Cascading effects of defensive endosymbionts

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Abstract

Defensive endosymbionts are now understood to be widespread among insects, targeting many different threats, including predators, parasites and disease. The effects on natural enemies can be significant, resulting in dramatic changes in the outcome of interactions between insects and their attackers. Evidence is now emerging from laboratory and field work that defensive symbionts can have important effects on the surrounding insect community, as well as on vulnerable enemy species; for example, by reducing prey available for the trophic level above the enemy. However, there is a need for more experimental work across a greater taxonomic range of species in order to understand the different ways in which defensive symbionts influence insect communities.

Highlights

Defensive endosymbionts are widespread among insects, targeting many different threats

Recent evidence shows defensive symbionts can indirectly impact the surrounding insect community

Most studies hitherto have used aphids; more taxonomic breadth is needed in future work

Introduction: symbiont-mediated defence and indirect effects

Many insects harbour endosymbiotic microorganisms which rely on their insect host for resources and transmission opportunities [1]. Symbionts which are indispensable to the host, notably those providing nutritional supplements to an otherwise inadequate diet [2], are universally prevalent within their host species. Symbiont species that are not required for host growth or reproduction may also persist at high frequencies, through parasitic manipulation of the host [3], providing conditional benefits [4], or a combination of the two [5].

One way in which facultative symbionts can secure their own future is by defending their insect host against biological threats, termed ‘symbiont-mediated protection’ [6]. This protection can have a significant impact on both hosts and enemies. For example, the symbiotic bacterium *Spiroplasma* sp. can protect *Drosophila neotestacea* against a sterilising parasitic nematode, *Howardula aoronymphium* [7]. In experimental populations, *Spiroplasma* spreads in the presence of nematodes, but declines in their absence, suggesting a cost to the host [8]. This effect is presumed to underlie the recent spread of *Spiroplasma* among populations of *D. neotestacea* in North America [7]. The presence of a defensive symbiont can therefore have important direct consequences, but the effects are also predicted to travel further through the food web through indirect interactions [9-11]. In this review, I will consider how effects of defensive endosymbionts can propagate through an ecosystem beyond the immediate host and the susceptible natural enemy.

There is some debate about how strictly the term ‘trophic cascade’ should be defined, with some authors suggesting it should be limited to effects of predators propagating downward through a food web across more than one trophic level, while others favour a broader definition that encompasses any effect across more than one trophic link in the food web [12]. Here, I will assess the evidence and potential for defensive endosymbionts to have indirect (non-trophic) effects throughout the food web, including both strictly cascading effects, and other ‘knock-on’ indirect effects (see Figure 1).

Indirect effects of defensive symbionts

(i) effects on the trophic levels below the symbiont host (trophic cascade)

Where a herbivorous insect is protected by a symbiont from a natural enemy, or other potential threat, the pressure exerted on its food plants will increase. In agricultural systems, biological control of herbivorous insects via their natural enemies is one means of protecting crops and reducing reliance on pesticides [13]. Protective symbionts could provide pest insects with a means of overcoming this control [14]. In aphids, a number of bacterial symbionts have been shown in the laboratory to protect against parasitoids [15-17]; these symbionts could allow aphids to escape otherwise effective biological control. Herzog and colleagues [18] conducted cage experiments using a mixed-genotype asexually-reproducing population of peach-potato aphids (*Myzus persicae*), one genotype of which harboured a symbiont, *Regiella insecticola*. Aphids of this genotype were not particularly successful competitors, but nevertheless dominated in the presence of parasitoids, due to their high resistance. Similarly, Oliver and colleagues [19] initiated cage experiments using multiple asexually-reproducing clonal lines of pea aphids (*Acyrthosiphon pisum*) with and without facultative symbionts, and found that the proportion of aphids with a protective symbiont (*Hamiltonella defensa*) increased in the presence of parasitoids, but decreased in their absence. Nevertheless, direct evidence for a cascading negative effect of protective symbionts on insect food plants or prey species remains lacking at present, and a clear priority for future research.

