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1 **Sublethal pesticide exposure in non-target terrestrial ecosystems: from known effects on**
2 **individuals to potential consequences on trophic interactions and network functioning**

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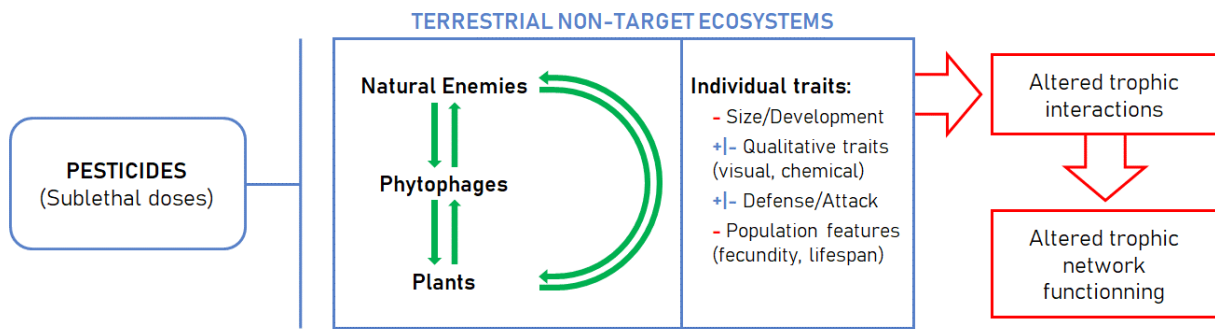
17 **Abstract**

18 Over the last decades, the intensification of agriculture has resulted in an increasing use of
19 pesticides, which has led to widespread contamination of non-target ecosystems in agricultural
20 landscapes. Plants and arthropods inhabiting these systems are therefore chronically exposed
21 to, at least, low levels of pesticides through direct pesticide drift, but also through the
22 contamination of their nutrient sources (e.g. soil water or host/prey tissues). Pesticides
23 (herbicides, acaricides/insecticides and fungicides) are chemical substances used to control
24 pests, such as weeds, phytophagous arthropods and pathogenic microorganisms. These
25 molecules are designed to disturb specific physiological mechanisms and induce mortality in
26 targeted organisms. However, under sublethal exposure, pesticides also affect biological
27 processes including metabolism, development, reproduction or inter-specific interactions even
28 in organisms that do not possess the molecular target of the pesticide. Despite the broad current
29 knowledge on sublethal effects of pesticides on organisms, their adverse effects on trophic
30 interactions are less investigated, especially within terrestrial trophic networks. In this review,
31 we provide an overview of the effects, both target and non-target, of sublethal exposures to
32 pesticides on traits involved in trophic interactions between plants, phytophagous insects and
33 their natural enemies. We also discuss how these effects may impact ecosystem functioning by
34 analyzing studies investigating the responses of Plant-Phytophage-Natural enemy trophic
35 networks to pesticides. Finally, we highlight the current challenges and research prospects in
36 the understanding of the effects of pesticides on trophic interactions and networks in non-target
37 terrestrial ecosystems.

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44 **Graphical abstract**

45

46 **1. Introduction**

47 The capacity of pesticides to increase yield and to regulate crop production, their low cost and
 48 easy usage have contributed to their worldwide spread (Popp et al., 2013). This expansion of
 49 pesticide use, urged by agrochemical industries, led to a shift in agricultural practices, rooting
 50 pesticides as a standard and unavoidable solution for efficient food production (Clapp, 2021).
 51 This technological lock-in in agricultural activities has led to the global current consumption of
 52 two to three million tons of pesticides annually (Popp et al., 2013; Sharma et al., 2019).
 53 Pesticides are chemical substances classified into three main categories, herbicides,
 54 insecticides/acaricides and fungicides that control pests, such as weeds, phytophagous
 55 arthropods and pathogenic fungi, respectively. Each category includes several modes of action
 56 designed to target specific proteins and related physiological or biochemical processes. In
 57 addition to the rising concern of resistant pest outbreaks that make pesticides less efficient (Bass
 58 et al., 2015; Neve et al., 2014), a major concern relative to pesticide use is the wide
 59 contamination of terrestrial and aquatic ecosystems (Arias-Estévez et al., 2008; Björklund et
 60 al., 2011; Silva et al., 2019).

