduced free-living species and its  
221 parasites are associated with the addition of new nodes and links across different trophic  
222 levels that should increase connectivity and complexity. For the quantitative food web, shifts  
223 in trophic interactions and patterns of energy flow might be caused by cascading effects  
224 arising from the modified phenotypic traits of the native hosts (e.g. through parasite spillover,  
225 Fig. 1, Table 1) and introduced hosts (e.g. through parasite acquisition). Empirical evidence  
226 for these food web shifts supports the opinion I have expressed here that there is considerable  
227 potential for introduced parasites to substantially alter native food web structure (Boxes 1-3).  
228 There are, however, a series of factors, such as enemy release and biotic resistance, which  
229 strongly influence how these alterations will be manifest (Table 1). Nevertheless, it should be  
230 noted that these alterations are resulting from an aspect of human-mediated global change  
231 that is usually irreversible and often associated with exploitation of ecosystem services and  
232 their management (Box 1) [58]. Thus, from a management perspective, this emphasises the  
233 requirement for risk-based regulations and policies to be implemented on the global  
234 movements of free-living species that minimises opportunities for inadvertent parasite co-  
235 introduction [1,2].

236

237 Research perspectives require the further testing of hypotheses relating to the potential  
238 shifts in food web structure that arise from introduced parasites of different functional groups  
239 and with contrasting lifecycles, and in relation to the factors outlined in Table 1. Approaches

240 can integrate the qualitative food web approaches that have dominated native parasite food  
241 web research with stable isotope analyses that can help reveal the more quantitative  
242 perspectives, including parasite-host trophic relationships [27], the effect of parasite loading  
243 on trophic niche [55] and the modifications to energy flow between trophic levels (Box 1).  
244 Evolutionary perspectives can be informed by the potential development of rapid and  
245 inheritable acquired immune responses of naïve hosts to introduced parasites [8]. The outputs  
246 of this research will then be important in refining the underlying theory that bridges the fields  
247 of parasitology, invasion ecology and evolution (Table 1). Aspects of these research  
248 perspectives are likely to be already progressing, albeit indirectly, through the use of  
249 introduced parasites in classical biological control programmes (CBC) that represent large-  
250 scale field experiments on introduced parasites in food webs (Box 3). That the parasite's  
251 natural host is already present and invasive in the food web increases their probability of  
252 establishment and so their utility to this field.

253

254 In closing, I emphasise that the increasing rate of species introductions is accelerating the  
255 rate of non-native parasite introductions and their consequences in the receiving ecosystems  
256 depends on their host specificity. Should parasite spillover occur then the native components  
257 of the food web are likely to be altered. If the parasite is host-specific then only impact the  
258 invaded component of the food web would be affected, potentially diminishing its effect.  
259 Indeed, in these circumstances, the parasite may protect the native aspects of the food web  
260 through diminishing the interaction strength of the invader. Irrespective, the increasing  
261 presence of non-native species and their parasitic fauna in food webs might be resulting in  
262 their irreversible structural re-organisations and represents a further consequence of global  
263 change.

264

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411 Table 1. Factors affecting the structural consequences of introduced parasites in food webs and examples of their potential outcomes

| Factor                               | Implication   | Potential outcome for food web structure  |
|--------------------------------------|---|---|
| Lifecycle of the introduced parasite | (i) Parasites with complex lifecycles require definitive intermediate and final hosts absent in the new range and fail to establish | No change in food web structure.  |
|                                      | (ii) Parasites with complex lifecycles might spillover at their different lifestages to native hosts at different trophic levels    | Shifts in the topological food web through new links and the quantitative food web via host phenotypic modifications. |
|                                      | (iii) Parasites with direct lifecycles infect only the introduced species   | Minor changes in food web topology.   |
| Enemy release                        | The introduced free-living species hosts a reduced number of parasites than in their native range.                                  | Minor changes in food web topology.   |
| Biotic resistance                    | The introduced host and their parasites fail to establish as they are out-competed, predated and/or parasitized by native species.  | No change in food web structure.  |
| Parasite spillover                   | Co-introduced parasites are transmitted to native species through host-switching.   | Shifts in the topological food web through new links and the quantitative food web via host phenotypic modifications. |