It is important to note that symbionts could have direct as well as indirect consequences for host insect food plants. As well as protecting against parasitoids [17] and fungal pathogens

[20], the bacterial symbiont *R. insecticola* has been shown to improve food plant utilization [21,22]. The symbiont *H. defensa* can infect the whitefly *Bemesia tabaci* [23], although a protective function has not been demonstrated in this host. However, *H. defensa* in whiteflies is associated with increased virus transmission between food plants [24,25]. It will therefore be important in future field studies to distinguish whether any negative observed effects on plants are indeed the cascading consequence of releasing a herbivorous insect from a natural enemy, or the direct result of altering insect–plant interactions [26].

Protective symbionts can also interact directly with plants, and thence the wider community [26]. Some parasitoids can detect the specific volatiles emitted by plants under herbivore attack, in order to locate herbivorous prey. Defensive symbionts in aphids can alter the profile of volatile compounds emitted by their food plants, and thus reduce their attractiveness to parasitoids [27]. Likewise, the symbiotic polydnaviruses of some parasitoids have recently been shown to alter volatile emissions from the food plants of prey insects, with consequences for the surrounding insect community [28,29]. While the latter are perhaps not strictly defensive symbionts, being an integral part of the parasitoid attack responsible for subduing the prey immune system, their example illustrates the power of symbionts to alter the insect community via stimulating plant responses. It seems highly likely that further examples will emerge as we examine protective symbiotic associations in their community context.

(ii) effects at the same trophic level as the symbiont host

Releasing an insect from its natural enemies is expected to have negative consequences for any competitors. Sanders and colleagues [30] addressed the potential for defensive symbionts in aphids to suppress competitor aphid species as part of a laboratory-based cage study, in which three aphid species (sharing the same host plant species) were subjected to parasitism by three species-specialist parasitoids. This system is stable in the absence of symbionts [31]. One of the aphids (*A. pisum*) had a larger population size if it harboured a symbiont (*H. defensa* again) that protected against its species-specialist parasitoid. The relative density of the other two aphid species (*A. fabae* and *Megoura viciae*) consequently decreased. However, absolute population sizes of the competitor aphids were not affected.

The presence of a protective endosymbiont could also impact insects feeding on different resources. Where two insect species share an enemy, an increase in the population of one prey insect may have a detrimental effect on the population of the other prey insect, even where the two do not compete directly. This indirect effect arises because the natural enemy population increases with that of the first insect, thus increasing pressure on the second, an effect termed 'apparent competition' [32]. Conversely, one would predict that if the population of a shared enemy were to be depressed by the presence of a protective symbiont in one potential prey species, populations of all other prey species would reap the benefits ('apparent mutualism').

A recent laboratory study [33] used an experimental design capable of revealing these kinds of indirect interactions. Two aphid species (*A. fabae* and *M. persicae*), feeding on a common host plant, were subjected to parasitism by a single shared parasitoid (with equivalent parasitoid-free cages). Treatments comprised cages in which neither, one, or both aphid species housed a protective bacterial symbiont (*H. defensa*). Where neither aphid was protected, both aphid species became extinct in the presence of the parasitoid. Where both aphids were protected, both species persisted. Where only one aphid species was protected, both still became extinct, with the large number of wasps produced by the vulnerable aphid presumed to cause damage to the resistant aphid either through repeated oviposition injuries or disturbing aphids to the extent of preventing feeding [33]. This is, in effect, a form of apparent competition, although it is hard to know whether such a phenomenon is likely to be important in the field, where dispersal of the parasitoids would be likely to mitigate the disturbance effect. Nevertheless, this result shows the potential for protective symbionts to impact indirectly beyond their own host, and should certainly inspire future field work.

(iii) effects at the same trophic level as the natural enemy

Defensive symbionts are frequently highly specific in the enemies they target. Defence by aphid symbionts against parasitoids is limited to narrow taxonomic groups [34,35], while the aphid symbiont *Regiella insecticola* has been shown to provide protection against two different aphid-specific fungal pathogens but not against a third, generalist, fungal infection [36]. Even among those with wide-ranging effects there will be enemies unaffected: for example, *Spiroplasma* in *Drosophila* impacts several distantly-related parasitoid species, but at least two other parasitoids are resistant [37]. The symbiont-mediated suppression of one (or more) natural enemy species could thus present opportunities for any resistant enemies.