61 In agricultural and related adjacent ecosystems, trophic systems involving plants, phytophages
 62 and their arthropod natural enemies have great ecological and economic importance (Gurr et
 63 al., 2003; Ives et al., 2000; Wilby and Thomas, 2002). In fact, several phytophagous arthropods
 64 are agricultural pests, annually causing crop losses ranging from 5 to 50% (Gurr et al., 2003;

65 Oliveira et al., 2014). Natural enemies, whether they are predatory arthropods or parasitoid
66 insects, induce the death of phytophagous insects by killing them either directly, or indirectly,
67 as a result of their development on or into their hosts (Eggleton and Gaston, 1990). These Plant-
68 Phytophage-Natural enemy (hereafter mentioned as PPNe) trophic systems are based on
69 nutrient and energy flows (nitrogen compounds, sugars, lipids, water) circulating vertically
70 from a trophic level to another (Stam et al., 2014). Species within these systems also interact
71 through chemical signals involving non-volatile and volatile organic compounds (VOCs)
72 perceived by upper trophic levels (Stam et al., 2014; Unsicker et al., 2009). The tight links
73 between plants, phytophagous insects and natural enemies lead to bottom-up and top-down
74 regulations of populations through the modulation of abundance and/or quality of interacting
75 species between trophic levels. For example, a decrease in plant quality can reduce the fitness
76 of phytophagous insects and therefore their availability and/or quality as hosts/preys for natural
77 enemies (Bottom-up regulation; Stenberg, 2015; Zaugg et al., 2013). On the other hand, natural
78 enemies can reduce phytophage populations to densities at which plants experience low levels
79 of herbivory and therefore display an increased fitness (Top-down regulation ; Halaj and Wise,
80 2001; Zaugg et al., 2013). Such capacity of natural enemies to improve yield is crucial for
81 agrosystems and is used in biocontrol strategies (Roudine et al., 2023; Rutledge et al., 2004;
82 Stiling and Cornelissen, 2005). This regulation process also relies on mutualistic interactions
83 between plants and natural enemies, plants providing protective habitats, food subsidies, and
84 attractive signals allowing natural enemies to increase their efficiency to control pests (Quispe
85 et al., 2017; Tylianakis et al., 2004; Unsicker et al., 2009).

86 In agricultural landscapes, terrestrial PPNe trophic systems are chronically exposed to a wide
87 diversity of pesticides and related degradation products, either directly in crop fields or in non-
88 target adjacent refuge ecosystems such as field margins, vegetated buffer strips, or flowering
89 strips (Björklund et al., 2011; Krutz et al., 2005; Serra et al., 2013). These contaminations may

90 occur through spray drift during application or through subsequent runoffs in soil water (Loewy
91 et al., 2011). On the one hand, edaphic contaminations resulting from leaching lead to exposure
92 and contamination of the trophic system through pesticide transfer from the plant to upper
93 trophic levels (Calvo-Agudo et al., 2019; Goulson, 2013; Stapel et al., 2000). On the other hand,
94 spray-drift leads to direct deposition of pesticides onto organisms, and consequently to tissue
95 contamination due to diffusion through plants' or insects' cuticle (Balabanidou et al., 2018;
96 Wang and Liu, 2007).