|  |  |   |
|--|--|---|
| Parasite spillback   | Native parasites infect the introduced free-living species that:<br>(i) become a competent host that acts as infection reservoirs for native hosts; or<br>(ii) become an incompetent host acting as an infection sink. | Shifts in the topological food web through new links and the quantitative food web via host phenotypic modifications in native and/or introduced hosts. |
| Naïve hosts rapidly develop inheritable anti-parasite traits | Host populations suffering an epizootic due to initial low parasite resistance and tolerance acquire inheritable immunity and anti-parasite behaviours in two to three generations                                     | Decreased host populations that substantially reorganise food web topology and disrupt trophic relationships are temporary.                             |
| Co- infections of native and introduced parasites            | Hosts with modified phenotypic traits are infected with a number of native and introduced parasites.   | Shifts in the quantitative food web might relate to infections by native and/or introduced parasites.   |

412 **Glossary**

413 **Competent host:** A host species that is capable of supporting and transmitting the parasite.

414 **Connectance:** A food web metric expressing the proportion of possible links in a food web  
415 that are realized.

416 **Complex lifecycle:** A parasite lifecycle that requires more than one host species for  
417 completion through use of intermediate and final hosts.

418 **Direct lifecycle:** A parasite lifecycle involving a single host species.

419 **Food web topology:** A qualitative representation of feeding interactions that illustrates who  
420 eats who in the food web, but with no information on the strength of those feeding  
421 interactions.

422 **Macro-parasite:** Defined here as relatively large parasites such as cestode tapeworms; can  
423 be seen with the naked eye.

424 **Micro-parasite:** Defined here as parasites requiring microscopy to view, such as viruses,  
425 bacteria and fungi.

426 **Nestedness:** An expression of the extent to which species with a low number of food web  
427 links have a sub-set of the links of other species, and is determined by characteristics such as  
428 network size and connectivity.

429 **Parasite spillover:** The cross-species transmission of a non-native parasite from its  
430 introduced free-living host to a native free-living host.

431 **Parasite spillback:** The cross-species transmission of a non-native parasite from its acquired  
432 native free-living host via spillover back to its introduced free-living host.

433 **Paratenic host:** A host that maintains the lifecycle of the parasite but is not needs for its  
434 development.

435 **Quantitative food web:** a representation of feeding interactions within an ecosystem that  
436 illustrates both the presence and strength of feeding interactions within that ecosystem.

437 **Qualitative food web:** a representation of the feeding interactions within an ecosystem that  
438 illustrates who eats whom but provides no information about the strength of the feeding  
439 interactions.

440 **Robustness:** Refers to the probability of secondary extinctions arising from species'  
441 removal; often defined as the proportion of species that must be removed to result in 50 % of  
442 species going extinct as they lack resource species. It is a topological measure of stability.

443 **Stability:** The likelihood of interacting species within the food web being persistent and  
444 usually expressed as a continuous metric that measures this likelihood. A stable food web  
445 tends to be one with minimal secondary extinctions following species removal.

446

447

448 **Box 1. Alterations to food-web structure by introduced parasites**

449 Direct empirical evidence for shifts in food web topology arising from the introduction of  
450 free living species with their parasites is provided by invasive fishes in the pelagic food web  
451 of Lake Takvatn, Norway [4]. Introductions into this sub-Arctic lake of Arctic charr  
452 *Salvelinus alpinus* and three-spined stickleback *Gasterosteus aculatus* and their co-  
453 introduced parasites strongly altered pelagic food web structure through increasing: (i)  
454 species richness from 39 to 50 species (the two fishes plus nine parasites); (ii) the number of  
455 nodes and trophic links in the topological food web; (iii) food-chain length; and (iv) the total  
456 number of trophic levels in the food web [4]. Food web complexity also increased, revealed  
457 through increased linkage density, degree distribution, vulnerability to natural enemies,  
458 omnivory and nestedness, all of which might have consequences for network functioning and  
459 stability [4]. The study concluded that when parasites are co-introduced with their free-living  
460 hosts, substantial alterations in the structure of the qualitative food web can result, especially  
461 when the parasites are tropically transmitted with complex lifecycles that form new links  
462 across multiple trophic levels. It thus underpins the importance of accounting for both native  
463 and introduced hosts and parasites in food-web studies.