Evidence for such an effect has been found in both laboratory and field studies. In North America, pea aphids are attacked predominantly by a single parasitoid, *Aphidius ervi*, and to a much lesser extent by another aphidiine braconid, *Praon pequodorum* [38]. The latter species appears not to be impacted by *H. defensa* [39]. Although *P. pequodorum* is the superior competitor within an aphid ("multiparasitism"), it is less efficient at foraging than *A. ervi* [38], and so is an inferior competitor in cage experiments [40]. However, *P. pequodorum* can nevertheless persist and dominate in cages if prey aphids are infected with *H. defensa* [40]. The outcome of multiparasitism by the parasitoids *Aphelinus abdominalis* and *A. ervi* has likewise been shown to vary depending on whether or not the host aphids possess a strain of *H. defensa* providing asymmetric protection against the two species [41].

Protective symbionts can also alter community composition in the field. The symbiont *H. defensa* provides the black bean aphid, *Aphis fabae*, with protection from its most important parasitoid, *Lysiphlebus fabarum* [42]. In replicated field plots, aphids with *H. defensa* were found to suffer lower rates of parasitism than those without the symbiont [43]. In addition, the parasitoid species composition was different, with a greater diversity and more even species distribution of parasitoids in plots where the aphids carried *H. defensa*, because the dominant parasitoid was absent [43]. In a field study using pea aphids, overall parasitism rates were not found to be affected by symbiont presence, but species composition was strongly affected: the symbiont reduced the parasitism rate for the specific susceptible enemy, and so presumably provided opportunities for other species to exploit [44]. However, it should be noted that where the most common enemies are not susceptible to a particular defensive symbiont, there may be no noticeable impact of that symbiont on the surrounding insect community [45], presumably because symbiont presence does not significantly alter the opportunities available to other enemy species.

Not all indirect effects involving defensive symbionts are advantageous for non-susceptible natural enemies. In the population cage experiments of Sanders and colleagues mentioned above [30], presence of a symbiont increased the resistance of its aphid host to a parasitoid, leading to an increase in population density relative to two competitor aphid species. Subsequently, the two parasitoids specific to the competitor aphid species became extinct in the cages. The loss of the additional parasitoids is assumed to have resulted from an inability to locate suitable prey, coupled with many individuals wasting time and resources by ovipositing in the most common, but unsuitable, aphid. Whether such an effect is likely to pertain outside a constrained cage setting is uncertain; however, the study demonstrates that defensive symbionts can produce significant community perturbations via indirect effects.

(iv) effects on the trophic levels above the natural enemy

The removal of a natural enemy via a protective symbiont may produce a ‘bottom-up’ knock-on effect on the trophic level above. Once again, the only examples come from aphids. Aphid parasitoids (‘primary parasitoids’) are attacked in turn by two distinct types of secondary parasitoid: ‘mummy’ parasitoids which attack only after the parasitoid has pupated and the host aphid is dead; and ‘true’ hyperparasitoids which attack during the larval stage in the living aphid [32,46]. In the laboratory, the success rate of true hyperparasitoids has been shown to depend on whether the aphids are infected with defensive symbionts. Pea aphids with protective *H. defensa* produced a smaller number of viable primary parasitoids, and so fewer hosts were available for secondary parasitism [47]. The effects are similar in the field. Rothacher and colleagues [43] found that hyperparasitoid numbers were significantly lower in experimental plots where black bean aphids harboured *H. defensa*, although the proportion of parasitized aphids which produced hyperparasitoids was similar.

An extensive observational study examining parasitism rates of the grain aphid *Sitobion avenae* in the field suggests that mummy parasitoids are negatively affected by presence of putatively protective endosymbionts [48]. This study used molecular detection of symbiotic bacteria in field-collected aphids, and found significantly lower rates of secondary parasitism, in particular by mummy parasitoids, in aphids that carried a symbiont. The authors speculate that the effect arose from lower perceived primary parasitoid quality in the presence of symbionts [49].

Conclusions

Protective microbial endosymbionts are now recognized as an important element of insect defence against natural enemies [10,50]. However, the number of experimental or observational studies of cascading and other indirect effects remains rather small. In addition, the vast majority of studies mentioned in this review have been from a single insect family;

very few examples from other insect groups are available. Aphids have many advantages for conducting community ecology studies, but lack of research from other taxonomic groups is undoubtedly limiting, and prevents general conclusions from being established.