97 Numerous studies on terrestrial PPNe organisms reported the effects of high doses of pesticides,
98 mainly field application rates, and focused on target-related effects, i.e. the effects on the
99 specific biological processes targeted by pesticides in the targeted phyla (e.g., herbicides
100 inhibiting photosynthesis in plants, insecticides inhibiting nervous activity in insects) (Guedes
101 et al., 2016). Many studies also examined the effects of a wide range of pesticides at lower
102 doses on target organisms and, to a lesser extent, on non-target organisms, among various taxa
103 (reviewed in Parween et al., 2016; Teder and Knapp, 2019; Table S1). These lower doses
104 usually remain non-lethal or sublethal (i.e. leaving a majority of individuals alive), and therefore
105 lead to more discrete effects such as physiological disturbances, impairments in development
106 and reproduction, or changes in behavior. However, reviews on the effects of pesticides rarely
107 focus on species interactions and trophic system functioning, especially in terrestrial food webs,
108 despite available empirical data on individuals' traits that are key to trophic interactions. Our
109 aim is to review the effects of sublethal and non-lethal pesticide exposures on PPNe food webs
110 by analyzing relevant features of each trophic level in the context of trophic interactions and,
111 when available, the responses of interacting organisms (Table S1). Indeed, understanding the
112 impacts of a stress on biotic interactions is essential to link individual trait responses to
113 community/food web responses (Gross et al., 2009; Schmitz et al., 2015). This review provides
114 a better understanding of the cascading effects of pesticides between trophic levels and of the

115 consequences on trophic system functioning. First, it focuses on the few studies examining the
116 effects of pesticides on PPNe networks, mainly at high doses. The review then reports how
117 exposures to lower, sublethal doses of pesticides may alter host/prey selection by phytophages
118 and natural enemies and, more generally, how they may modulate the emission of signals that
119 regulate interactions between species. Then, it analyzes how sublethal pesticide exposures may
120 affect attack and defense mechanisms of PPNe organisms, and how they impact hosts'/preys'
121 nutritional value while considering the consequences on upper trophic levels. It last assesses
122 how such exposures may affect the dynamics of the populations of each trophic level and
123 therefore of the trophic system functioning. It finally discusses the implications of the outlined
124 results in the scope of agriculture, pesticide use and pest management strategies.

125 **2. Methodology (509 words)**

126 To identify the studies investigating the effect of pesticides on PPNe interactions and complete
127 trophic networks, a first literature search was carried out by using keyword-based screening in
128 the publication databases (Google scholar, web of knowledge, etc.): pesticides (OR herbicide
129 OR insecticide OR fungicide) AND trophic interaction (OR trophic network OR trophic chain).
130 Then, a more specific literature search was performed to identify the studies focusing on non-
131 lethal and sublethal effects at lower doses on single or interacting organisms by using the
132 following keywords: pesticides (OR herbicide OR insecticide OR fungicide) AND low (OR
133 non-lethal OR sublethal OR residual) AND dose (OR concentration OR level).

134 This screening of the literature allowed to collect a panel of studies ranging from 1970 to 2023
135 that were then sorted according to several criteria. First, only publications assessing the
136 responses of land plants, terrestrial herbivorous arthropods and/or arthropod natural enemies
137 were kept. Second, empirical studies using ecologically relevant exposure routes for
138 investigating consequences on trophic interactions (i.e. through food consumption for insects
139 or root uptake for plants) were selected. Third, publications investigating traits relevant in the

140 scope of trophic interactions (cues for other trophic levels, attack/defense mechanisms,
141 metabolism and physiology related to quality as hosts, population features) or directly assessing
142 the responses of interacting organisms to pesticides were considered. This procedure excluded
143 numerous studies that only assessed survival/damage responses of organisms to pesticide
144 exposure such as standardized dose-response studies for ecotoxicological assays. Finally,
145 publications investigating pesticide effects on organisms surviving doses inducing high
146 mortality rates in arthropods ($>LC_{30}$ i.e. above the concentration inducing 30% of mortality
147 within the population) or high damages/impairments in plants ($>EC_{30}$ i.e. above the
148 concentration inducing an effect on individuals within the population) were excluded, even if
149 doses were described as low (Cutler et al., 2022; Jalal et al., 2021). These thresholds of lethality
150 (arthropods) and growth inhibition/damage (plants) are commonly used in ecotoxicological
151 assays and considered relevant to characterize the intensity of pesticide effects on a given
152 species (Callow and Forbes, 2003; Hill et al., 2000). Studies of non-target effects considering
153 high doses, sometimes equivalent to field rates, were conserved as the effects remained mainly
154 sublethal or even non-lethal (García et al., 2002; Saska et al., 2016; Schneider et al., 2009).

