

# *Multiple global change impacts on parasitism and biocontrol services in future agricultural landscapes*

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**Suggested title: Multiple global change impacts on parasitism and biocontrol services in future agricultural landscapes**

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1 **ABSTRACT:**

2 Parasitoids are a significant mortality factor in the population dynamics of many arthropods  
3 involved in key ecological processes such as herbivore-plant and predator-prey interactions.  
4 Parasitoids are therefore widely used in biocontrol programs. Global change phenomena  
5 influence these natural and anthropocentric roles of parasitoids and here we review the effects  
6 of the main drivers and their interplay. Land use intensification modifies landscape structure  
7 and elevates agroecosystem loads of fertilizers and pesticides creating risks for parasitism  
8 and loss of biocontrol services. Climate change can affect parasitoids directly, affecting  
9 physiology and survival, or indirectly via phenological and other effects (plant chemistry,  
10 herbivore-induced plant volatiles HIPVs) on their hosts, endosymbionts and plants. Biological  
11 invasions have the potential to modify native host-parasitoid systems and elevate risk of novel  
12 pest dynamics, requiring restoration of biocontrol. The interplay between these global change  
13 drivers may thus exacerbate the overall risk to parasitism in future agricultural landscapes. To  
14 make more accurate predictions, future studies could focus on the impact of interacting global  
15 change drivers on parasitoids and the biocontrol services they provide. Moreover, host and  
16 parasitoid specificity appear to be a key driver in assessing the effects of global change on  
17 parasitoids.

18

19 **KEY WORDS:** Parasitoid, land use intensification, climate change, biological invasion,  
20 ecological interactions, sustainable agriculture, pest management, host specificity.

21

22

## 23 INTRODUCTION:

24 The magnitude, spatial extent and rapidity of current environmental changes is  
25 unprecedented. The main global changes that threaten biodiversity and have the potential to  
26 disrupt herbivore-plant, predator-prey and parasitoid-host interactions are land use  
27 intensification, climate change and biological invasions (Early et al. 2016; Foley et al. 2005;  
28 IPBES 2019; Laliberté et al. 2010; Pecl et al. 2017; Pimm and Raven, 2000; Sala et al. 2000;  
29 Vanbergen et al. 2020; Walther et al. 2002). Aside from disruption to the natural world, global  
30 change phenomena threaten the biodiversity, ecosystem functions and services upon which  
31 humanity depends (IPBES 2019).

32 Changing land-use patterns can result in conversion (i.e., altering natural habitats for  
33 human use) or intensification (e.g., greater intensity and/or frequency of disturbance,  
34 increased use of external inputs; Foley et al. 2005) (Figure 1). Despite the negative effects of  
35 land-use intensification, the practice has expanded globally with an increase of 64% in arable  
36 production, 57% in livestock numbers and 112% in built-up areas until 2040 (van Asselen and  
37 Verburg 2013). Climate change leads to an increase in global average temperature and  
38 increases in the frequency and duration of drought events or the frequency of catastrophic  
39 and unpredictable events (IPCC 2021). Global warming induces shifts in phenology,  
40 physiological changes and range shifts in species (Walther et al. 2002) (Figure 1). Ectothermic  
41 species such as insects, “the little things that run the world” (Wilson, 1987), must therefore  
42 respond to these large temperature variations and extreme climatic events by adapting and/or  
43 moving, or by going extinct. Finally, human-induced biological invasions can lead to the  
44 collapse of classical biogeographic regions (Capinha et al. 2015) and considerable social,  
45 economic and ecological damage (Blackburn et al. 2011), altering ecosystems and  
46 endangering food security (Schweiger et al. 2010; Ziska et al. 2011) (Figure 1).

47

### 48 [Insert Figure 1 here]

49 **Figure 1.** Impacts on the (a) biocontrol services provided by parasitoids of (b) climate change,  
50 (c) land use intensification and (d) biological invasions. These global change drivers impact  
51 on, directly and indirectly, the primary producer (non-crop or crop plant) and secondary (insect  
52 herbivores or pests) and tertiary (parasitoids) trophic levels. HIPVs: herbivore-induced plant  
53 volatiles. Images sourced from thenounproject.com (CC-BY: Ayumi Aya; Baboon designs;  
54 Carpe Diem; Denimao; Megan Strickland; Phạm Thanh Lộc; Varvarvarvarra; Yu luck) and  
55 following websites: <https://www.google.fr/maps/>.

56

57 Insect parasitoids have a life cycle that is divided into parasitic larval stages and a free-  
58 living adult stage. The female parasitoid in the adult stage deposits an egg inside or outside  
59 its host (typically another insect or arthropod) and the resulting larva develops by feeding on  
60 the body of the host, resulting in its death. They are considered important natural enemies of  
61 insect pests, as they play a critical role in terrestrial communities by regulating lower trophic

62 levels, such as insect herbivores (Heimpel and Miles, 2017; Jervis 2005). The effectiveness  
63 of parasitoids as biocontrol agents has been demonstrated against a large number of different  
64 pest invertebrates (Heimpel and Mills, 2017), and are responsible for a large number of  
65 biocontrol successes from an economic and environmental point of view (LaSalle 1993). In  
66 addition, parasitoids often demonstrate high host specificity since they attacks hosts mainly  
67 from the same family, thus reducing the ecological risks of introducing a biocontrol agent into  
68 a new environment (classical biocontrol) (Heimpel and Mills, 2017). Therefore, the hosts alone  
69 represent both the food source and physiological environment of the developing immature  
70 parasitoids. The effects of global changes on host fitness and populations may then, in turn,  
71 be transmitted up the food chain to influence parasitoids. Parasitoids are haplodiploid, having  
72 lower standing genetic variation and mutation rates compared to their hosts (which are  
73 typically diploid) in responding to global changes (Biale et al. 2020; Le Lann et al. 2021; Smith  
74 and Shaw, 1980).

75         Given the magnitude of global change phenomena, and the importance of parasitoids  
76 in the natural world and in biological pest control, here we review the literature to assess the  
77 likely impacts of land use intensification, climate change and biological invasions to predict  
78 likely community- and individual-level effects on host-parasitoid interactions and biocontrol.

79

## 80 **1 – AGRICULTURAL INTENSIFICATION**

81 Intensification of land use, characterised by increased use of external inputs, frequent  
82 disturbance and ecosystem homogenisation, is a major driver of worldwide decline in  
83 biodiversity and ecosystem degradation (Foley et al. 2005). Land use intensification effects on  
84 the environment (e.g., vegetation, habitat resources) drive changes in pest and parasitoid  
85 populations from the individual- to community-level. In this section, we consider how  
86 conventional agricultural intensification through external input use (pesticide and nitrogen) and  
87 crop/landscape management impact pests and their parasitoids (primary and secondary)  
88 (Figure 2).

89         Conventional agricultural intensification can occur both at local and landscape scales.  
90 At the local scale, the intensification of management results from the adoption of short crop  
91 rotations, increased monocultures, increased inputs of fertilizers and pesticides, deep  
92 ploughing, increased field sizes and high levels of mechanisation (Tscharntke et al. 2005). As  
93 a consequence, where these practices are extended to a large number of fields, the entire  
94 landscape will be modified with widespread conversion of perennial and natural habitat to  
95 crops, habitat fragmentation and loss of landscape complexity in space and time (Tscharntke  
96 et al. 2005). This correlation between local practice and landscape simplification means it is  
97 important to consider the effect of agricultural intensification on pests, parasitoids and their  
98 interactions.

99 **[Insert Figure 2 here]**

100 **Figure 2.** Impacts of conventional agricultural intensification on plant-host-insect-parasitoid-  
101 hyperparasitoid individuals and food web stability and diversity. Direct and indirect as well as  
102 positive or negative effects of landscape simplification and intensive use of external inputs  
103 (pesticides and nitrogen fertilizer) are illustrated. Images sourced from thenounproject.com  
104 (CC-BY: Carpe Diem; Megan Strickland; Phạm Thanh Lộc; Yu luck) and following websites:  
105 [monsafety.wordpress.com](https://monsafety.wordpress.com); [morningagclips.com](https://morningagclips.com); <https://www.google.fr/maps/>.  
106

## 107 **1.1. Direct and indirect effects of external inputs on host-parasitoid interactions**

### 108 **1.1.1. Impact of pesticides**

109 Agriculture relies heavily on chemical pesticides to control crop pests in a cost-effective way  
110 (Cooper and Dobson, 2007). However, these substances have non-negligible adverse effects  
111 such as lethal and sublethal impacts on non-target organisms, development of pest resistance  
112 and secondary pest outbreaks, as well as pollution of water, soil and bioaccumulation of  
113 residues in food chains (Cloyd 2012; Desneux et al. 2007; Pinheiro et al. 2020; Weinzierl  
114 2008). The sensitivity of parasitoids to plant protection products depends on their biology  
115 (guild, developmental stage, sex, age), the pesticide regime (type and dose of pesticide used,  
116 the method and timing of application) and the mode of action of the active substances (Cloyd  
117 2012; Desneux et al. 2006a; 2006b). Among chemical pesticides, insecticides such as  
118 organophosphates and pyrethroids are generally more toxic (Ohta and Takeda, 2015; Pinheiro  
119 et al. 2020) than herbicides and biopesticides, which have less impact on parasitoid survival  
120 and fecundity (Khan and Ruberson, 2017; Pinheiro et al. 2020).

121 Pesticides can affect parasitoids through direct contact with spray droplets or treated  
122 surfaces (Krischik et al. 2007; Longley and Jepson, 1996; Stapel et al. 2000), or mediated by  
123 plant uptake of pesticides in the soil or pore water that can lead to cumulative bottom-up effects  
124 on higher trophic levels (Kampfraath et al. 2017; Mullin and Croft 1985). Persistent pesticide  
125 contamination of host and parasitoid food sources (pollen, nectar, and host exudates such as  
126 honeydew) required for survival, egg maturation in synovigenic females, and reproduction  
127 (Benelli et al. 2017; Cowles and Eitzer, 2017; Jervis and Kidd, 1996; Pinheiro et al. 2020),  
128 significantly increases the risk of exposure and harm to parasitoids (Pinheiro et al. 2020).

129 Direct and indirect (via their hosts) contact with pesticides can alter parasitoid host  
130 locating and food foraging behaviors in a number of ways (Desneux et al. 2007; Kampfraath  
131 et al. 2017; Wang et al. 2016). Pesticides induce modifications of the chemical constituents of  
132 plants, thereby affecting the nutritional value or attractiveness of pollen or nectar foods to the  
133 free-living adult parasitoids (Hervé et al. 2014; Serra et al. 2015). Pesticides can interfere with  
134 parasitoid behaviours reliant on chemical signals. Pesticide exposure can reduce the host  
135 location ability of parasitoids by disrupting the detection of kairomones involved in olfactory  
136 orientation during foraging (Desneux et al. 2004a; 2004b) or communication using sex  
137 pheromones (Desneux et al. 2004b; Stapel et al. 2000; Tappert et al. 2017). The use of

138 pyrethroids, in particular, can impair the mobility and orientation ability of parasitoids when  
139 searching for food sources or host plants (Schoonhoven et al. 2005). Greater aggregation of  
140 parasitoids (*Aphidius* spp. Braconidae, Hymenoptera) on crop plants and higher parasitism  
141 rates were observed in the absence of pesticide use, implying repellency from treated areas  
142 (Longley and Jepson, 1996) and a lowering of parasitoid exposure (to some extent) to  
143 pesticides (Desneux et al. 2005). In some cases, however, parasitoid adults exposed to  
144 residual pesticide doses retain their ability to orient towards host odors (Desneux et al. 2006a;  
145 2006b), or these abilities may be recovered after sublethal exposure (Desneux et al. 2004c;  
146 Longley and Jepson, 1996).

147 Exposure to pesticides can also modify the survival or physiological function of  
148 parasitoids. Direct and indirect contact with pesticides can reduce survival at various  
149 developmental stages (Bueno et al. 2008; Fontes et al. 2018; Khan and Ruberson, 2017).  
150 Adult parasitoids exposed to pesticides suffer increased short-term mortality (Asadi et al.  
151 2019; Bayram et al. 2010; Cheng et al. 2021; Ohta and Takeda, 2015). For example, the  
152 pesticide Metomil reduces the survival of *Trichogramma pretiosum* (Hymenoptera:  
153 Trichogrammatidae) eggs, larvae, and pupae by 96%, 91%, and 67%, respectively, with only  
154 5% of parasitoids exposed to pesticides being viable (Bueno et al. 2008). Negative sublethal  
155 effects have been seen on parasitoid larval and pupal development as well as on fertility, sex  
156 ratio or oviposition ability (Cheng et al. 2021; D'Ávila et al. 2018; Kampfraath et al. 2017;  
157 Vianna et al. 2009). *Aphidius ervi*, following exposure to pesticides, demonstrated  
158 uncoordinated and irreversible female ovipositor extrusion leading to failure of parasitism  
159 (Desneux et al. 2004c). Pesticides can modify host immune defences, for example, exposure  
160 of the host *Drosophila melanogaster* to the pesticide Dieldrin leads to a 25% reduction in  
161 immune defenses against the parasitoid *Leptopilina boulardi* (Delpuech et al. 1996), which  
162 could affect, in turn, the development of immature parasitoids.