464

465 That this study highlighted that trophically transmitted parasites with complex lifecycles  
466 will cause the most substantial shifts in food web structure suggests that globally invasive  
467 parasites with complex lifecycles, such as the Asian tapeworm *Bothriocephalus*  
468 *acheiolognathi*, might have already resulted in major reorganisations in food web structure.  
469 This trophically-transmitted freshwater parasite has been introduced around the world  
470 through the aquaculture industry [59]. In their invasive range, species within six copepod  
471 genera have been identified as intermediate hosts and at least 200 fish species as final hosts  
472 [59]. Transmission can also be through piscivory by fish and birds (postcyclic transmission)

473 [59]. Thus, as already measured in [4], their widespread introduction might have resulted in  
474 substantial shifts in food webs structure and complexity. Quantitative food web impacts  
475 might also be likely through their host impacts, as they cause substantial phenotypic  
476 modifications, albeit with a variable severity according to the fish host and infected lifestage  
477 [55]. In particular, infected *Cyprinus carpio* were discovered to be feeding at lower trophic  
478 levels than uninfected individuals, changing the symmetry of their competitive interactions  
479 [55] and potentially impacting trophic diversity and disrupting patterns of energy flow.  
480

481 **Box 2. Emerging infectious diseases and epizootics**

482 Epizootics are often associated with emerging infectious diseases (EIDs) [8,9]. These include  
483 parasites which have recently increased in incidence, host species and/or geographic extent  
484 [8,9,54,58]. Their effects can be severe, mediating community dynamics, shrinking host  
485 ranges and potentially extirpating local populations [8,9,58]. Consequently, they could  
486 disrupt food web topology, potentially decrease robustness via secondary extinctions and  
487 cause shifts in trophic relationships [9,44,45]. Examples of introduced pathogens in UK food  
488 webs responsible for substantial declines of native species are crayfish plague *Aphanomyces*  
489 *astaci* impacting native crayfish *Austopotamobius pallipes* following spillover from  
490 introduced signal crayfish *Pacifastacus leniusculus* [60] and the parapoxvirus that spilled-  
491 over from invasive grey squirrels *Sciurus carolinensis* to native reds *Sciurus vulgaris* [61].  
492 The disease emergence associated with *Gyrodactylus salaris* in Norway dramatically reduced  
493 populations of Atlantic salmon *Salmo salar* in 45 rivers [62] and triggered large-scale  
494 eradication efforts [62]. This highlights that EIDs in economically important species are often  
495 highly managed [9] and although outbreaks can have substantial food web implications,  
496 structural changes might be temporary if their management enables population recovery  
497 (Table 1).

498

499 Epizootics can also have profound effects on native ecological-engineering species, such  
500 as grazing animals that can have consequences for plant communities and food web structure.  
501 For example, EIDs impacting grazing animals can have substantial implications on the  
502 prevailing vegetation cover, as revealed by the cattle disease Rinderpest [63]. Savannah  
503 ecosystems comprise open grasslands, woodlands and closed thickets of broad-leaved shrubs;  
504 in the Serengeti National Park, Tanzania, the small tree *Euclea divinorum* facilitates  
505 establishment of the closed thickets [63]. Under current park management this, however, is



506 not occurring, with the existing thickets estimated as having established between 1890 and  
507 1920 when their growth was enabled by a Rinderpest epizootic that extirpated the park's  
508 ungulates and severely reduced the cattle population [63]. Rinderpest has subsequently been  
509 successfully managed at a regional and global level, preventing further outbreaks and  
510 inhibiting further thicket establishment [64].

511

512 Control of engineering invasive species has utilised introduced pathogens to facilitate  
513 ecosystem restoration that might have invoked cascading food web effects. The *Myxoma*  
514 virus has been used widely to control invasive rabbit numbers and enabled severely grazed  
515 vegetation to recover in impacted food webs [65]. In the case of the sub-Antarctic Macquarie  
516 Island, *Myxoma* decreased rabbit numbers and enabled recovery of tall tussock grassland;  
517 when rabbit numbers subsequently recovered to former levels then a uniform pattern of  
518 degraded vegetation and increased bare ground returned [65].