155 Selected literature was then categorized by “type of organism”, corresponding to the trophic
156 level on which the study focused, and by the number of interacting trophic levels (Bredeson et
157 al., 2015; Deng et al., 2019; Tran et al., 2004; Yao, 2015; Table S1). For instance, several
158 studies assessed the responses of a single trophic level or of more trophic levels but not
159 necessarily in interaction (Cordeiro et al., 2013; Ricupero et al., 2020). When the responses of
160 different trophic levels were assessed, the study was accounted once for each level (Figure 4,
161 5). In addition, the species, pesticide and dose were filled out for each study. Concerning the
162 effects on traits, they were characterized based on the main highlights summarized in the
163 publication abstract, and categorized following the different sections of this review (Figure 4;
164 Table S1).

165 **3. What can we draw from responses of complete PPNe systems to pesticides at field**
166 **rates?**

167 Most of the current literature on the effects of low pesticide doses focuses on one to two
168 organisms at most, usually in controlled conditions and without involving interactions. Only
169 few studies assessed the effects of low doses of pesticides on interacting organisms and only
170 two focused on complete PPNe trophic systems (Table S1; Bredeson et al., 2015; Uhl et al.,
171 2015). There are a few more studies investigating the effects of pesticides on PPNe systems at
172 field doses, which are generally partially lethal to one organism of the network (Table S1).
173 Here, we summarize the effects of pesticides on complete PPNe trophic systems, to better
174 understand how pesticides could affect their functioning.

175 Studies carried out on various PPNe systems investigated the effects of insecticides at field rates
176 (Bommarco et al., 2011; Calvo-Agudo et al., 2019; Douglas et al., 2015; Kampfraath et al.,
177 2017; Zhang et al., 2016) but also at lower doses (Bredeson et al., 2015; Uhl et al., 2015).
178 Imidacloprid applied on soil at field rates, reduced both the fitness of the phytophagous insect,
179 *Nemobius sylvestris* (Orthoptera: Trigonidiidae), feeding on *Fragaria vesca* plantlets
180 (Rosaceae) and the predation efficiency of its spider natural enemy, *Pisaura mirabilis* (Araneae:
181 Pisauridae) (Uhl et al., 2015). Similar effects were found in response to lower rates of
182 insecticides, equivalent to those found in field margins, suggesting that insecticides may induce
183 negative effects at both field application and residual levels (Bredeson et al., 2015; Uhl et al.,
184 2015). Several studies carried out on various PPNe models however showed that edaphic
185 exposure to field-rate insecticides could significantly reduce plant biomass and fitness as well
186 as natural enemy efficiency without affecting phytophages (Bommarco et al., 2011; Douglas et
187 al., 2015; Kampfraath et al., 2017). This bypass is thought to be due to a lower sensitivity of
188 phytophages to chemical stress compared to their natural enemies (Jonsson et al., 2012;
189 Monsreal-Ceballos et al., 2018). Indeed, phytophages are frequently exposed to natural toxic

190 compounds (see section 5.2.1.2) which often leads to increased pesticide tolerance, mostly
191 through detoxication or sequestration mechanisms (Alyokhin and Chen, 2017; Heckel, 2014).
192 Nevertheless, opposite effects were also reported in one field study on a wheat-aphid-parasitoid
193 system, where insecticide seed coating decreased aphid infestation with no significant impact
194 on ladybird, hoverfly and parasitoid populations (Zhang et al., 2016). In addition, sequestration
195 and accumulation of insecticides or of their degradation products in specific tissues or
196 byproducts of phytophages may lead to an acute exposure of natural enemies. Calvo-Agudo et
197 al. (2019) observed a negative effect of plant exposure to insecticides on parasitoid fitness
198 through pesticide circulation from the plant up to aphid honeydew.