163 The lethal and sublethal effects of pesticides on individuals and populations may lead  
164 to modifications of the structure of the arthropod community. Pesticide use by disrupting top-  
165 down control in an agroecosystem may promote secondary pest outbreaks (Guedes et al.  
166 2017, 2016; Lu et al. 2012; Zhao et al. 2017, 2016). This might be due to altered community  
167 dynamics as seen in the case of imidacloprid application that modulated competition among  
168 aphid species to induce a shift in both aphid and natural enemy species dominance  
169 (Mohammed et al. 2019). In Banana plantations, parasitoid abundance and species richness  
170 were inversely related to rates of insecticide application (Matlock and de la Cruz, 2002).  
171 Deltamethrin treatment resulted in initial reductions of aphid, primary parasitoid and  
172 hyperparasitoid populations by 78%, 90% and 47% respectively (Longley et al. 1997).  
173 Nonetheless, populations of primary and secondary parasitoids were able to re-invade treated  
174 ecosystems, suggesting the existence of reservoir areas hosting natural enemy populations,



175 and parasitoids may limit aphid population growth soon after a deltamethrin application  
176 (Desneux et al. 2005).

177

### 178 **1.1.2. Impact of nutrient inputs:**

179 Because of its importance to plant productivity, fertilizers supplying Nitrogen (N) are frequently  
180 used in agricultural production (McNeill and Southwood, 1978; Stiling and Moon, 2005).  
181 Fertilization can modify plant primary and secondary metabolites causing a variety of bottom-  
182 up effects on tritrophic, parasitoid interactions via a number of mechanisms (Chen et al. 2010;  
183 Pekas and Wackers, 2020; Sarfraz et al. 2009). Fertilisation tends to generate bottom-up  
184 increases in the strength or frequency of herbivore–plant, predator–prey and parasitoid–host  
185 interactions, for example (e.g., De sassi et al. 2012; Moon and Stiling, 2002, 2000; Tylianakis  
186 et al. 2008) (Figure 2).

187 Many insect herbivores are able to distinguish between host plants of high and low  
188 nutritional quality and tend to prefer fertilized to unfertilized host plants for oviposition (Chen  
189 et al. 2008a, 2004; Prudic et al. 2005). Plant emissions of herbivore-induced plant volatiles  
190 (HIPV) are a well-known mechanism by which plants signal to and recruit natural enemies to  
191 attack herbivores. Parasitoids tend therefore to fly more frequently towards host-damaged  
192 plants e.g., *Cotesia marginiventris* (Cresson) (Röse et al. 1998), *Microplitis croceipes*  
193 (Cresson) (Röse et al. 1998) and *Cardiochiles nigriceps* Viereck (De Moraes et al. 1998).  
194 Nitrogen levels can alter positively, negatively or can have no effects on the production and  
195 release of these volatiles depending upon the plant (Chen et al. 2010). Well-nourished plants  
196 emitted several HIPVs enabling parasitoid recruitment in contrast with nitrogen-deficient plants  
197 (Becker et al. 2015; Chen et al. 2010; Han et al. 2014; Ibrahim et al. 2008; Winter and Rostás,  
198 2010). By contrast, the amount of volatile released decreased when N concentration in the  
199 nutrient solution increased in corn (*Zea mays* var Delprim) (Schmelz et al. 2003) and did not  
200 vary in tobacco (*Nicotiana attenuata*) (Lou and Baldwin, 2004).

201 Phytophagous insects that feed on well-nourished host plants exhibit higher growth  
202 rates, higher efficiency of food use, higher fecundity, and higher abundance (Awmack and  
203 Leather, 2002; Chen et al. 2010, 2004; Karowe and Martin, 1989; Mattson 1980; Moon and  
204 Stiling, 2000; Weibull 1987; Zhao et al. 2015). An increase in nitrogen input may therefore  
205 improve the nutritional quantity (enhanced size of host) or quality of the host supporting the  
206 immature developing parasitoid and/or synovigenic species that require host feeding (i.e.,  
207 feeding on host body fluids) for egg development, such effects of N may thus increase levels  
208 of parasitism (e.g., Chen et al. 2010; Gharekhani et al. 2020; Moon and Stiling, 2000; Pekas  
209 and Wackers, 2020; Sarfraz et al. 2009). High N concentration in the soil may also disrupt the  
210 herbivore immune system promoting parasitoid development. For instance, high nitrate  
211 concentration in the soil impairs the immune system of *Myzus persicae* allowing the parasitoid

212 *Diaeretiella rapae* (Hymenoptera: Braconidae) to emerge at rates 1.5 times higher than when  
213 the nitrate concentration is low (Chesnais et al. 2016). A high nitrogen concentration may,  
214 however, also reduce parasitism rates. The parasitism rate of *Diadegma insulare* when  
215 encountering its host *Plutella xylostella* decreased at high N concentration, despite increased  
216 parasitoid survival rates, suggesting no role for the host immune system in lower parasitisation  
217 (Sarfranz et al. 2009).

218 Some plant allelochemicals that function as defensive compounds are produced in  
219 greater quantities in well-fertilized conditions (Cipollini and Bergelson, 2001; Lou and Baldwin,  
220 2004) and are sequestered in the hemolymph of herbivorous insects. Development times and  
221 survival rates of adult parasitoids feeding on these insects and/or immature larvae developing  
222 in these hosts may therefore be altered (Campbell and Duffey, 1979; Duffey et al. 1986; van  
223 Emden 1995; Kester and Barbosa, 1991; for a review, see Turlings and Benrey, 1998; but see  
224 Schuler et al. 1999). For example, Lou and Baldwin (2004) noted that N addition increased  
225 nicotine production in tobacco. *Manduca sexta*, which is a specialist herbivore of tobacco, can  
226 sequester nicotine in its hemolymph with no ill-effects (Self et al. 1964). The parasitoid *Cotesia*  
227 *congregata* is, by contrast, more sensitive to nicotine and larval survival is reduced (Barbosa  
228 et al. 1991; Parr and Thurston 1972; Thorpe and Barbosa 1986). Nevertheless, the typical  
229 effect of most constitutive secondary metabolites involved in plant defense are negatively or  
230 even unrelated to N levels (Cipollini and Bergelson, 2001; Darrow and Bowers, 1999; Dudt  
231 and Shure, 1994; Hemming and Lindroth, 1999; Hol et al. 2003; Prudic et al. 2005; Stout et  
232 al. 1998; Wall et al. 2005), and parasitoids that feed on hosts developing on well-nourished  
233 plants generally perform better.

234

## 235 **1.2. Landscape simplification**

236 The pursuit of food productivity and efficiency, and the widespread adoption of conventional  
237 agricultural intensification has come with the costs of ecological homogenization, loss of  
238 biodiversity and ecosystem services, invasive pest outbreaks, and rising human health issues  
239 (Baude et al. 2019; IPBES 2019; Larsen and Noack, 2021). Landscape simplification arising  
240 from habitat conversion and adoption of industrial crop monocultures to increase the  
241 productivity of land is a globally widespread phenomenon (Baude et al. 2019; Larsen and  
242 Noack, 2021). As an example, cereals occupy most of the arable lands in the EU, with 121  
243 million hectares planted in 2019, in comparison to the 60 million hectares for all other crops.

244 Landscape complexity is a combination of composition and configuration of different  
245 habitats (Fahrig et al. 2011), and both these aspects have been shown to be important for  
246 natural enemies and biocontrol (Haan et al. 2019; Karp et al. 2018). A highly cropped  
247 landscape is often defined as a poorly diversified landscape (i.e., less complex landscape)  
248 compared to a landscape with a high proportion of natural and semi-natural habitats (Bianchi

249 et al. 2006; Karp et al. 2018; Veres et al. 2013). Landscapes with high configuration complexity  
250 can be defined as land having high connectivity between the different habitats, reduced patch  
251 size, increased richness of land cover types and increased irregularity of patch shapes  
252 (Dominik et al. 2018; Nelson and Burchfield, 2021).

253         Such differences in landscape compositional or configurational complexity are another  
254 factor affecting parasitoid biocontrol efficiency (Jonsson et al. 2012) (Figure 2). This is  
255 because highly simplified landscapes lack the diversity of ecological resources to fulfil the  
256 trophic needs (host and non-host) and life-histories of parasitoids. Parasitoids need diversified  
257 food sources as they can be pollinators during their adult stage and carnivores during their  
258 larval stage (Gurr et al. 2017). Consequently, more diverse and structurally complex  
259 landscapes are hypothesised to harbour sufficient resources for different parasitoid species  
260 and life-histories in space and time, with potential gains in biocontrol efficacy in crop fields.  
261 For example, a landscape dominated by wheat in monoculture risks a sudden post-harvest  
262 drop in parasitoid populations and potential biocontrol due to a lack of spatial and temporal  
263 connections to alternative food sources (e.g., hosts or floral resources in semi-natural habitats  
264 or other crops). The implication is therefore that in highly simplified, intensively managed  
265 landscapes or habitats the efficacy of biocontrol will be reduced (Schellhorn et al. 2015).  
266 Conversely, greater habitat compositional and configurational complexity may promote  
267 parasitoid populations and high biocontrol efficacy (Dominik et al. 2018). The need for  
268 diversified food sources to support parasitoid life cycles (Gurr et al. 2017) can be met by  
269 agricultural land management. Plant diversity underpinning both host and parasitoid resources  
270 can be manipulated at the field (crop types), farm (crop diversity, field margin diversity, habitat  
271 composition and connectivity, field size and shape) and landscape (landscape complexity,  
272 semi-natural habitat cover and habitat composition and configuration) scale (Gillespie et al.  
273 2016).

274         In this section, we focus on the importance of agricultural landscape complexity on  
275 parasitoids and, where evidence allows, their food web interactions. We detail the impact of  
276 simplification of habitat composition and configuration on parasitoids.

277

### 278 **1.2.1. Effect of habitat composition simplification on parasitoids**

279 Parasitoid trophic dependence on their hosts means there can be a strong density-dependent  
280 link to host population dynamics (Gagic et al. 2012). Such a simple response may, however,  
281 be modulated by the composition of the landscape and the complexity of the host-parasitoid  
282 food-web. Agricultural landscape simplification can reduce parasitoid abundances  
283 (Letourneau et al. 2012) and parasitism efficacy (Elliott et al. 2018; Gagic et al. 2012; Grab et  
284 al. 2018; Plečaš et al. 2014). This lowering of population size or biocontrol is associated with  
285 the reduced cover of semi-natural habitats (e.g., forest, hedgerows) in intensive agricultural

286 landscapes that provide overwintering sites, pollen and nectar sources, or alternative prey and  
287 hosts that are key to maintaining parasitoid populations and biocontrol efficacy (Gillespie et  
288 al. 2016). The abundance of the Tachinidae, a common guild of parasitoid flies, increases with  
289 the presence of semi-natural habitats and perennial vegetation but is negatively correlated to  
290 the proportion of annual crop cover (Letourneau et al. 2012). Maintaining semi-natural habitats  
291 and perennial plants in landscapes is likely to be crucial for maintaining the populations of  
292 parasitoids that are active in adjacent short-cycle crop fields (Letourneau et al. 2012).  
293 Compositional complexity of agricultural landscapes is also important as parasitoids use  
294 different habitat types during the year and frequently disperse among habitats. Proximity of  
295 different habitats is thus crucial for the spillover of parasitoids and biocontrol services from  
296 semi-natural to cropped areas (Elliott et al. 2018). Along with greater parasitism efficacy in  
297 complex landscapes, the proportion of pests is often lower due to dilution or reduced  
298 apparency of their food resources in the more compositionally complex landscapes and is  
299 associated with higher yields (Grab et al. 2018, but see Plećaš et al. 2014). This suggests that  
300 there may be a direct benefit of landscape diversification on yields and farm incomes through  
301 reduction in pest pressure.

302         Agricultural landscape simplification through cropland expansion can also increase  
303 parasitoid abundance and parasitism rates (Hawro et al. 2017; Zhao et al. 2015), although  
304 effects vary according to the ecology or life-history of different species or functional groups.  
305 Where host density responds positively to crop monocultures due to a concentration of plant  
306 resources (e.g., aphid pests of cereals) there may be a corresponding density-dependent  
307 primary parasitoid response in a tri-trophic interaction (Gagic et al. 2012; Hawro et al. 2017).  
308 Agricultural simplification may therefore impact parasitoid food webs through bottom-up forces  
309 transmitted along the links in the plant - host insect - parasitoid - hyperparasitoid food web  
310 (Lohaus et al. 2013). Agricultural intensification can increase the complexity of aphid-  
311 parasitoid food webs (e.g., interaction evenness), in contrast to the hypothesis that organic  
312 and low intensity farming preserve species richness and food web complexity (Lohaus et al.  
313 2013). For example, parasitoids able to overwinter in the oilseed rape crops are unaffected by  
314 changes in the area of surrounding semi-natural habitat, highlighting how specific ecology  
315 dictates parasitoid responses to landscape-scale habitat complexity (Berger et al. 2018; Haan  
316 et al. 2020).