Protective symbionts have the potential to cause important indirect effects within the ecosystems of their hosts. As more insect groups are investigated we can hope to improve our picture of the influence of protective endosymbionts, not only on their own host and its direct interactions, but also on the broader ecological communities in which they are ‘hidden players’ [26].

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References

1. Duron O, Hurst GDD: **Arthropods and inherited bacteria: from counting the symbionts to understanding how symbionts count**. *BMC Biol.* 2013, **11**:45.

2. Douglas AE: **The microbial dimension in insect nutritional ecology**. *Funct. Ecol.* 2009, **23**:38-47.

3. Duron O, Bouchon D, Boutin S, Bellamy L, Zhou LQ, Engelstadter J, Hurst GD: **The diversity of reproductive parasites among arthropods: *Wolbachia* do not walk alone**. *BMC Biol.* 2008, **6**:12.

4. Hurst GDD, Hutchence KJ: **Host Defence: Getting By with a Little Help from Our Friends**. *Curr. Biol.* 2010, **20**:R806-R808.

5. Zug R, Hammerstein P: **Bad guys turned nice? A critical assessment of Wolbachia mutualisms in arthropod hosts**. *Biol Rev* 2015, **90**:89-111.

6. Brownlie JC, Johnson KN: **Symbiont-mediated protection in insect hosts**. *Trends Microbiol.* 2009, **17**:348-354.

7. Jaenike J, Unckless R, Cockburn SN, Boelio LM, Perlman SJ: **Adaptation via symbiosis: recent spread of a *Drosophila* defensive symbiont**. 2010, **329**:212-215.

8. Jaenike J, Brekke TD: **Defensive endosymbionts: a cryptic trophic level in community ecology**. *Ecol Lett* 2011, **14**:150-155.

9. Ferrari J, Vavre F: **Bacterial symbionts in insects or the story of communities affecting communities**. *Philos. Trans. R. Soc. B-Biol. Sci.* 2011, **366**:1389-1400.

10. Oliver KM, Smith AH, Russell JA: **Defensive symbiosis in the real world – advancing ecological studies of heritable, protective bacteria in aphids and beyond**. *Funct. Ecol.* 2014, **28**:341-355.

11. McLean AHC, Parker BJ, Hrček J, Henry LM, Godfray HCJ: **Insect symbionts in food webs**. *Phil. Trans. R. Soc. Lond. B* 2016, **371**:20150325.

12. Ripple WJ, Estes JA, Schmitz OJ, Constant V, Kaylor MJ, Lenz A, Motley JL, Self KE, Taylor DS, Wolf C: **What is a Trophic Cascade?** *Trends Ecol Evol* 2016, **31**:842-849.

13. van Lenteren JC: **A greenhouse without pesticides: fact or fantasy?** *Crop Protection* 2000, **19**:375-384.

14. Vorburger C: **Symbiont-conferred resistance to parasitoids in aphids – Challenges for biological control**. *Biol Control* 2018, **116**:17-26.

15. Oliver KM, Russell JA, Moran NA, Hunter MS: **Facultative bacterial symbionts in aphids confer resistance to parasitic wasps**. *Proc. Natl Acad. Sci. U.S.A.* 2003, **100**:1803-1807.

16. Oliver KM, Moran NA, Hunter MS: **Variation in resistance to parasitism in aphids is due to symbionts not host genotype**. *Proc. Natl Acad. Sci. U.S.A.* 2005, **102**:12795-12800.

17. Vorburger C, Gehrer L, Rodriguez P: **A strain of the bacterial symbiont *Regiella insecticola* protects aphids against parasitoids**. *Biol. Lett.* 2010, **6**:109-111.

18. Herzog J, Muller CB, Vorburger C: **Strong parasitoid-mediated selection in experimental populations of aphids**. *Biol. Lett.* 2007, **3**:667-669.

19. Oliver KM, Campos J, Moran NA, Hunter MS: **Population dynamics of defensive symbionts in aphids**. *Proc. R. Soc. B* 2008, **275**:293-299.