199 In the meantime, a few field studies focused on the effects of herbicides on arthropod
200 communities, to assess their non-target effects on trophic networks (Albajes et al., 2009;
201 Atwood et al., 2018; Kampfraath et al., 2017). Glyphosate treatment in herbicide-tolerant corn
202 fields led to significant shifts in both primary and secondary consumer communities, which
203 could ultimately disturb ecosystem functioning (Albajes et al., 2009). While leafhopper and
204 aphid phytophagous insects as well as mymarid parasitoids were more abundant on herbicide-
205 treated plots, phytophagous thrips and ichneumonid parasitoids were predominant in untreated
206 plots. Moreover, natural enemies were significantly harmed by an herbicide (2,6-
207 dichlorobenzonitrile, DCBN), either through bottom-up effects or directly *via* non-target effects
208 of the herbicide and its degradation products, while phytophagous insects such as aphids
209 seemed to be much less affected (Kampfraath et al., 2017).

210 Most of these studies underline that, in complete PPNe systems, exposure of plants to field rates
211 of pesticides can lead to deleterious effects on phytophages, but mostly on natural enemies,
212 even when they are exposed only through the food chain (Calvo-Agudo et al., 2019; Douglas
213 et al., 2015; Kampfraath et al., 2017). However, depending on the considered molecule and its
214 dose, the effects observed can strongly differ in terms of traits, species, and trophic level

215 affected. It thus seems that, even though pesticide effects are still observed under lower rates
216 of pesticide exposure (Bredeson et al., 2015; Uhl et al., 2015), studies at field rates are not
217 sufficient to provide a comprehensive understanding of how terrestrial trophic systems react to
218 sublethal doses of pesticides. Due to the scarcity of studies on complete PPNe systems under
219 low pesticide exposure, and the bias toward studies on insecticides compared to other pesticides
220 (Table S1), it is necessary to consider the numerous studies carried out on single organisms or
221 2-partner interaction systems exposed to sublethal rates of pesticides to better understand how
222 they affect trophic interactions. This can be achieved by focusing on pesticide effects on traits
223 that shape interactions within trophic networks (e.g. host/prey cues for the upper trophic level,
224 attack/defense mechanisms, host/prey quality...).

225 **4. How sublethal doses of pesticides affect cues for patch and host/prey selection within**
226 **PPNe systems: from the emission of chemical and physical cues to their perception**

227 **4.1. Pesticide effects on olfactory cues in plants and phytophages**

228 Plants emit Volatile Organic Compounds (VOCs) in species specific mixtures characterized by
229 their composition and concentration (Aartsma, 2017; Anderson and Anton, 2014). These
230 cocktails of volatile compounds give cues to arthropods, including phytophages and natural
231 enemies, about the location and physiological state of plants. Moreover, under phytophagy,
232 VOC profiles can change due to active defense responses from plants. Their effects range from
233 phytophage repelling to natural enemy attraction (Aartsma, 2017; Bernasconi et al., 1998;
234 Clavijo McCormick et al., 2012; Das et al., 2013; Heil, 2008; Moraes et al., 2001; Sarkar et al.,
235 2014). Insects also emit VOCs, such as pheromones involved in intraspecific communication
236 (e.g. sexual, aggregation and alarm) and kairomones associated to activity byproducts (e.g.
237 feces and secretions such as honeydew), that can be used by natural enemies for host/prey
238 location and choice (Benelli et al., 2014; Lewis et al., 1976) . Here, we report how low doses
239 of pesticides alter olfactory cues emitted by plants and phytophages, and how they disturb the
240 perception of these cues by natural enemies.