317         Finally, effects of landscape compositional simplification on parasitoids can be  
318 positive, negative or idiosyncratic. In highly-simplified landscapes, host(aphid)-parasitoid food-  
319 webs can be more complex, but less stable due to high levels of temporal change in the host-  
320 parasitoid network in intensively-managed fields, likely due to bottom-up fluxes in aphid  
321 abundance (Gagic et al. 2014, 2012). Food webs stability can therefore be decreased in  
322 landscapes with high agricultural intensification, although the overall richness of parasitoids

323 may remain high in intensified agricultural lands (Gagic et al. 2012). High levels of agricultural  
324 intensification can produce distinct parasitoid species assemblages where the constituent  
325 species are low-dispersing specialised parasitoid leading to a lack of connectivity between  
326 local populations and higher species turnover (Gagic et al. 2014). Different effects of  
327 landscape simplification on parasitoids according to traits such as dispersal capacity  
328 complicate the formation of clear predictions (Gagic et al. 2014). Interestingly, parasitism rates  
329 and hyperparasitism rates seem higher in fields with high landscape (Gagic et al. 2012). The  
330 response of host-parasitoid interactions and parasitism rates to landscape compositional  
331 complexity are therefore complex and variable (Haan et al. 2019). Much of this can be  
332 explained by variation in species assemblage composition, richness or abundance between  
333 regions and regional differences in management practices or intensity (Hawro et al. 2015;  
334 Plećaš et al. 2014; Thies et al. 2011). Differences in the relative strength of bottom-up and  
335 top-down forces on the different trophic levels (host - parasitoid - hyperparasitoid) are another  
336 factor that can shape the impact of landscape composition on abundance and parasitism  
337 (Ulina et al. 2019).

338

### 339 **1.2.2. Effect of habitat configuration simplification on parasitoids**

340 Habitat configuration at the landscape scale can have a significant impact on parasitoids  
341 (Berger et al. 2018; Dominik et al. 2018; Haan et al. 2020; Martin et al. 2016; Ulina et al. 2019).  
342 Parasitoid abundance tends to be greater in fields embedded in fragmented landscapes with  
343 high edge densities. The configurational effect of a landscape can reduce the impact of  
344 landscape composition (Haan et al. 2020). In a study led in oilseed rape (OSR) fields, proximity  
345 to the forest favoured agricultural pest colonisation of the crop from nearby forest where they  
346 overwinter, but there was no concomitant spillover of parasitoid populations. Consequently,  
347 the larger the OSR field and the greater the distance to the forest edge, the lower the pest  
348 density and the greater the biocontrol efficacy of the more mobile parasitoids to locate and  
349 suppress the pest population (Berger et al. 2018). Additionally, the parasitoids were able to  
350 overwinter in the OSR field (Berger et al. 2018) and do not need shelter or alternative food  
351 from the forest. A consequence of these differential ecological patterns and processes is that  
352 host-parasitoid food webs were more asymmetrical in larger fields (Berger et al. 2018).  
353 However, it is very important to point out that this situation may be highly specific to OSR  
354 crops. Indeed, these crops are rich in pollen and nectar available during the winter and  
355 cropping disruptions (pesticides applications, harvest, ploughing or fertilizing) are rare during  
356 the winter period. As parasitoids often only need hosts, pollen, nectar and shelter to survive  
357 and as this crop fulfils all these needs, it is not surprising to find these results. It is important  
358 to keep in mind that the results might not be the same in winter wheat fields for example.

359 Other studies have demonstrated that habitat configuration complexity increased  
360 parasitoid abundance and richness in rice systems (Dominik et al. 2018; Martin et al. 2016;  
361 Ulina et al. 2019). Abundance and richness was elevated by greater structural connectivity of  
362 rice fields (Dominik et al. 2018) and the small-grain of rice landscapes with high connectivity  
363 between fields (Ulina et al. 2019) facilitating the spillover of the parasitoids (Martin et al. 2016).  
364 Conversely, greater habitat fragmentation reduced the presence of parasitoids in rice fields  
365 (Dominik et al. 2018). Interestingly, the parasitoids were more affected by landscape  
366 configuration complexity than by the presence of their hosts (Dominik et al. 2018) or by the  
367 amount of semi-natural habitats (Martin et al. 2016) suggesting that landscape configuration  
368 could be a crucial factor in preserving natural enemy efficiency in cropped lands. A conclusion  
369 is that the proximity of diversified resources seems more important than the diversity of  
370 resources alone (Martin et al. 2016).

371 Habitat configuration complexity may have no particular impact on hosts or parasitoids  
372 and parasitism rates (Hawro et al. 2015; Plečáš et al. 2014; With and Pavuk, 2019). This can  
373 be when the effects of habitat composition overcome habitat configuration complexity (With  
374 and Pavuk, 2019; but see Haan et al. 2020) or host availability overcomes the direct effect of  
375 habitat configuration on parasitoids and parasitism rates (Hawro et al. 2015). As noted above,  
376 the effects of habitat configuration on parasitism and biocontrol can markedly differ between  
377 geographic regions and years due to variation in population sizes, species pools or turnover  
378 (Hawro et al. 2015, Plečáš et al. 2014).

379

### 380 **1.3. Synthesis and perspectives**

381 The use of chemical pesticides has negative effects on the survival of parasitoids and on their  
382 reproductive capacity, whereas nitrogenous chemical inputs overall positively affect parasitoid  
383 populations through bottom-up improvements in host quantity and or quality. The use of bio-  
384 pesticides is one proposed solution to the impact of chemical pesticides on non-target  
385 organisms, but the results are mixed and it seems that similarly adverse effects on parasitoid  
386 populations are possible (Alves et al. 2019; Biondi et al. 2013). Consideration of the use of  
387 refuge zones around the pesticide treated areas may allow the reinvasion of these areas by  
388 natural enemies, but the precise scale and configuration of such refuges remains a research  
389 active area. Furthermore, the policy to reduce the use of agrochemicals is encouraging the  
390 development of new pest control methods and the use of biocontrol as an ecosystem service.  
391 The combined use of pesticides and parasitoids is not incompatible and can be considered in  
392 integrated pest management (IPM) programs if these interventions are carefully timed (Biondi  
393 et al. 2013; Desneux et al. 2007; Milonas et al. 2021; Rakes et al. 2021; Williams et al. 2003).  
394 However, this field of study sorely lacks practical, working examples. Most studies assessing  
395 bottom-up effects of external inputs on parasitoids are conducted under laboratory conditions

396 and in the case of pesticide use, only the impact of sublethal effects on reproduction is mainly  
397 considered. To satisfactorily assess the impact of pesticides on parasitoids, additional field  
398 studies are needed (Pinheiro et al. 2020). In addition, very few studies have been conducted  
399 on hyperparasitoids despite their primary role in the success of biocontrol programs using  
400 parasitoids (Frago et al. 2012; Schooler et al. 2011; Vyas et al. 2020). Furthermore, it is  
401 expected that the bottom-up effects of N and pesticide use would be more important in  
402 organisms higher up the food chain through bioaccumulation, but this does not appear to be  
403 the case since the hyperparasitoid population was less impacted by pesticide use than the  
404 primary parasitoids (e.g., Longley et al. 1997). Further studies are needed to determine the  
405 precise effects on hyperparasitoids because if they are found to be less impacted than primary  
406 parasitoids, the pressure supported by bottom-up effects of land use intensification and top-  
407 down effects unbalancing primary parasitoid/secondary parasitoid populations may drastically  
408 modulate primary parasitoid populations and reduce the ecosystem services they provide.

409         Enhancing natural enemy abundance and biocontrol can be done by manipulating  
410 landscape configuration and composition, although they are often highly interconnected and  
411 hard to disentangle in their effects (Haan et al. 2020; Martin et al. 2019). Landscape  
412 composition complexity has contrasting effects on parasitoids and parasitism rates with  
413 positive (Elliott et al. 2018; Gagic et al. 2012; Grab et al. 2018; Plećaš et al. 2014), negative  
414 (Hawro et al. 2017; Zhao et al. 2015) and neutral (Gagic et al. 2012) responses reported. Such  
415 variability and inconsistency may arise from regional variation in species group identity (Thies  
416 et al. 2011) or food web structure acting on the parasitoid (Ulina et al. 2019). The positive  
417 effect of landscape configuration on parasitoids seems more consistent (but see Plećaš et al.  
418 2014; Hawro et al. 2015; With and Pavuk, 2019). Moreover, recent studies have shown that  
419 effects of landscape composition variables can be secondary to effects of landscape  
420 configuration (Haan et al. 2020) showing the importance of the latter as a potential lever to  
421 increase biocontrol. Indeed, a growing number of studies have highlighted the impact of  
422 landscape configuration on parasitoids capacity to survive and parasitize in a given landscape  
423 (Martin et al. 2016; Berger et al. 2018; Ulina et al. 2019).

424         From these assessments, we can conclude that manipulating landscape configuration  
425 to increase parasitoid populations might be a viable option to activate natural biocontrol in  
426 future agricultural landscapes. Some key steps to activate natural biocontrol services from  
427 parasitoids may include: 1. enhancing connectivity between the different food resources of  
428 parasitoid species or life-history stages to facilitate population persistence and spillover of  
429 parasitoids, 2. promote small field sizes to enable parasitoid spillover to reach the centre of  
430 fields, 3. increase the proximity between diversified resources in order to help parasitoids find  
431 complementary food resources (e.g., pollen and nectar, prey) and hosts. While reducing field  
432 sizes in highly intensified crop systems might be a good lever to improve parasitoid

433 effectiveness, this might not necessarily be associated with increased cover of semi-natural  
434 habitats as they are not always efficacious in preserving parasitoids in a landscape (Berger et  
435 al. 2018). It might, however, be that increased crop diversity and use of complementary crop  
436 rotations or co-planting that divide current large monocultures into smaller, more diverse units  
437 (Shellhorn et al. 2011) can provide the spatio-temporal continuity of diversified food resource  
438 patches to enhance natural parasitism rates and reduce dependency on pesticide  
439 applications.

440

## 441 **2 - CLIMATE CHANGE**

442 Host–parasitoid systems can be disrupted when species respond differently to a climate  
443 change (Jefferies and Lewis, 2013), although a species' biological adaptations and evolutionary  
444 history shape responses to different aspects of climate change (e.g., Ewald et al. 2015;  
445 Sinclair et al. 2016). In this section, we discuss the likely and observed effects of climate  
446 change on parasitoids and on their interactions with their hosts, and identify some current  
447 challenges for making predictions in this area (Figure 3). Evidence for effects on parasitoids  
448 of climate change induced bottom-up effects often comes from semi-natural ecosystems (e.g.,  
449 forests), but we consider such findings here as they can still inform on potential impacts in  
450 agricultural systems.

451

452 **[Insert Figure 3 here]**

453 **Figure 3.** Direct and indirect effects of climate change (temperature and water regime  
454 changes, increased atmospheric CO<sub>2</sub>) on ecological mechanisms producing positive and/or  
455 negative impacts on plant-host-parasitoid interactions (and their symbionts). Images sourced  
456 from thenounproject.com (CC-BY: Carpe Diem; Denimao; Megan Strickland; Phạm Thanh  
457 Lộc).

458

### 459 **2.1. Direct impacts of climate change on parasitoids**

460 Temperature is a key factor affecting parasitoid performance (Abarca and Spahn, 2021; Hance  
461 et al. 2007; Le Lann et al. 2021). It does so, however, in a non-linear way with gains in  
462 performance from a lower thermal limit up to an optimal temperature, followed by an abrupt  
463 decrease as the highly constrained upper thermal limit is approached (Furlong and Zalucki,  
464 2017; Stoks et al. 2017). Parasitoid responses to global warming will therefore depend upon  
465 how current and future conditions align with their evolved thermal performance. Temperature  
466 performance may be trait-dependent, and that alone could alter host–parasitoid interactions  
467 under climate change (Foray et al. 2014). Under increased temperatures, parasitoids could  
468 develop faster, but at the expense of reduced body size and energetic resources (Foray et al.  
469 2014; Moore et al. 2020; Schreven et al. 2017). A meta-analysis by Wu et al. (2016a) found  
470 differences in temperature response between *Trichogramma* parasitoid species, widely used



471 as inundative biocontrol agents, related to the geographical source of the species and were  
472 therefore likely due to evolved thermal adaptations among species.