20. Scarborough CL, Ferrari J, Godfray HCJ: **Aphid protected from pathogen by endosymbiont**. *Science* 2005, **310**:1781.

21. Tsuchida T, Koga R, Matsumoto S, Fukatsu T: **Interspecific symbiont transfection confers a novel ecological trait to the recipient insect**. *Biol. Lett.* 2011, **7**:245-248.

22. Tsuchida T, Koga R, Meng XY, Matsumoto T, Fukatsu T: **Characterization of a facultative endosymbiotic bacterium of the pea aphid *Acyrthosiphon pisum***. *Microb. Ecol.* 2005, **49**:126-133.

23. Zchori-Fein E, Brown JK: **Diversity of prokaryotes associated with *Bemisia tabaci* (Gennadius) (Hemiptera : Aleyrodidae)**. *Ann. Entomol. Soc. Am.* 2002, **95**:711-718.

24. Gottlieb Y, Zchori-Fein E, Mozes-Daube N, Kontsedalov S, Skaljac M, Brumin M, Sobol I, Czosnek H, Vavre F, Fleury F, et al.: **The Transmission Efficiency of Tomato Yellow Leaf Curl Virus by the Whitefly *Bemisia tabaci* Is Correlated with the Presence of a Specific Symbiotic Bacterium Species**. *J. Virol.* 2010, **84**:9310-9317.

25. Su Q, Pan HP, Liu BM, Chu D, Xie W, Wu QJ, Wang SL, Xu BY, Zhang YJ: **Insect symbiont facilitates vector acquisition, retention, and transmission of plant virus**. *Sci. Rep.* 2013, **3**:1367.

26. Frago E, Dicke M, Godfray HCJ: **Insect symbionts as hidden players in insect–plant interactions**. *Trends Ecol. Evol.* 2012, **27**:705-711.

27. Frago E, Mala M, Weldegergis BT, Yang C, McLean A, Godfray HCJ, Gols R, Dicke M: **Symbionts protect aphids from parasitic wasps by attenuating herbivore-induced plant volatiles**. *Nature Comm* 2017, **8**:1860.

28. Zhu F, Cusumano A, Bloem J, Weldegergis BT, Villela A, Fatouros NE, van Loon JJA, Dicke M, Harvey JA, Vogel H, et al.: **Symbiotic polydnavirus and venom reveal parasitoid to its hyperparasitoids**. *Proc Natl Acad Sci USA* 2018, **115**:5205-5210.

29. Cusumano A, Zhu F, Volkoff A-N, Verbaarschot P, Bloem J, Vogel H, Dicke M, Poelman EH: **Parasitic wasp-associated symbiont affects plant-mediated species interactions between herbivores**. *Ecol Lett* 2018, **21**:957-967.

30. Sanders D, Kehoe R, van Veen FJF: **Experimental evidence for the population-dynamic mechanisms underlying extinction cascades of carnivores**. *Curr. Biol.* 2015, **25**:3106-3109.

31. Sanders D, Sutter L, van Veen FJF: **The loss of indirect interactions leads to cascading extinctions of carnivores**. *Ecol. Lett.* 2013, **16**:664-669.

32. van Veen FJF, Morris RJ, Godfray HCJ: **Apparent competition, quantitative food webs, and the structure of phytophagous insect communities**. 2006, **51**:187-208.

33. Hertäg C, Vorburger C: **Defensive symbionts mediate species coexistence in phytophagous insects**. *Funct Ecol* 2018, **32**:1057-1064.

34. Asplen MK, Bano N, Brady CM, Desneux N, Hopper KR, Malouines C, Oliver KM, White JA, Heimpel GE: **Specialisation of bacterial endosymbionts that protect aphids from parasitoids**. *Ecol. Entomol.* 2014, **39**:736-739.

35. McLean AHC, Godfray HCJ: **Evidence for specificity in symbiont-conferred protection against parasitoids**. *Proc. R. Soc. Lond. B* 2015, **282**:20150977.

36. Parker BJ, Spragg CJ, Altincicek B, Gerardo NM: **Symbiont-mediated protection against fungal pathogens in pea aphids: a role for pathogen specificity?** *Appl. Environ. Microbiol.* 2013, **79**:2455-2458.