241 Sublethal doses of pesticides alter the spectrum of VOCs emitted under phytophagy and
242 therefore disrupt attraction of natural enemies (Figure 1). This can occur through their impact
243 on plant metabolism. For example, exposure of maize to non-lethal, field rates of glyphosate
244 led to a significant decrease in the emission of shikimic acid derivatives such as indole, known
245 to attract natural enemies (Aljbory and Chen, 2018; D'Alessandro et al., 2006). However,
246 several studies underlined that herbicides could also increase herbivore-induced VOC
247 production by plants and attract natural enemies (Rao, 1996; Rao et al., 1999; Xin et al., 2012).
248 Indeed, low doses of 2,4-Dichlorophenoxyacetic acid (2-4D), an herbicide acting as homolog
249 of auxin phytohormone, strongly promoted defense pathways in rice and led to higher

250 production of defensive VOCs such as the sesquiterpenes (E,E)- α -farnesene and (E)- β -
251 caryophyllene (Xin et al., 2012). Application of 2,4-D therefore increased the attraction of the
252 natural enemies of the leafhopper *Nilaparvata lugens* (Hemiptera: Delphacidae) (Xin et al.,
253 2012). This attraction of natural enemies could occur by directly affecting plant metabolism
254 and related VOC biosynthesis, but also by modulating plant signaling pathways, especially
255 those involved in plant defenses (see section 5.2).

256 Inhibition of phytophage pheromone or kairomone production by pesticides has been rarely
257 documented (Table S1). Exposure to sublethal doses of thiacloprid (neonicotinoid) and
258 azinphosmethyl (organophosphate) insecticides, but also to non-lethal doses of several
259 herbicides such as diclofop, led to a decrease in the quantity of pheromones produced by female
260 moths (Lepidoptera: Tortricidae and Noctuidae) (Navarro-Roldán and Gemeno, 2017; Trimble
261 et al., 2004; Hanin et al., 2008 respectively). Since parasitoids often use sex pheromones to
262 locate their host, a pesticide-induced shift in quantity or quality of these olfactory cues may
263 disrupt host-parasitoid interactions (Hardie et al., 1991; Powell et al., 1993). Concerning
264 kairomones, no study has to our knowledge reported direct effects of pesticides on their
265 production nor their composition. However, given that pesticides can alter insects' metabolism
266 (see section 6.2), the quantity and composition of these insect activity byproducts are also likely
267 to be altered.

268 **4.2. Pesticide effects on visual and contact cues in plants and phytophages**

269 In most arthropod species, visual and contact cues become critical over short distances because
270 VOCs generally do not provide information precise enough for the discrimination of individuals
271 close to each other (Bernays and Chapman, 1994; Morehead and Feener, 2000). Moreover,
272 these additional cues allow to precisely assess the quality of the host/prey (Bernays and
273 Chapman, 1994; Mackauer et al., 1996; Muratori et al., 2006; Prokopy and Owens, 1983).

274 While cues' assessment modalities vary within both phytophages and natural enemies, size
275 remains a determining factor in host/prey choice (Bernays and Chapman, 1994; Mackauer et
276 al., 1996; Muratori et al., 2006). Any detrimental effect of sublethal doses of pesticides on plant
277 and phytophage size could therefore decrease attraction of upper trophic levels and alter trophic
278 interactions (Figure 1, Lauro et al., 2005; Lacoume et al., 2006).

279 Plant growth is inhibited by sublethal rates of herbicides from very different families, including
280 synthetic auxins like 2-4 D, photosynthesis inhibitors like triazines and phenylureas, or even
281 inhibitors of specific metabolic pathways such as glyphosate (Baillard et al., 2021; Boutin et
282 al., 2004; Colquhoun et al., 2012; Florencia et al., 2017; Marrs and Frost, 1997; Mateos-Naranjo
283 and Perez-Martin, 2013; McCown et al., 2018; Ramel et al., 2009; Scholtes et al., 2019; Sulmon
284 et al., 2004). Fungicides and insecticides were also shown to have non-target deleterious effects
285 on plant height and mass, even at low doses (Çavuşoğlu et al., 2012b; Duran et al., 2015; Serra
286 et al., 2013, 2015). An increase of plant growth was however observed punctually, for
287 fungicides from the benzimidazole family, due to pesticide structural similarities with growth-
288 promoting phytohormones such as cytokinins (García et al., 2002; Schruft, 1970; Thomas,
289 1974, 1973).