473 The consequence of temperature changes for any particular host–parasitoid  
474 interaction will depend on the combination of life-history impacts that result. Romo and  
475 Tylianakis (2013) found higher temperature reduced longevity of *Diaeretiella rapae*  
476 parasitoids, but increased emergence success, resulting in greater suppression of aphid pests  
477 *Brevicoryne brassicae* on *Brassica oleracea*. However, changes to individual life-history  
478 elements do not necessarily result in changes to overall parasitism outcomes. Moreno-  
479 Delafuente et al. (2021) found a reduced development time of the parasitoid *Aphidius colemani*  
480 parasitizing its aphid host *Rhopalosiphum padi* under the combination of increased  
481 temperature and CO<sub>2</sub> level, but parasitism rate was unaffected. Nevertheless, since the upper  
482 thermal limit is generally higher for the host than its associated parasitoid, increased  
483 temperatures should generally favour the host over its parasitoid (Agosta et al. 2018; Moore  
484 et al. 2021; Stoks et al. 2017). In addition, the tight constraints on upper thermal limits for  
485 insects leave limited adaptation potential, especially for species already under thermal stress  
486 (Hoffmann et al. 2013), and may lead to reduced parasitoid reproductive rates as limited lipid  
487 resources are allocated to body maintenance instead (Denis et al. 2013).

488 As climate change advances, parasitoid behaviour will also be impacted, often in non-  
489 linear ways, by exposure to episodic extreme temperatures (e.g., heat waves). Such  
490 behavioural alterations are likely to affect host location and parasitism success, but the  
491 direction of the effect appears to vary between species and the behavioural traits measured.  
492 Valls et al. (2020) found that heat shock during foraging reduced parasitoid activity, resulting  
493 in a reduction in the number of aphids parasitized. In a different species combination, high  
494 temperature exposure has been shown to reduce search time and increase parasitism rate  
495 (Jiang et al. 2018). In the latter example, at higher temperature the parasitoid also appeared  
496 better able to discern unsuitable hosts that had been infected by a virus (Jiang et al. 2018).  
497 Flying and walking capacities may also be affected by changes in temperature; Jerbi-Elayed  
498 et al. (2015) found that flying and walking capacities of parasitoids were reduced and  
499 increased, respectively at higher temperatures in association with a reduction in reproductive  
500 potential. Overall different responses between species and traits hamper predictability and  
501 indicate that a detailed understanding of each host-parasitoid combination is necessary.

502 Warmer conditions due to global climate change may paradoxically increase  
503 parasitoids' exposure to cold temperature extremes (Abarca and Spahn, 2021). This is  
504 because warmer autumnal conditions may delay diapause induction, while warm winter  
505 conditions will shorten diapause (Bale and Hayward, 2010) leading to increased parasitoid  
506 mortality and reduced longevity and fecundity (reviewed in Hance et al. 2007). Mirroring the  
507 upper thermal limit, the lower thermal limit of parasitoid activity is probably higher than that of

508 their host (Liu et al. 2016), and parasitoid species extending their activity window as a  
509 response to warmer temperatures may have a limited adaptation potential to cold extremes,  
510 as found in *Aphidius avenae* (Hymenoptera: Braconidae: Aphidiinae) (Alford et al. 2020).

511 Other aspects of climate change such as atmospheric and water regime changes are  
512 most likely to affect parasitoids indirectly through bottom-up effects on vegetation and hosts  
513 (section 2.2.). Research on the potential direct effects of elevated CO<sub>2</sub> and increased  
514 atmospheric pollutants on parasitoids and parasitism is scarce in comparison to temperature,  
515 perhaps due to the more specialist experimental infrastructure required. Ozone pollution can  
516 negatively affect host searching behaviour of the *Drosophila* parasitoid *Asobara tabida* (Gate  
517 et al. 1995), but is unclear if this due to direct physiological impairment (e.g., of olfactory  
518 systems) – as demonstrated in insect pollinators (Vanderplanck et al. 2021) – or by host  
519 kairomone degradation by air pollutants (e.g., Himanen et al. 2009).

520

## 521 **2.2. Plant- and host-mediated impacts of climate change on parasitoids**

522 Because parasitoid fitness is tightly linked with host quality (Godfray 1994), climate change  
523 effects of increased temperature, elevated atmospheric CO<sub>2</sub> (eCO<sub>2</sub>) and droughts may induce  
524 bottom-up (plant- and host-mediated) impacts on both parasitoid behavior and development  
525 (Thomson et al. 2010).

526 A fundamental mechanism underpinning plant–host–parasitoid tri-trophic interactions  
527 is the attraction of parasitoids via herbivore-induced plant volatiles (HIPVs) (Dicke and  
528 Baldwin, 2010; Du et al. 1998; Turlings et al. 1991). Climate-induced abiotic stressors are  
529 likely to affect HIPV emissions by plants, jeopardizing this chemical communication between  
530 plants and parasitoids (Becker et al. 2015; Harvey, 2015; Jamieson et al. 2017; Yuan et al.  
531 2009). The effect of climate change on plant–parasitoid interactions via HIPVs is multifaceted  
532 with effects manifesting through changes in the volume, composition, perception by insects,  
533 or environmental persistence of HIPVs (Ode et al. 2006; Pinto et al. 2007). Increased eCO<sub>2</sub>  
534 from 360 to 720 μl l<sup>-1</sup> in *Brassica oleracea* caused a reduction in the emission of two HIPVs  
535 induced by the host *Plutella xylostella*, and the associated parasitoid *Cotesia plutellae* no  
536 longer responded to the plant signal (Vuorinen et al. 2004). Conversely, Himanen et al. (2009)  
537 found increased emissions of most terpenoids of *Brassica napus* under equivalent elevated  
538 eCO<sub>2</sub> had no effect on attraction of *Cotesia vestalis* to *P. xylostella* host-infested plants.

539 Drought stress can also have negative, positive or negligible impact on HIPV emissions  
540 and parasitoid recruitment. Drought altered HIPVs of *Citrus* trees infested with *Diaphorina citri*  
541 preventing attraction of their parasitoid *Tamarixia radiata* (Martini and Stelinski, 2017).  
542 Similarly, *B. oleracea* HIPV emissions induced by the aphid *Myzus persicae* were reduced  
543 under drought, lowering parasitoid recruitment, particularly for the specialist species  
544 *Diaeretiella rapae* (Tariq et al. 2013). In contrast, drought elicited no change in parasitoid

545 attraction in the *Brassica oleracea* – *Mamestra brassicae* – *Microplitis mediator* system  
546 (Weldegergis et al. 2015), indicating how outcomes can differ according to species identity.

547 Disentangling plant- and host-mediated effects on parasitoid performance requires  
548 complex experimentation and clear examples are therefore scarce. Effects discussed in this  
549 section may in fact be the result of plant-mediated effects on herbivores, that then have knock-  
550 on consequences for their parasitoids. Temperature increases can have complex, multi-  
551 generational and multi-directional effects on host–parasitoid interactions. Ittis et al. (2020)  
552 experimentally separated the effects of warming on adults of the parasitoid *Trichogramma*  
553 *cacoeciae* and their parasitic offspring (eggs) in the host *Lobesia botrana* (Tortricidae).  
554 Warming of the parental generation reduced the pupal mass and the nutritional quality of their  
555 eggs, which resulted in a reduced emergence rate of the next generation. However, direct  
556 warming of the parasitized host (e.g., during parasitoid development) did not significantly affect  
557 the host–parasitoid interaction in that generation. One adaptation to high temperature by  
558 koinobiont parasitoids is their ability to manipulate the behaviour of their hosts to mummify in  
559 a more optimal temperature environment (Hance et al. 2007). Without which, host reaction to  
560 heat stress may protect them against parasitism, as seen with greater survival of  
561 *Acyrtosiphon pisum* aphids from parasitism by *Aphidius ervi* after exposure to a heat shock  
562 (Trotta et al. 2018).

563 Climate change may alter the chemistry of primary (N, P, C, amino acids) and  
564 secondary plant metabolites with a defensive function (Harvey, 2015; Ode et al. 2014). Under  
565 eCO<sub>2</sub> plants capture more carbon relative to nitrogen resulting in a decrease in foliar nitrogen  
566 content impairing herbivores' performance and potentially their quality as hosts for parasitoids  
567 (Bezemer et al. 1998; Jeffs and Lewis, 2013; Thomson et al. 2010). It can also reduce plant  
568 quality and thereby increase host feeding, lengthen host development and alter host fecundity  
569 (Schulze-Sylvester and Reineke 2019; Stacey and Fellowes, 2002; Sun et al. 2011; Wang et  
570 al. 2014). Roth and Lindroth (1995) found that eCO<sub>2</sub> both reduced foliar nitrogen content and  
571 increased foliar phenolic and starch content in aspen trees. This increased leaf consumption,  
572 slowed development, and reduced final weight of gypsy moth *Lymantria dispar* L. larvae, which  
573 led to greater mortality and slightly reduced female body size of the parasitoid *Cotesia*  
574 *melanoscela*. Reduced vegetation quality can also increase parasitism, however. Lower foliar  
575 nitrogen content increased leafminer mortality in a natural *Quercus* community, partly due to  
576 the plant effect, but mainly through increased parasitism (Stiling et al. 1999). The knock-on  
577 consequences for parasitoids of eCO<sub>2</sub> effects on host quality may therefore be positive (Sun  
578 et al. 2011) or negative (Schulze-Sylvester and Reineke, 2019), while impacts on parasitism  
579 rates remain unresolved (Schulze-Sylvester and Reineke, 2019; Sun et al. 2011; Wang et al.  
580 2014).

581 O<sub>3</sub> and water stress have also been shown to alter plant chemistry and consequently  
582 herbivorous host performance and the performance of their parasitoids (Aslam et al. 2013;  
583 Johnson et al. 2011; Munir et al. 2016). Holton et al. (2003) found a decreased nitrogen content  
584 but increased tannin content in the quaking aspen *Populus tremuloides* under eO<sub>3</sub>, while eCO<sub>2</sub>  
585 only caused decreased nitrogen content. Forest tent caterpillars *Malacosoma disstria* had an  
586 improved performance under eO<sub>3</sub> at ambient CO<sub>2</sub> levels, but a reduced performance under  
587 eCO<sub>2</sub> and O<sub>3</sub>, while their parasitoids *Compsilura concinnata* (Diptera) had an increased  
588 mortality under eO<sub>3</sub>. Wade et al. (2017) found that continuous drought reduced the plant  
589 biomass of *Hordeum vulgare* L. while a drought/deluge regime (reduced rainfall events but not  
590 rainfall volume), did not. The drought/deluge regime also increased the nitrogen and amino  
591 acid foliar content, and increased by 15 % the mass of aphids *Sitobion avenae*,  
592 *Metapolophium dirhodum*, and *Rhopalosiphum padi* and by 66 % the mass of ladybirds  
593 *Harmonia axyridis*. However, the parasitism rate was not affected (Wade et al. 2017). Finally,  
594 drought stress may increase or decrease host quality. For example, slower development and  
595 reduced body size of *S. avenae* aphids on drought-stressed wheat reduced *Aphidius*  
596 parasitism rate (Ahmed et al. 2017; Nguyen et al. 2018). Ahmed et al. (2017) also showed that  
597 aphid species adapted to more humid conditions could no longer defend against parasitoids  
598 under drought which could improve parasitism success rate and biocontrol. Similarly,  
599 Kansman et al. (2021) found an improved suppression of *R. padi* aphids by *Aphidius colemani*  
600 under water limitation. While water stress increased aphid size and maximized parasitoid  
601 performance, parasitism rate was lowest under high-water stress, although this was  
602 accompanied by simultaneously poor aphid performance driving their abundance down  
603 (Kansman et al. 2021). Conversely, Calatayud et al. (2002) found improved immune  
604 responses of mealybugs on water-stressed, water-resistant cassava plants, leading to a  
605 higher rate of encapsulation of their endoparasitoid.

606 Overall, climate change drivers may directly or indirectly reduce host nutritional  
607 quality which will reduce parasitoid fitness (Facey et al. 2014) or reduced host immunity to  
608 parasitism which may lead to the opposite. The impact of these different climate change  
609 drivers tend to have a negative impact on parasitoid behavior and performance even if the  
610 response seems species-specific. Combinations of these climatic factors are likely to result in  
611 different outcomes compared to their individual effects (Romo and Tyljanakis, 2013). However,  
612 there is little research to date on *plant-* and *host-mediated* impacts of combined climatic factors  
613 or extreme climatic events on parasitoids performance or adaptation potential.