37. Mateos M, Winter L, Winter C, Higareda-Alvear VM, Martinez-Romero E, Xie J: **Independent origins of resistance or susceptibility of parasitic wasps to a defensive symbiont**. *Ecol Evol* 2016, **6**:2679-2687.

38. Schellhorn NA, Kuhman TR, Olson AC, Ives AR: **Competition between native and introduced parasitoids of aphids: nontarget effects and biological control**. *Ecology* 2002, **83**:2745-2757.

39. Martinez AJ, Kim KL, Harmon JP, Oliver KM: **Specificity of Multi-Modal Aphid Defenses against Two Rival Parasitoids**. *PLoS One* 2016, **11**:e0154670.

40. Kraft LJ, Kopco J, Harmon JP, Oliver KM: **Aphid symbionts and endogenous resistance traits mediate competition between rival parasitoids**. *PLoS One* 2017, **12**:e0180729.

41. McLean AHC, Godfray HCJ: **The outcome of competition between two parasitoid species is influenced by a facultative symbiont of their aphid host**. 2017, **31**:927-933.

42. Vorburger C, Sandrock C, Gouskov A, Castaneda LE, Ferrari J: **Genotypic variation and the role of defensive endosymbionts in an all-parthenogenetic host-parasitoid interaction**. *Evolution* 2009, **63**:1439-1450.

43. Rothacher L, Ferrer-Suay M, Vorburger C: **Bacterial endosymbionts protect aphids in the field and alter parasitoid community composition**. *Ecology* 2016, **97**:1712-1723.

44. Hrček J, McLean AHC, Godfray HCJ: **Symbionts modify interactions between insects and natural enemies in the field**. *J. Anim. Ecol.* 2016, **85**:1605-1612.

45. Lenhart PA, White JA: **A defensive endosymbiont fails to protect aphids against the parasitoid community present in the field**. 2017, **42**:680-684.

46. Sullivan DJ, Völkl W: **Hyperparasitism: multitrophic ecology and behavior**. *Annu. Rev. Entomol.* 1999, **44**:291-315.

47. McLean AHC, Hrček J, Parker BJ, Godfray HCJ: **Cascading effects of herbivore protective symbionts on hyperparasitoids**. 2017, **42**:601-609.

48. Ye Z, Vollhardt IMG, Parth N, Rubbmark O, Traugott M: **Facultative bacterial endosymbionts shape parasitoid food webs in natural host populations: A correlative analysis**. *J Anim Ecol* 2018, **0**.

49. Schmid M, Sieber R, Zimmermann YS, Vorburger C: **Development, specificity and sublethal effects of symbiont-conferred resistance to parasitoids in aphids**. *Funct. Ecol.* 2012, **26**:207-215.

50. Kaltenpoth M, Engl T: **Defensive microbial symbionts in Hymenoptera**. *Funct Ecol* 2014, **28**:315-327.

Highlighted references

33. Hertäg C, Vorburger C: **Defensive symbionts mediate species coexistence in phytophagous insects**. *Funct Ecol* 2018, **32**:1057-1064.

Laboratory experiment using artificial communities of two aphid species and a single shared parasitoid. Outcomes for all species depend on the symbiont infection status of both aphids.

40. Kraft LJ, Kopco J, Harmon JP, Oliver KM: **Aphid symbionts and endogenous resistance traits mediate competition between rival parasitoids**. *PLoS One* 2017, **12**:e0180729.

Experimental laboratory study demonstrating that asymmetric symbiont-mediated protection can mediate competitive relationships between parasitoids.

43. Rothacher L, Ferrer-Suay M, Vorburger C: **Bacterial endosymbionts protect aphids in the field and alter parasitoid community composition**. *Ecology* 2016, **97**:1712-1723.

Field experiment showing significant effect of protective symbionts on parasitism rates of aphids, with consequences for parasitoid community composition, and for hyperparasitoid numbers.

44. Hrček J, McLean AHC, Godfray HCJ: **Symbionts modify interactions between insects and natural enemies in the field**. *J. Anim. Ecol.* 2016, **85**:1605-1612.