519

520

521 **Box 3. Classic biocontrol: field experiments on introduced parasites in food webs**

522 As classic biological control (CBC) is the deliberate introduction of the natural enemies of an  
523 introduced species into their invaded region then aspects of their study have high utility in  
524 informing how non-native parasites may alter the structure of native food webs [66]. Relevant  
525 ecological theories and hypotheses to CBC include enemy release and parasite spillover.  
526 Indeed, ERH provides CBC with its underlying principles as it assumes the invasion success  
527 of the target species was the loss of its native enemies so that their introduction into the new  
528 range will control it [39,66,67].

529

530 CBC has been argued by practitioners as being the most environmentally desirable control  
531 method as it has limited ecological consequences beyond the target species. However, the  
532 traditional CBC approach, the release of generalist parasites to control the invader, suggests  
533 that substantial impacts have been incurred in native non-target species as a result of  
534 spillover, including local extinctions, [66,67]. For example, Hawkins and Marino [68] found  
535 that of 313 introduced parasitoids released in North America for CBC, 51 were present on  
536 non-target native insects. In field experiments in the USA on the parasitoid fly *Compsilura*  
537 *concinata*, Boettner *et al.* [69] found high levels of parasitism (up to 100 %) in two native  
538 silk moths that could have been responsible for local extinctions. Henneman and Memmott  
539 [67] studied a remote and relatively pristine Hawaiian swamp within a region where at least  
540 122 releases of parasitic wasps and flies have been released to control Lepidopteran  
541 agricultural pests [67]. They recovered 216 parasitoids from 58 native moth species of which  
542 83 % were introduced through CBC and a further 14 % were from accidental introductions;  
543 only 3 % were native species [67]. Thus, introduced parasites from CBC had profoundly  
544 reorganised the trophic relationships in this quantitative food web.

545        These examples all suggest that the release of generalist, non-native parasites is likely to  
546 result in some degree of spillover to native species and alter food web structure. More  
547 contemporary applications of CBC has, however, started to test the use of specialist enemies  
548 that will not spillover and, if successful at controlling the target species, will diminish their  
549 interaction strength with native species [70]. By contrast to the release of generalist parasite,  
550 this aspect of CBC should consequently inform how host-specific introduced parasites might  
551 protect the native components of food webs from introduced free-living species [70].  
552

553 Figure 1. (i) Graphical and (ii) matrices representing a simple five-node native food web [27]  
554 before (a) and after (b) the introduction of a free-living non-native species, and before (c) and  
555 after (d) the spillover of its parasite with a complex lifecycle to a native final host. Native  
556 taxa are represented as basal (B), grazer (G1, G2) and predator (C1, C2) and the introduced  
557 free-living non-native species as  $C_{INV}$ . In (c) and (d), the parasite introduced with  $C_{INV}$  is  
558 represented as P; it has an adult stage (A) using (c)  $C_{INV}$  and (d)  $C_{INV}$  and C1 as a host, a free-  
559 living larval stage (L1), and a parasitic larval stage (L2) that uses G2 as an intermediate host.  
560 Transmission from intermediate host to final host requires the consumption of an infected  
561 intermediate host.

562 In (i), the rectangular box at the top of (c) and (d) contains the three life stages of P, the  
563 dashed ellipsoids indicate parasites occurring within hosts, and arrows represent feeding links  
564 that also indicate the direction of energy flow (note the predator–parasite links are not shown  
565 for brevity).

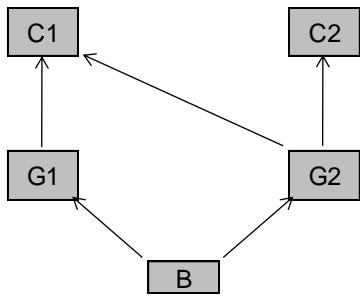
566 In (ii), the consumers are rows and resources are columns, and the shaded boxes indicate an  
567 interaction. In (c) and (d) there are four quadrants (clockwise from the top left): predator–  
568 prey, predator–parasite, parasite–parasite and parasite–host. In the initial free-living web (a),  
569 20 % of the possible links (directed connectance) are present [27]; after the introduction of  
570 the free-living species (b), this reduces to 19 %. The inclusion of the introduced parasite (c)  
571 increases connectance to 26.5 % and parasite spillover to C1 increases it to 29 %.