614

### 615 **2.3. Endosymbiont-mediated impacts of climate change on parasitoids**

616 Host–parasitoid interactions can be influenced strongly by the presence of endosymbiotic  
617 bacteria, with several bacterial species able to increase host resistance to parasitism (Oliver

618 et al. 2014). Changes in temperature could profoundly affect endosymbionts, with implications  
619 for host–parasitoid interactions (Corbin et al. 2017). The protection provided by the aphid  
620 symbiont *Hamiltonella defensa* is temperature-dependent (Bensadia et al. 2006), probably  
621 due to heat damage to the bacterium. Consequently, we might expect diminished  
622 endosymbiont protection against parasitoids in heat-sensitive bacteria faced with increased  
623 frequency of episodic heat waves or sustained higher temperatures. Other symbiont species  
624 are able to withstand heat damage, and may thus offer redundancy in symbiont-mediated  
625 protection from parasitism (Guay et al. 2009; Heyworth et al. 2020). Symbionts shown to  
626 protect aphids from heat stress can also exacerbate host vulnerability to parasitoids e.g., aphid  
627 harboring X-type symbionts are more susceptible to parasitism than cured aphids (Heyworth  
628 and Ferrari, 2016). One symbiont that can at least occasionally increase aphid resistance to  
629 parasitism (*Serratia symbiotica*; Oliver et al. 2003) is found more frequently in hot  
630 environments (Henry et al. 2013), possibly due to an ability also to protect the insect host  
631 against heat stress (Montllor et al. 2002). In environments where heat stress becomes more  
632 common, we might anticipate parasitoid resistance, because of the selection pressure due to  
633 rising frequencies of *S. symbiotica*.

634         When other elements of the ecosystem are included, the picture becomes ever more  
635 complex. Host feeding on drought-stressed plants may influence symbiont-infected and  
636 symbiont-free aphids differently, and speculative modelling work indicates this could disrupt  
637 co-existence of symbiont-free and symbiont-infected aphids, with knock-on effects on  
638 parasitism (Preedy et al. 2020). Impacts of climate change (including temperature and eCO<sub>2</sub>)  
639 on emission of plant volatiles (see above) could interact with known effects of herbivore  
640 symbionts on plant volatiles (Frago et al. 2017), but experimental evidence of the direction  
641 and magnitude of such interactions is currently lacking.

642         Symbionts are, however, not limited to herbivorous hosts; many parasitoids also carry  
643 symbiotic bacteria. In several species of *Trichogramma*, *Wolbachia* endosymbiont presence  
644 is correlated with heat tolerance (Pintureau and Bolland, 2001; Wu et al. 2016b). Considering  
645 the symbiont status of parasitoid genotypes is therefore one aspect of predicting biocontrol  
646 potential under climate warming or extreme heatwave event scenarios. Alternatively, changing  
647 climate could result in significant changes to symbiont frequencies and/or identities in both  
648 insect herbivores and their parasitoids, but if the consequence of symbiont turnover is to  
649 maintain insect phenotypes, this would result in very little visible change in the external insect  
650 communities.

651

## 652 **2.4. Community structure and species interactions**

653 Climate change may affect both species assembly within communities and interactions within  
654 food webs (Thierry et al. 2019). Tougeron et al. (2018) identified a recent species

655 diversification over nine years in a temperate winter cereal aphid-parasitoid-hyperparasitoid  
656 community, that was partially explained by increased minimum temperatures and the reduced  
657 frequency of frost events. Salazar-Mendoza et al. (2021) similarly found that the species  
658 richness of fruit flies and their associated parasitoids and parasitism rate were higher at lower  
659 elevations. Under climate change, such displacement of the favourable 'climate envelope'  
660 hosting a high diversity and abundance of parasitoids towards higher latitudes could leave  
661 lower latitudes depleted due to harsher temperatures.

662           The community-level parasitism rate may also be affected by the precipitation regime.  
663 Over a large spatial scale, parasitism rate correlates negatively with increased variability of  
664 precipitation (Stireman et al. 2005), which is predicted to be drastically exacerbated by climate  
665 change (Pendergrass et al. 2017). Similarly, Salcido et al. (2020) found that weather  
666 anomalies leading to flooding events were likely at least partially responsible for the strong  
667 decline in species richness of caterpillars and parasitoids, interaction richness and overall  
668 parasitism rate in a tropical Costa Rican community over a 22-year survey. Changes in  
669 temperature regimes may alter species relative abundances and interaction strengths. Under  
670 simulated heatwave conditions, Gillespie et al. (2012) found a reduced total parasitism rate  
671 but an increased competition for hosts between *Aphidius matricariae* and *Aphelinus*  
672 *abdominalis* parasitizing *Myzus persicae* aphids. Enhanced competition under heatwaves was  
673 also found between hyperparasitoids (Chen et al. 2019). Conversely, competition was  
674 unchanged in a *Drosophila* (host) – *Asobara* (parasitoid) community under increased  
675 temperatures, and reduced parasitism rate was instead a direct consequence of reduced  
676 parasitoid performances (Thierry et al. 2021). Finally, Bonsignore et al. (2020) found that  
677 short-term cold stress affected the relative frequencies of parasitoids emerging from Asian  
678 cynipid gall wasps in chestnut trees. Range expansions due to climate change provide an  
679 additional source of changes in community structure and interactions. For example,  
680 Audusseau et al. (2021) found that range expansion of one nettle-feeding butterfly (*Araschnia*  
681 *levana*) was associated with an increased parasitism rate in existing resident nettle-feeding  
682 butterfly species.

683           The impacts of other aspects of climate change on species interactions, notably  
684 drought, remain understudied. However, temperature and rainfall will, of course, act in  
685 combination. Derocles et al. (2018) found that increased temperatures and rainfall  
686 synergistically exacerbated asymmetry of interactions in a wheat–aphid–parasitoid  
687 community, with aphid abundances doubled but with overall similar parasitism rate. This could  
688 lead to outbreaks of the main pest species, but perhaps also secondary outbreaks of minor  
689 pest species due to the enhanced interaction asymmetry relaxing top-down control. In a 42-  
690 year survey in cereal fields, Ewald et al. (2015) found that braconid abundances increased in  
691 hot/dry years and decreased in cold/wet years, but aphid or chalcid wasp abundances were

692 less strongly correlated to extreme events, suggesting the dominant parasitoid groups in a  
693 community may shift if average weather patterns change. However, climate change may not  
694 always have a major impact on more functionally diverse communities with multiple natural  
695 enemies: combined eCO<sub>2</sub>, higher temperature and decreased precipitation reduced survival  
696 of nematodes, but not parasitoid wasp, ladybird or spider survival (van Doan et al. 2021).

697

## 698 **2.5. Impacts of climate change on phenology**

699 Changes in climate are already driving changes in insect phenologies (Abarca and Spahn,  
700 2021; Forrest, 2016). These changes can arise from direct physiological effects of warmer  
701 climates such as speed of development, knock-on effects of changing plant phenologies (e.g.,  
702 timing of leaf burst), and changes to previously reliable signals for developmental timing (e.g.,  
703 for entering or exiting diapause). All these alterations could have consequences for host–  
704 parasitoid interactions, especially if they result in a mismatch between host and parasitoid  
705 phenologies.

706 A straightforward physiological effect of climate change is that higher temperatures  
707 can result in a faster life cycle. For instance, increased temperatures reduce development time  
708 in *Spodoptera exigua*, allowing a temporal escape from its parasitoid *Cotesia marginiventris*  
709 and hence a dramatic reduction of pest control (Dyer et al. 2013). This is also the case where  
710 higher temperatures reduced the temporal occurrence of cynipid chestnut gall wasp  
711 (*Dryocosmus kuriphilus*, Hymenoptera: Cynipidae) and increased asynchrony with parasitoids  
712 (Bonsignore et al. 2019). Similarly, increased temperatures from 20 to 35 °C reduced the  
713 period of susceptibility of the emerald ash borer *Agrilus planipennis* to parasitoid attacks (Duan  
714 et al. 2014).

715 Climate change may also affect host–parasitoid phenology through bottom-up plant  
716 mediated effects. Warmer spring temperatures may cause plant phenology to be shifted earlier  
717 disrupting the higher trophic levels. This was the case in a fern-moth-parasitoid system, where  
718 the host and parasitoid were slower at tracking this phenological shift, resulting in an increased  
719 asynchrony between the trophic levels (Morse, 2021). In the sycamore, *Acer pseudoplatanus*,  
720 warmer spring temperatures caused earlier budburst but delayed the emergence of aphids  
721 while parasitoid attacks were advanced (Senior et al. 2020). An increase in 1.9°C has also  
722 caused a phenological shift in wheat growth, increasing the abundance and reproduction  
723 period of aphids *Sitobion avenae*, but left parasitoid abundance unaffected and lowered the  
724 parasitism rate (Han et al. 2019).

725 Diapause is generally induced and ended by environmental cues, such as day length  
726 or temperature at higher latitudes and rainfall in tropical regions (Bale and Hayward, 2010).  
727 Warmer winters in temperate regions may cause diapause termination, and the differences in  
728 lower thermal limits between hosts and parasitoids may cause asynchrony in their respective

729 development (Hance et al. 2007). In the passion vine hopper *Scolytopa australis* Walker  
730 (Homoptera: Ricaniidae), abnormally warm summer temperatures disrupted the diapause-  
731 induced synchrony between the pest and its normally univoltine egg parasitoid *Centrodora*  
732 *scolytopae* Valentine (Hymenoptera: Aphelinidae), and this caused the parasitoid to have a  
733 second unsuccessful generation (Gerard 2004). Over the long term, this could cause a drastic  
734 reduction in the abundances of parasitoids.

735         Where insect herbivores and their parasitoids exhibit a different phenological  
736 response to climate change a mismatch can occur, to the benefit or detriment of either party.  
737 In general, greater mismatch will favour the herbivore while greater synchrony will benefit the  
738 parasitoid. Asynchrony is most likely where parasitoids and their hosts use different  
739 phenological cues (or respond differently to the same cue). Insect life-history is an important  
740 element of whether or not synchrony is likely to be affected. For example, if parasitoid  
741 diapause depends entirely on the host, synchrony will be maintained, whereas asynchrony  
742 can develop if spring emergence of host and parasitoid is controlled by different cues and  
743 becomes decoupled (Damien and Tougeron, 2019).

744         Asynchrony between hosts and parasitoids has been found under experimental  
745 warming in natural forest caterpillar-wasp communities: both caterpillars and hosts emerged  
746 earlier, but the effect was stronger for caterpillars leading to partial decoupling (Abarca and  
747 Lill, 2019). In a 10-year survey of cereal leaf beetles in Utah, warm spring temperatures  
748 advanced the population growth of beetles but not of parasitoid wasps, causing enhanced  
749 asynchrony and reduced parasitism (Evans et al. 2013). In other systems, warmer spring  
750 temperatures may instead increase host–parasitoid synchrony: the host butterfly *Melitaea*  
751 *cinxia* and its parasitoid *Cotesia melitaeorum* show some asynchrony under normal  
752 temperatures. This is notably due to the different colours of the caterpillars (dark) and the  
753 parasitoid cocoons (pale) as dark-coloured caterpillars basking in the sun increase their body  
754 temperature. In addition, the ability of caterpillars to move to seek a warmer microclimate and  
755 thus develop more quickly - under warmer temperatures parasitoid phenology is advanced,  
756 reducing asynchrony (Van Nouhuys and Lei, 2004).

757         Outcomes from experimental studies range from dramatic reductions in parasitism  
758 rate (e.g., Dyer et al. 2013) to no major change in parasitism (Bale and Hayward, 2010).  
759 However, by incorporating understanding of insect life histories, including the cues that are  
760 used to align development with food-plants (in the case of herbivores) or insect hosts (in the  
761 case of parasitoids), experimental laboratory studies and field observations, it may become  
762 possible to predict the likely impacts of climate change on phenology for a range of specific  
763 systems (Forrest 2016).

764  
765



## 766 **2.6. Impacts of climate change on species distributions**

767 Insects may respond to changing climate, altering their geographic distribution. As  
768 temperatures change, range expansions and contractions will be observed, according to the  
769 thermal limits of the insects involved and the speed with which they are able to track the  
770 changing environment. Just as with phenological responses to climate change, geographic  
771 shifts may be different for herbivores and their natural enemies, altering the rates of parasitism.  
772 Crop distributions will also be change with new climate and herbivorous pests might be able  
773 to track such changes faster than their natural enemies, especially parasitoids which have a  
774 reduced dispersal capacity relative to their hosts' (Thomson et al. 2010).

775         Such decoupled range shifts and the release of parasitism pressure has been  
776 observed in natural communities: Menéndez et al. (2008) observed a northward expansion of  
777 the brown argus butterfly *Aricia agestis* in Great Britain, with a reduced parasitism rate in the  
778 newly colonized areas. Similarly, parasitism pressure by parasitoid wasps was released at the  
779 expanding margin of fig wasps' geographic distribution (Mackay et al. 2020). In an Arctic  
780 community, a community shift over 22-years from parasitoids of Lepidoptera to parasitoids of  
781 pollinator Diptera related to increased summer temperatures caused greater lepidopteran  
782 herbivory but reduced dipteran pollination (Kankaanpää et al. 2020).