Field experiment showing that aphid symbionts can provide protection against specific parasitoids in the field, and that other parasitoid species, rather than the aphids, benefit from this.

48. Ye Z, Vollhardt IMG, Parth N, Rubbmark O, Traugott M: **Facultative bacterial endosymbionts shape parasitoid food webs in natural host populations: A correlative analysis**. *J Anim Ecol* 2018, **0**.

Field survey finding that facultative symbiont presence in aphids correlates with community characteristics, implying potential for effects on parasitoids and hyperparasitoids.

Box 1: Glossary

Endosymbiont: a symbiont living internally within the host, whether in the gut, haemolymph or intracellularly

Facultative symbiont: a symbiont which is not required for growth or reproduction, and is not universally prevalent within the host species

Food web: the complete network of trophic interactions within a community, comprising numerous different food chains

Host: an insect which houses a symbiont (prey insects of parasitoids are usually also referred to as hosts, but that terminology has been avoided here to prevent confusion)

Hyperparasitoid/secondary parasitoid: a parasitoid which uses another parasitoid to support its development

Parasitoid: an organism whose life-cycle is intermediate between predation and parasitism: development requires a single individual of another organism, which is killed in the course of successful development.

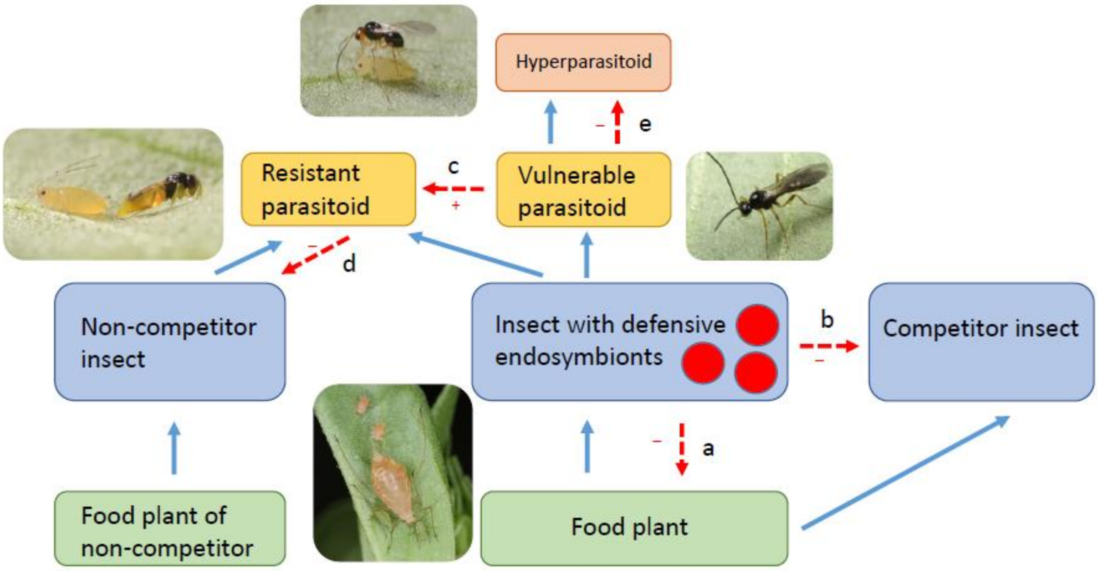

Figure 1. A representative food web incorporating protective endosymbionts. Trophic interactions are shown with blue arrows; illustrative potential effects (positive + and negative –) due to protective symbionts with dashed red arrows: **(a)** negative effects on food plants due to herbivorous insect release from parasitoid; **(b)** negative effects on competitors due to insect release from vulnerable parasitoid; **(c)** positive effects on resistant parasitoid due to reduced competition from vulnerable parasitoid; **(d)** negative effects on non-competitor insect due to increased numbers of shared, resistant parasitoid; **(e)** negative effects on hyperparasitoids due to reduced population of vulnerable parasitoid prey. Photographs clockwise from left: *Aphelinus abdominalis* with *Acyrthosiphon pisum* (Jan Hrček); *Alloxysta victrix* with *A. pisum* (Jan Hrček); *Aphidius ervi* (Ian McLean); *A. pisum* feeding on *Vicia faba* (Kevin Foster).