572

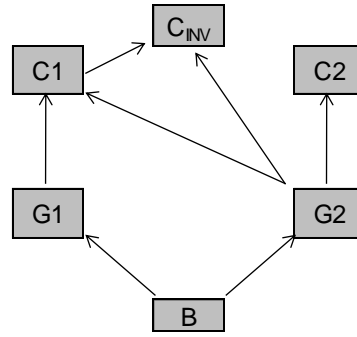
573

(i)

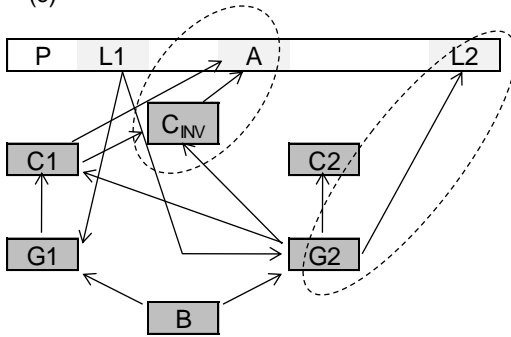
(a)



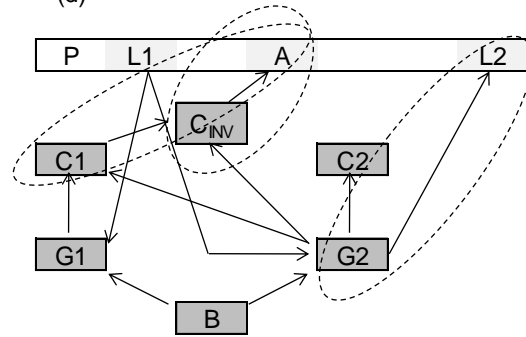
(b)



(c)

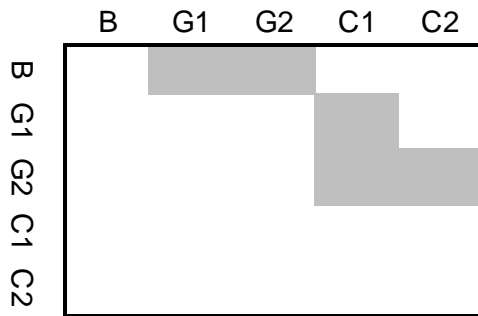


(d)

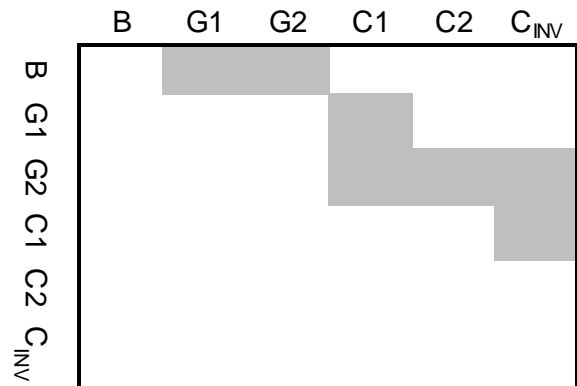


(ii)

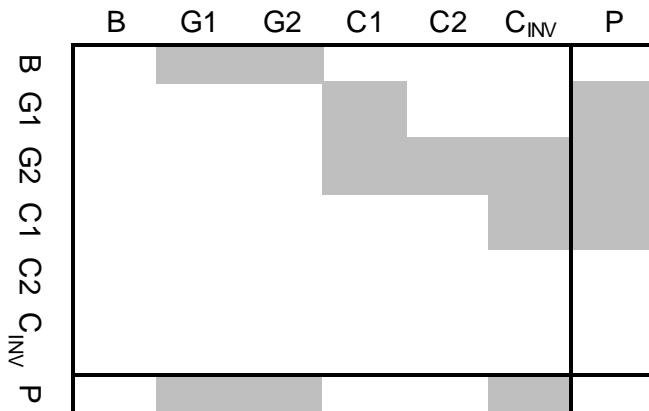
(a)



(b)



(c)



(d)



Figure 1.