783         Parasitic interactions are predicted to be the most sensitive to climate-induced  
784 species range shifts: parasitoids were less able to track climate change and host range shifts,  
785 compared to mutualist or commensal species (Singer et al. 2013). Modelling approaches  
786 applied to crop pest–natural enemy communities predict changes in the distribution of crop  
787 damage under climate change. In Australia, Furlong and Zalucki (2017) predicted a decoupling  
788 between regions suitable for the lepidopteran pest *Plutella xylostella* and its parasitoid  
789 *Diadegma semiclausum* that would shrink the parasitoids northern range, whilst allowing  
790 continued crop damage by the pest. Conversely, the light brown apple moth *Epiphyas*  
791 *postvittana* is sensitive to warm temperatures and is predicted to shift towards temperate  
792 southern Australia, where it could increase crop damage unless generalist parasitoids with a  
793 large geographic distribution are able to control it (reviewed in Thomson et al. 2010). Climate-  
794 induced range shifts may potentially result in improved pest control in high latitude regions  
795 where biocontrol has failed historically: *Peristenus digoneutis* (Hymenoptera: Braconidae) is  
796 predicted to expand northwards throughout Canada and northern Europe, where it could  
797 improve the control of *Lygus* bugs (Olfert et al. 2016). Similarly, the distribution of  
798 *Trichogramma ostriniae* is predicted to expand in northeastern China and North America with  
799 climate change, potentially biocontrol of its host *Ostrinia nubilalis*.

800         Potential host–parasitoid spatial decoupling and the success of introduced parasitoid  
801 biocontrol agents will depend on the life history of both the parasitoids and the host. For  
802 instance, warmer temperatures in the southern part of their range have been shown to cause

803 emerald ash borer *Agrilus planipennis* to overwinter deeper in the wood of their host plant,  
804 where they are no longer accessible to their parasitoid *Tetrastichus planipennisi* (Gould et al.  
805 2020). Under climate change, therefore, the suitable geographic area for the establishment of  
806 the parasitoid introduced as a biocontrol agent is predicted to shrink dramatically at the  
807 southern margin of their range. At the northern extent, the increased frequency of extreme  
808 cold events induced by climate change may also compromise ash borer control due to  
809 parasitoid mortality (Duan et al. 2020).

810

## 811 **2.7. Synthesis and perspectives**

812 To conclude, the potential of climate change to impact parasitoids, and especially host–  
813 parasitoid interactions, has been widely studied in laboratory and field systems, in both  
814 manipulation and observational studies. It is clear that climate change has the potential to  
815 disrupt host-parasitoid interactions, but with variable outcomes for the rate of parasitism.  
816 Indeed, herbivores would benefit from these changes by avoiding parasitism. Hosts may have  
817 a reduced development time shortening the risk of exposure to parasitoids. The upper thermal  
818 limit of the host is generally higher than its parasitoid and a greater phenological mismatch  
819 may favour the herbivore, particularly as herbivores tend to track their host plants faster than  
820 parasitoids. Herbivores that are favoured by climate change through bottom-up effects could  
821 cause major pest outbreaks and important crop damage as they overwhelm the potential  
822 biocontrol that parasitoids provide. However, precise outcomes depend on individual species’  
823 characteristics, and these drive differences in relative importance of the multiple aspects of  
824 parasitoid and host life-history that combine to determine parasitism rates. In addition, few  
825 studies incorporate the multiple components of predicted climate change simultaneously. It is  
826 important to recognise that insect responses to climate change are not fixed – we would expect  
827 to see both plastic and evolutionary adaptation, even if the evolutionary response cannot keep  
828 pace with the rate of climate change. The laboratory experimental work we review in this  
829 manuscript does not take into account potential plastic transgenerational responses to  
830 changing conditions that might mitigate some impacts in subsequent generations. Likewise,  
831 in observational field studies where parasitoids are expanding their range more slowly than  
832 their hosts, this may be only a temporary lag that will be overcome in future years (Stone et  
833 al. 2012), provided that the parasitoid can persist within its original range in the meantime. In  
834 addition, effects of climate change such as altering distributions or phenologies of herbivores  
835 could provide opportunities for new host–parasitoid interactions. Host shifts, especially by  
836 generalist parasitoids, might thus permit biocontrol of herbivores to continue, even if the  
837 species assemblage changes. Invasion events show the potential for such shifts: for example,  
838 native parasitoids beginning to attack invasive *Cameraria ohridella* leaf miners in the UK  
839 (Pocock and Evans, 2014). Human introductions (biocontrol agents) are likely to be particularly

840 vulnerable to climate change. New introductions of biocontrol agents should therefore take  
841 into account efficacy not only in the current environment, but in projected future thermal  
842 scenarios. Rather than predicting general patterns or even specific instances of changes to  
843 parasitism in a changing climate, it may be more important for biocontrol to focus on  
844 understanding what makes a particular system more robust to perturbations such as those  
845 predicted to result from climate change. In particular, diverse or highly connected ecosystems  
846 are more ecologically resilient than simplified ecosystems, i.e., they are better able to resist  
847 and recover from disturbances and could provide a sustainable solution to limit the impact of  
848 climate change (Feit et al. 2021; see 1.2 and 4.1).

849

### 850 **3 - BIOLOGICAL INVASION**

851 Invasions by non-native or alien species (IAS) often extirpate species and profoundly modify  
852 native populations and community structure (David et al. 2017; Mack et al. 2000; Ragsdale et  
853 al. 2011; Vanbergen et al. 2018) (Figure 4). Intact, diverse or highly connected species  
854 networks may limit the probability of successful invasions because high diversity of species  
855 and phenotypic or functional traits may saturate the niche space available to the invading  
856 organism (David et al. 2017; Smith-Ramesh et al. 2017). Ecosystems with unoccupied niches  
857 space due to simpler, homogenous communities are thus more vulnerable to invasion. For  
858 example, the most concerned ecosystems include where the ecosystem was evolutionary  
859 isolated (islands) or where it has been highly modified by anthropogenic disturbance (David  
860 et al. 2017; Dawson et al. 2017; Frost et al. 2019; Vanbergen et al. 2018). Moreover,  
861 successful establishment of alien invasive species in a novel ecosystem is predicated on an  
862 adaptive advantage arising from a lack of coevolution between the native and alien species,  
863 where the latter prevails due to an advantage in competitive or trophic interactions (David et  
864 al. 2017; Díaz et al. 2019). Empirical data and simulation modelling suggest that species with  
865 larger body sizes and dietary generalists are generally more successful invaders across  
866 different trophic levels (Frost et al. 2019; Lurgi et al. 2014).

867

868 **[Insert Figure 4 here]**

869 **Figure 4.** The pathways and mechanisms by which the introduction of an Invasive Alien  
870 Species (IAS) can directly and indirectly affect community interactions and structure producing  
871 positive and negative effects on plant-host-parasitoid interactions. Black arrows represent  
872 interactions between native organisms in the absence of IAS, while green arrows represent  
873 potential interactions created by the introduction of IAS (plant, pest or parasitoid). Potential  
874 pathways to invader modification of native host-parasitoid systems include: (a) Invader  
875 occupies a vacant ecological niche; (b) Increased complementarity of parasitoid/pest actions;  
876 (c) Classical biocontrol program to introduce an agent to (re)establish top-down control of a  
877 pest; (d) Native herbivore/parasitoid able to control invading plant/pest; (e) 'Central-to-Reap,  
878 Edge-to-Elude' trait strategy enabling invasion. Images sourced from thenounproject.com  
879 (CC-BY: Baboon designs; Carpe Diem; Megan Strickland; Phạm Thanh Lộc).

880

881 Mathematical modelling can simulate the eco-evolutionary dynamics of trait-mediated  
882 invasion of networks. One such analysis of invader fitness in different community contexts  
883 (e.g., mutualistic, antagonistic, food webs) predicted key adaptive mechanisms in a 'central-  
884 to-reap, edge-to-elude' trait strategy (Hui et al. 2021). This meant that the invader should  
885 possess traits that position it to take advantage of positive (facilitator organisms, optimal  
886 resources) while avoiding negative (predation, competition) interactions in the novel  
887 environment. In the case of host-parasitoid communities, for a novel herbivore species to  
888 successfully invade and avoid parasitism, its traits should minimally overlap with the trait space  
889 of its optimal native consumer to reduce consumption rates by resident parasitoids. Whereas,  
890 to maximize consumption rates, the traits of an invading parasitoid should overlap with the  
891 central position of its optimal resource (native host) in the trait space of the resident resource  
892 community (Hui et al. 2021). This balance and alignment of traits (e.g., trophic niche  
893 partitioning) in the parasitoid community has implications for top-down regulation, for instance  
894 complementarity among parasitoid species in host resource use reduces competition that can  
895 lead to greater levels of community parasitism rates (Peralta et al. 2014; Wang et al. 2021).

896 This importance of trait space is central to the 'enemy release' hypothesis, which  
897 postulates that if a host or prey species (host plant, insect herbivore host) species is  
898 translocated beyond its natural range it is able to occupy and thrive in the novel enemy-free  
899 space lacking coevolved antagonists. Invasion of North American forests by the gypsy moth  
900 (*Lymantria dispar* L.; Lepidoptera) provides an illustration of this phenomenon with very low  
901 post-invasion parasitism rates and little sharing of parasitoids with native lepidopteran hosts  
902 (Timms et al. 2012). Ecosystem transformation by land conversion can create enemy-free  
903 space, such as with the invasion of *Solanum myriacanthum* plants into pastures cleared of  
904 tropical forest where a native butterfly (*Mechanitis menapis*) experienced a lack of parasitism  
905 compared to the native host plant (*S. acerifolium*) (Despland and Santacruz, 2020).

906 There is, however, variation in the degree that native parasitoid species are unable to  
907 adapt to the novel host insect (e.g., see Desneux et al. 2010, Ragsdale et al. 2011; Asplen et  
908 al. 2015). For instance, invasion of Europe and North America by the Asian fruit fly pest  
909 *Drosophila suzukii* showed how the composition of the native parasitoid community might limit  
910 the impact of the invading herbivore (Chabert et al. 2012). Parasitoid host range was important  
911 with specialist parasitoid species unable to switch to the novel fruit fly host, perhaps due to a  
912 lack of pre-adaptations to cope with the immunocompetence of the novel host or a lack of  
913 appropriate cues stimulating parasitoid attack. In contrast, generalist parasitoids with a  
914 naturally broad host range were able to include this invader in their diet (Chabert et al. 2012).  
915 Therefore, contrary to the enemy release hypothesis, certain native parasitoids may be able  
916 to adopt novel hosts to the extent they may regulate the invading herbivore population, as  
917 shown by the capacity of *Encarsia noyesi* (Hymenoptera: Aphelinidae) parasitizing the

918 invasive whitefly, *Aleurodicus rugioperculatus* (Hemiptera: Aleyrodidae) (Boughton et al.  
919 2015) and of *Necremnus tutae* (Hymenoptera, Eulophidae) parasitizing the invasive moth *Tuta*  
920 *absoluta* (Lepidoptera: Gelechiidae) (Biondi et al. 2018). Indeed, enemy-free space may only  
921 facilitate the initial phase of novel pest species establishment and outbreaks because the  
922 invasion process is spatially and temporally dynamic. As the pest moves across the novel  
923 landscape, it may encounter new competent enemies able to attack it (geographic spread-  
924 hypothesis) or parasitoids may adapt over time to the novel host and include it in their host  
925 range (adjustment-hypothesis) (Grabenweger et al. 2010). Compared with native hosts,  
926 invasive herbivores may, however, be suboptimal hosts that lower the reproductive success  
927 of native parasitoids, this raises the potential risk that the parasitoid populations are so  
928 disrupted by the invader that overall biocontrol pressure is relaxed in the longer term and  
929 secondary outbreaks of native pests re-emerge (Abram et al. 2014). Conversely, native  
930 herbivores may be suboptimal hosts for invasive parasitoids, reducing their ability to control  
931 populations of exotic herbivores from the same geographic area (i.e., apparent competition;  
932 e.g., Monticelli et al. 2021).

933 Indirect trophic interactions such as apparent competition may also drive patterns in  
934 parasitism rates and host abundance across community or habitat networks (Chailleux et al.  
935 2014) and differences in abundance across host species could lead to one-way indirect  
936 interactions with strong structuring effects on host–parasitoid communities (Muller et al. 1999;  
937 Valladares et al. 2001). One experimental study of host-parasitoid networks across the  
938 interface of plantation and natural forest revealed how host sharing among parasitoids  
939 determined attack rates and host population changes (Frost et al. 2016). Moreover, host-  
940 parasitoid food webs in areas of natural and production habitats functioned as a landscape-  
941 scale metaweb of host-parasitoid interactions (Frost et al. 2016). Still, herbivores with  
942 overlapping parasitoid communities could exhibit independent population dynamics, or even  
943 positive indirect interactions such as apparent mutualism (Tack et al. 2011). These findings  
944 necessitate consideration of the whole landscape matrix of crop and non-crop habitats in order  
945 to plan landscapes in ways that manage biocontrol services and restrict species invasions and  
946 pest outbreaks.

947 Alien invasive plants are common invaders worldwide and can exert a profound  
948 influence on the community of host-parasitoid interactions. The invasion of UK heathlands by  
949 an alien plant *Gaultheria shallon*, a densely growing, perennial shrub native to North America,  
950 modified the abundance of native herbivores and parasitoids and lowered parasitoid species  
951 richness. Its impact on the higher trophic levels varied with the degree of specialism, however,  
952 strongly reducing specialist abundance while leaving generalist unaffected. This invasion-  
953 induced decline of specialists disrupted top-down regulation releasing generalist species from  
954 competition via shared natural enemies (Carvalho et al. 2010). In another case, invasion of

955 Portuguese forests by *Acacia longifolia* simplified the plant communities in ways that led to  
956 declines in the biomass, abundance and species and interaction richness of galling insect  
957 herbivores, their parasitoids, and inquilines. (Lopez-Nunez et al. 2017). Such dramatic shifts  
958 in communities raise the spectre of disrupted top-down regulation of herbivores and the  
959 potential for novel outbreaks or population dynamics.

960 The effects of invasive plants on parasitism and biocontrol in the highly anthropogenic  
961 agricultural landscape remain to be seen (Carvalho et al. 2010; David et al. 2017). It is  
962 possible that in such highly simplified ecosystems with low species diversity that invasion risks  
963 are high and, in combination with other pressures like climate change, may facilitate profound  
964 shifts in the community structure and function of host-parasitoid systems. Pantel et al. (2017)  
965 suggests that, in agroecosystems, invasive species follow the same dynamics as when pests  
966 that have been previously excluded by pesticide application or host suppression are re-  
967 inserted. The role of network structure in facilitating or limiting invasion successes remains  
968 debatable. Insights from theoretical simulation models indicate that simpler, less connected  
969 food webs might be more resistant to invasions (Lurgi et al. 2014). In contrast, a global  
970 synthesis revealed that across all functional groups, invasion success was retarded by highly  
971 connected food webs (Smith-Ramesh et al. 2017).

972 As already mentioned (section 1 and 2), parasitoids use chemical cues from herbivore-  
973 induced plant volatiles (HIPV) to locate and attack potential hosts (Becker et al. 2015). Alien  
974 species invasions have the potential to modify emissions of these kairomones in ways that  
975 disrupt functioning of native host-parasitoid interactions. Plant responses in terms of HIPV  
976 emissions are the product of evolution and so the impact of an invader will likely depend on  
977 the phylogenetic relatedness between the invading and native species (Desurmont et al.  
978 2014). A recent laboratory study of HIPV emissions from *Vicia faba*, showed the volatile  
979 emissions induced by an invasive pentatomid bug (*Halyomorpha halys*) did not attract a native  
980 parasitoid and moreover when the invasive was co-feeding with a native pentatomid host  
981 (*Nezara viridula*) the parasitoid no longer successfully parasitized the native host (Martorana  
982 et al. 2017). This indicates the potential for invasive herbivores to disrupt established  
983 semiochemical signals, parasitoid behaviour and ultimately interaction webs.

984

#### 985 **4 - INTERACTIONS BETWEEN DRIVERS AND PERSPECTIVES**

986 The published studies of global change deal in isolation with the three drivers reviewed in the  
987 foregoing sections. Yet these drivers are interlinked via multiple ecological and anthropogenic  
988 processes. For example, increasing temperature can facilitate the successful establishment  
989 of invasive species; and land use intensification and the expansion of monocultures lead to an  
990 increased use of chemical inputs (fertilizers and pesticides). These drivers can then operate  
991 in the same ecosystem and could have additive, synergistic and antagonistic effects (Crain et

992 al. 2008) on the behaviour and developmental capacity of herbivores, and on parasitoids,  
993 modulating their role as biocontrol agents. In this section we aim to consider the important  
994 forms of interaction among global change drivers and provide relevant examples.

995 Overall, interactions among drivers seem to have mainly synergistic effects on  
996 biodiversity (Sala et al. 2000) although a more recent meta-analysis found that only 20 of 57  
997 experiments analysed identified synergistic interactions, with the remainder being non-  
998 synergistic effects (24 antagonistic and 13 additive) on biodiversity (Darling and Côté, 2008).  
999 Simple and predictable additive effects were rare, suggesting more complex interaction  
1000 outcomes are commonplace (Darling and Côté, 2008). In our review, general trends indicate  
1001 that some global change drivers will enhance the development of many herbivore species,  
1002 including fertilisation and landscape simplification, though eCO<sub>2</sub> and pesticide use could have  
1003 the opposite effect. By contrast, effects of these global change drivers on parasitoids - the  
1004 third trophic level - are more difficult to predict, being highly variable and species-dependent.  
1005 These interactive effects remain largely untested (Moon and Stiling 2000; Johns and Hughes  
1006 2002) and therefore represent a challenge in understanding how further global change will  
1007 impact the delivery of ecosystem services.

1008

#### 1009 **4.1. Climate change interacting with land use change intensification**

1010 While global change drivers frequently interact, several existing studies have demonstrated  
1011 that climate is the dominant driver of change for parasitism. Parasitoid abundance (Johnson  
1012 et al. 2011) or species richness (Corcos et al. 2018) increased with temperature and  
1013 decreased under drought, but were not modulated in either study by habitat diversity even  
1014 though a higher diversity of floral resources is known to support higher density and diversity  
1015 of parasitoids (Tews et al. 2004). Parasitoid distribution and species richness are highly  
1016 dependent on the distributions of their hosts, and this may be more strongly impacted by  
1017 temperature than by habitat diversity (Corcos et al. 2018; Johnson et al. 2011); suggesting  
1018 that changes in climate may override in some cases the positive effect of habitat diversification  
1019 on parasitoid communities. Lakeman-Fraser and Ewers (2014) have shown that there were  
1020 positive effects between habitat fragmentation and latitude (as a surrogate for temperature)  
1021 on both the herbivores and parasitoid density but negative effects on the herbivory and attack  
1022 rate. These results suggest that the effects of global changes on parasitoids are primarily the  
1023 result of bottom-up processes. Synergistic effects of warming temperature and nitrogen input  
1024 have also been shown to promote both herbivores and parasitoids densities by increasing  
1025 host availability and size (i.e., quality) promoting parasitoid oviposition and development (De  
1026 Sassi et al. 2012). By contrast, only the negative impact of the most severe level of drought  
1027 stress in interaction with fertiliser cascaded up to parasitoid level (Shehzad et al. 2020),  
1028 suggesting that only major impacts of global change on hosts may transmit to their parasitoids.

1029 Ewald et al. 2015 demonstrated that braconid parasitoid abundances in cereal fields  
1030 responded positively to hot/dry years and negatively to cold/wet years, but pesticide was the  
1031 most important factor explaining the population trend. This suggests that a decrease in the  
1032 use of pesticides could reduce the impact of climate change on the parasitoid population  
1033 density. The effects of crop fertilizer use on herbivore and parasitoid populations may also  
1034 modify the impact of the increased atmospheric concentration of CO<sub>2</sub> causing climate change  
1035 on trophic interactions. For example, increased atmospheric CO<sub>2</sub> is associated with lower  
1036 concentrations of nitrogen and other minerals in crop plants (Myers et al. 2014); greater use  
1037 of fertilizer inputs may reduce these impacts of increased CO<sub>2</sub> on plant quality (Chen et al.  
1038 2010).

1039         Together with the multitude of direct and indirect interactions that may occur at species  
1040 and community levels, and effect scales ranging from microhabitat to inter-continental,  
1041 predicting the overall effects of global change on parasitoids is a complex problem. Farmer  
1042 decision-making adds another layer of uncertainty in understanding how global change drivers  
1043 will impact biocontrol in future landscapes. For example, farmers could modify crop varieties  
1044 or species, fertilizer inputs, and irrigation use, to compensate for yield losses or adapt to  
1045 changes in climate (Challinor et al. 2014). These crop management responses could have a  
1046 range of important positive or negative impacts on parasitism including changes in crop  
1047 attractiveness or resistance to herbivores, and changes in habitat availability at the field or  
1048 landscape level. There are opportunities for synergisms, where broader climate change  
1049 adaptation actions enhance biocontrol services. Farmers may seek to diversify agricultural  
1050 production and engage in agri-ecological practices to stabilise their yields and incomes (e.g.,  
1051 Harkness et al. 2021). Crop diversification to spread risk of yield impacts and commodity price  
1052 fluctuations due to climate change is one way for farm management to become more resilient  
1053 (Degani et al. 2019, Haile et al. 2017, Harkness et al. 2021). These additional crops could also  
1054 increase the potential for parasitoid populations to survive and find complementary food and  
1055 shelter resources, whilst providing other ecosystem services such as soil erosion prevention,  
1056 soil biota preservation, pollination services and micro-climate stabilisation (Degani et al. 2019).  
1057 These changes in agricultural practices are therefore aimed at increasing the resistance and  
1058 resilience of agroecosystems to climate change and land use intensification. They will need to  
1059 be applied as soon as possible as we already see strong effects of climate change on  
1060 agricultural production (Haile et al. 2017). Global agricultural policies will need to be put in  
1061 place in order to help farmers switch from one system to another. New research will need to  
1062 be done and new knowledge acquired. This long-term process is therefore urgent to  
1063 implement if we want the agricultural system to be as resilient as possible.

1064

1065



1066 **4.2. Biological invasion facilitated by both climate change and land use intensification**

1067 Global warming may also lead to an increase in biological invasions as an increase in  
1068 temperature can favour the establishment success rate of invasive species immigrating from  
1069 countries with higher temperature. For example, in continental China, a 1°C increase in  
1070 temperature has been associated with a 0.5 species/year increase in the establishment rate  
1071 of invasive alien insects (Huang et al. 2011). The invasion of exotic species relative to global  
1072 warming results in the geographic expansion of the niche of several species from different  
1073 trophic levels migrating simultaneously or in a rapid succession. Such rapid community  
1074 changes could affect local communities. In particular, a laboratory experiment demonstrated  
1075 that the simultaneous arrival of a new herbivore and its parasitoid had a negative effect on the  
1076 survival and parasitism rate of native organisms (Carrasco et al. 2017). Simple and low-  
1077 diversified species networks found in simplified cultivated landscapes may also facilitate the  
1078 successful invasions of introduced organisms due to the large cultivated areas availability and  
1079 the novel enemy-free space lacking coevolved antagonists (David et al. 2017; Smith-Ramesh  
1080 et al. 2017; Despland and Santacruz, 2020). In addition, use of crop fertilizer increased plant  
1081 quality, again facilitating the successful establishment of invasive species in a new  
1082 environment (Han et al. 2014). Overall, effects of land-use intensification and climate change  
1083 have the potential to elevate the risk of invasions by alien organisms that can modify native  
1084 host-parasitoid interactions.

1085

1086 **4.3. Is specificity of organisms the key?**

1087 Parasitoids are specialists in that they generally attack hosts belonging to the same family of  
1088 insect hosts, unlike predators that tend to behave in more generalised way to consume more  
1089 various prey with the principal limit on predation being body size. For this reason, parasitoids  
1090 are preferred over predators in biocontrol programs because the likelihood of non-target  
1091 impacts is reduced and control efficacy on target pest populations is high (Heimpel and Mills,  
1092 2017). However, the host specificity of parasitoids still varies between extreme specialists that  
1093 are only able to develop in a single host species compared to more generalist parasitoids that  
1094 are able to attack hosts belonging to different tribes or even a few families (Godfray 1994).  
1095 Parasitoid specialization can also occur at the plant level where some are able to specialize  
1096 on all potential hosts feeding on a specific host plant (Monticelli et al. 2021).

1097 Our review, demonstrate that the impact of interacting and non-interacting global  
1098 change drivers on parasitoids depends mainly on the effects on their hosts. This is mostly due  
1099 to the strong dependence of a parasitoid on its host as the entire nutritional and physiological  
1100 environment of the immature stage (Godfray 1994). Understanding the effect of global  
1101 changes on parasitoids therefore requires a good understanding of the effects on herbivores  
1102 which both appear to depend on the degree of ecological specialisation (Rand and Tscharrntke,

1103 2007; Tylianakis et al. 2008) (Figure 5). Specialist herbivores, by definition, have coevolved  
1104 with their hosts enabling them to have a high fitness through optimal use of resources and  
1105 circumventing host defenses (e.g., Carolan et al. 2009; Wittstock et al. 2004; Zust and  
1106 Agrawal, 2016). Whether the specialist or generalist is more affected depends on the global  
1107 change driver in question. For example, unlike generalist herbivores, the specialist aphid  
1108 *Acyrtosiphon pisum* is able to produce salivary metalloproteases which break down plant  
1109 defensive proteins even under drought stress enabling its generalist parasitoid to maintain a  
1110 high parasitism rate (Carolan et al. 2009; Nguyen et al. 2018). By contrast, habitat  
1111 fragmentation more strongly impacts habitat specialists than generalists, which are able to  
1112 exploit alternative hosts/habitats in the landscape (Rossetti et al. 2017).

1113

1114 **[Insert Figure 5 here]**

1115 **Figure 5.** Figure 5. Potential scenarios of the impact of different drivers of global change (a:  
1116 climate change, b: land use intensification and c: biological invasions) on (A) populations and  
1117 (B) communities of pests and parasitoids depending on host specificity. (A) Generalist pest  
1118 fitness is directly or indirectly (via host-plants) more strongly affected by global change drivers  
1119 (a-c) compared to specialist pests as the specialist organisms have co-evolved with their  
1120 hosts. (d) Global change (a-c) enhances induction of plant secondary (defence) metabolites  
1121 strongly reducing fitness of generalist pests and parasitoids through lower host (insect or plant)  
1122 quality. (e) Global change does not induce plant secondary metabolites, or the generalist pest  
1123 is able to excrete the toxic compounds, reducing the negative bottom-up effects compared to  
1124 the (d) scenario. (f) Strong coevolution means specialist parasitoids are able to optimise and  
1125 track changes in their host due to global change thereby lessening the impact. (g) Global  
1126 change elevates induction of plant secondary metabolites that specialist pests sequester,  
1127 strongly lowering generalist parasitoid fitness. (h) Global change does not induce secondary  
1128 metabolites, or the specialist pest is able to detoxify, reducing the negative bottom-up effects  
1129 compared to the (g) scenario. (B) Specialist pest communities are affected strongly by global  
1130 change compared to generalist communities because generalist species can switch hosts  
1131 according to their availability. (i) Both generalist and specialist parasitoids persist in the  
1132 modified environment when generalist hosts are affected only slightly by global change,  
1133 although parasitoids that specialize on particular plant species/families may suffer more than  
1134 true generalist parasitoids. (j) Generalist parasitoids switch to the most abundant alternative  
1135 host when their specialist hosts are greatly impacted by global change. (k) Specialist  
1136 parasitoids suffer greatly from global change impacts on specialist hosts. Images sourced from  
1137 thenounproject.com (CC-BY: Ayumi Aya; Baboon designs; Carpe Diem; Denimao; Phạm  
1138 Thanh Lộc; Varvarvarra).

1139

1140 At the population level, we suggest that parasitoids growing in specialist hosts might  
1141 be less impacted by global change drivers that modulate the host physiology, compared to  
1142 parasitoids growing on generalist hosts suffering from those same drivers (Figure 5A, d-f). An  
1143 exception is when global change drivers induce the production of secondary metabolites in  
1144 plants that are toxic to higher trophic levels, since the host specificity of both herbivores and  
1145 parasitoids will dictate their ability to persist in such an environment. Indeed, a specialist  
1146 herbivore will be able to detoxify or sequester these toxic compounds (Heidel-Fischer and  
1147 Vogel, 2015) allowing both generalist and specialist parasitoids (detoxification) or only

1148 specialist parasitoids (sequestration) to maintain their population level (e.g., Chen et al. 2010;  
1149 Krauss et al. 2007; Monticelli et al. 2019; Nguyen et al. 2018; Paudel et al. 2016; Sun et al.  
1150 2020). A generalist herbivore is, however, either capable of excreting toxic compounds  
1151 enabling specialist and generalist parasitoids to develop normally, or they are unable to  
1152 circumvent the toxicity and both their quality as hosts and their population sizes diminish with  
1153 negative consequences for parasitoids (e.g., Francis et al. 2001; Monticelli et al. 2019).

1154         When considering global change drivers impacting the herbivore community (e.g.,  
1155 switch in herbivore species dominance, Mohammed et al. 2019) and parasitoid habitat (e.g.,  
1156 fragmentation and loss of natural habitats), the population of specialist parasitoids that are  
1157 highly dependent on their hosts may be more drastically impacted and may no longer be able  
1158 to regulate pest populations compared to generalist parasitoids which can switch to the most  
1159 dominant host (Elzinga et al. 2007) (Figure 5B, i-k). Regarding invasive species, a generalist  
1160 parasitoid will have an easier time establishing itself in an environment than a specialist  
1161 because it will have a greater number of potential hosts available. On the other hand, a  
1162 parasitoid that is a specialist of a crop pest previously introduced into the same area will have  
1163 a better chance of establishing than a generalist organism because its optimal host will be  
1164 present and potentially in large quantities, if not regulated by a local natural enemy (Monticelli  
1165 et al. 2021).

1166         We could therefore recommend the use of generalist parasitoids in biocontrol  
1167 programs when the herbivore community is modified by global change drivers and when the  
1168 herbivores are themselves generalists because they may suffer from effect of these drivers  
1169 while generalist parasitoid may be able to persist in such environment by consuming various  
1170 host species. Biological control programs involving crop plants consumed by specialist  
1171 herbivores may then favour both specialist and generalist organisms if plant quality is not  
1172 impacted and only specialist parasitoids if the crop plant is known to produce secondary  
1173 metabolites under stress. Therefore, the host specificity of both the parasitoid and their hosts  
1174 should be considered, and further assessments made to determine whether specialisation is  
1175 a key factor in predicting the effects of global change on parasitism with greater accuracy.

1176

## 1177 **5. CONCLUSION**

1178 Our review shows that parasitism and biocontrol services in future landscapes are highly likely  
1179 to be impacted by global change drivers. Land use **intensification** is associated with the use  
1180 of large proportions of land masses for agriculture which is supported by high levels of inputs.  
1181 For the associated phenomena of habitat loss, erosion of biodiversity and agrochemical use  
1182 there is strong evidence of adverse effects on parasitoid individuals, assemblages and  
1183 function though there is a paucity of research on the effects on hyperparasitoids (parasitoids

1184 that attack parasitoids) (Figure 6). Further effort to confirm these effects under field conditions  
1185 is still needed to solidify the conclusions and identify the underlying mechanisms (Figure 6).  
1186 Loss of biocontrol services as a result of intensification can entrench usage of insecticides  
1187 though there is growing research efforts into habitat manipulation approaches at the field or  
1188 landscape scale to reinstate parasitoid function. **Climate change** can affect parasitoids  
1189 directly, affecting aspects such as development time and survival, as well as indirectly via  
1190 phenological and other effects on their hosts, on endosymbionts, and on the first trophic level  
1191 via changes to plant chemistry and host-plant defences including herbivore-induced plant  
1192 volatiles (HIPVs). Whilst major, direct effects are often well studied, the complexity of potential  
1193 community level interaction permutations lead to many knowledge gaps and impaired capacity  
1194 to predict the effects of climate change (Figure 6). **Biological invasions** have increased  
1195 dramatically with increased human travel and trade, introducing alien species to vulnerable  
1196 recipient regions that were formerly isolated and with incompletely occupied niches. In this  
1197 context, parasitoid use in biocontrol is especially important to combat host (pest) insects that  
1198 have previously been translocated and released from control by enemies from their native  
1199 range. But the effects of alien species are often not easily remedied and include negative  
1200 effects on native parasitoids when, for example, an invasive herbivore triggers the production  
1201 of HIPVs that are not recognised by native parasitoids and even disrupts their capacity to  
1202 utilise native hosts (Figure 6).

1203 Impact of global change drivers on biodiversity loss are biome-dependent and  
1204 increased land use appears to be the driver with the strongest impact, followed by climate  
1205 change, nitrogen use, and biological invasions (IPBES 2019). When considering the impact of  
1206 global change drivers on parasitoids and their ability to regulate pest populations, it would  
1207 appear that the major driver is climate change represented by an increase in temperature.  
1208 **Potentially important interactions** can occur among each of the three major forms of global  
1209 change. For example, regional temperature increase resulting from climate change can  
1210 facilitate invasions; and the effects of temperature can affect biological responses to  
1211 agricultural inputs such as nitrogen. A major challenge for ecologists seeking to understand  
1212 the extent of global change phenomena is the multitude of direct and indirect interactions that  
1213 may occur at species and community levels. Simple, predictable additive effects appear to be  
1214 rare, and difficulties in making predictions are compounded by the fact that effects can occur  
1215 at spatial scales ranging from microhabitat to biome (Figure 6). Addressing this challenge in  
1216 future studies might be made more tractable by focusing on parasitoids and the biocontrol  
1217 services they provide. The high level of host specificity generally exhibited by parasitoids  
1218 simplifies the extent of potential interactions and makes them a useful taxon for studies of  
1219 wider effects on other taxa. It is, however, rarely considered and further studies and reviews  
1220 incorporating parasitoid host specificity as a key driver explaining the impact of global change

1221 drivers on parasitoids and their role as biocontrol agents are therefore needed (Figure 6).  
1222 Moreover, the long-recognised economic value of parasitoids in biocontrol programs, some  
1223 dating back well over a century, provides both the incentive to invest in research and a rich  
1224 evidence base from which effects on other taxa may be predicted.

1225

1226 **[Insert Figure 6 here]**

1227 **Figure 6. Confidence in the evidence-base for impacts on host-parasitoid interactions**  
1228 **of** global change drivers, their interactions, and the role of organism specificity in modulating  
1229 those impacts. The degree of confidence in each impact (black dot) is based on the quantity  
1230 and quality of the evidence in the literature reviewed, and the level of agreement between  
1231 studies using a four-box model for the qualitative communication of confidence (IPBES, 2019).  
1232 Confidence increases towards the top-right corner as suggested by the increasing strength of  
1233 shading. The terms are: Well established: comprehensive meta-analysis or other synthesis or  
1234 multiple independent studies that agree. Established but incomplete: general agreement  
1235 although only a limited number of studies exist; no comprehensive synthesis and/or the studies  
1236 that exist address the question imprecisely. Unresolved: multiple independent studies exist  
1237 but conclusions do not agree. Inconclusive: limited evidence, recognizing major knowledge  
1238 gaps.

1239

1240 **GLOSSARY**

1241 **Bottom-up effect:** the bottom-up effect is defined as the effect occurring from lower trophic  
1242 levels affecting the higher trophic level.

1243 **Conventional agricultural intensification:** Mechanized livestock management on an  
1244 industrial scale and large-scale monocultures in simplified rotations of high-yielding varieties  
1245 (including GMOs) that are dependent on agricultural inputs (fertilizers, pesticides).

1246 **Diploid:** Diploid organisms have chromosomes in pairs ( $2n$  chromosomes). Haploid  
1247 organisms have chromosomes in single copies ( $n$  chromosomes).

1248 **Ecosystem services:** Benefits from ecosystems including provisioning services or goods  
1249 (e.g., food, timber, water), essential regulating services mediated by biodiversity (e.g., crop  
1250 pollination, soil erosion prevention, water purification), and cultural services (e.g., recreation,  
1251 sense of place).

1252 **Food chain:** sequence of transfers of matter and energy in the form of food from organism to  
1253 organism.

1254 **Food web:** interconnection of food chains.

1255 **Haplodiploid:** Haplodiploidy characterizes a sex-determination mode in which males develop  
1256 from an unfertilized egg and females from a fertilized egg.

1257 **Organism fitness:** describes individual reproductive success.

1258 **Host specificity:** both the range and diversity of host species.

1259 **Idiobiont:** female parasitoid kills or permanently paralyzes the host during oviposition, thus  
1260 stopping its development.

1261 **Integrated pest management:** Pesticides should be used as a last resort and only when an  
1262 economic threshold of pest damage has been crossed. The use of less toxic products such  
1263 as biocontrol should be favored.

1264 **Inundative biocontrol:** release of large numbers of mass-produced biological control agents  
1265 to reduce the population of a pest.

1266 **Kairomones:** substance produced by a living being (transmitter), released into the  
1267 environment, which triggers a response in another species (receiver), providing a benefit to  
1268 the latter.

1269 **Koinobiont:** a parasitoid whose host continues to feed and grow after parasitisation.

1270 **Landscape composition:** landscape spatial characteristics studied when measuring the  
1271 arrangements, the positions and the orientations of the different landscape patches.

1272 **Landscape configuration:** variability and abundance of the different landscape attributes.

1273 **Phenology:** science that studies the influence of climatic variations on periodic phenomena  
1274 in the life of organisms.

1275 **Plant inter-specific diversity:** refers to plant species diversity.

1276 **Plant intra-specific diversity:** refers to plant genotypic or phenotypic diversity.

1277 **Pro-ovigenic:** eggs available for oviposition by pro-ovigenic parasitoids are mature at the time  
1278 of emergence or mature very quickly after emergence.

1279 **Synovigenic:** the maturation of the eggs is carried out throughout the life of the adult and the  
1280 number of eggs produced depends on carbohydrate sources.

1281 **Top-down regulation:** the top-down force refers to the impact of the higher trophic level  
1282 regulating the lower trophic level.

1283

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