290 Several pesticides decrease the size of phytophagous insects, even at low doses (Bohnenblust
291 et al., 2013; Daniels et al., 2009; Hahn et al., 2014; Li et al., 2010; Müller, 2017; Müller et al.,
292 2019). For example, exposure to a sublethal dose of thiamethoxam insecticide (neonicotinoid)
293 led to a decrease of *Rhopalosiphum padi* growth (Hemiptera: Aphididae) (Daniels et al., 2009).
294 Such effect on phytophage size was also demonstrated for non-target compounds such as
295 herbicides and fungicides (Bohnenblust et al., 2013; Clements et al., 2018; Hahn et al., 2014)
296 and could be explained by direct but still unknown pesticide actions on phytophage (Clements
297 et al., 2018) and/or by indirect effects related to host plant quality.

298 Among other visual cues used by arthropods for host/prey recognition, color often drives
299 host/prey choice, both by phytophages and natural enemies. For example, chlorophyll and
300 carotenoid contents signal plant quality as a host (high chlorophyll content being attractive and
301 high carotenoid content being repellent ; Archetti, 2000; Sauvion et al., 2013; Schaefer and
302 Rolshausen, 2006; Zhong et al., 2019). For most insects, bright colors often indicate toxicity
303 and pale colors usually reflect poor nutritional status (Langley et al., 2006; Libbrecht et al.,
304 2007; Taylor et al., 2014; Théry and Gomez, 2010). Thus, host/prey color set its attractivity for
305 phytophages and natural enemies (Langley et al., 2006; Libbrecht et al., 2007).

306 Pigment contents contributing to plant color can be modified by pesticides (Table S1, Figure
307 1). For example, sublethal levels of glyphosate reduced chlorophyll contents, leading to
308 yellowing and to decreased phytophage attraction (Mateos-Naranjo and Perez-Martin, 2013;
309 Munoz-Rueda et al., 1986; Serra et al., 2015; Zhong et al., 2019). Similarly, other herbicides
310 inducing leaf bleaching, such as photosynthesis inhibitors of the triazine (e.g. atrazine),
311 phenylurea (e.g. isoproturon), and bipyridyl (e.g. paraquat) families, could also affect host
312 choice by phytophages (Dodge, 1990). Concerning non-target effects, the insecticides
313 cypermethrin and deltamethrin, as well as the fungicide tebuconazole, decreased chlorophyll
314 and carotenoid contents in several plant species (Çavuşoğlu et al., 2012a; Duran et al., 2015;
315 Serra et al., 2013). However, these effects seem at least species-dependent, as low doses of
316 tebuconazole were found to increase chlorophyll and carotenoid contents in *Lolium perenne*
317 (Poaceae) (Serra et al., 2015).

318 In insects, color results from endogenous compounds synthesized from small metabolites such
319 as tryptophan or dopamine (melanin and ommochromes), or from exogenous compounds
320 mainly acquired from plants (carotenoids and flavonoids) (Hashimoto et al., 2021; Moran and
321 Jarvik, 2010; Sloan and Moran, 2012). To date, no direct effect of pesticides on insect color has
322 been recorded. However, stresses such as starvation and cold temperature alter body color to

323 paler shades in aphids due to energy reallocation processes (Wang et al., 2019; L. Zhang et al.,
324 2021). It is thus possible that sublethal doses of pesticides could lead to similar body color
325 alterations because of the energetic cost related to chemical stress responses (Castañeda et al.,
326 2009).

327 Many natural enemies, and especially predators, also rely on movement to find hosts/prey
328 (Théry and Gomez, 2010). Most neurotoxic insecticides induce paralysis or death at field rates
329 and decrease insect mobility at sublethal doses, which could reduce their localization by natural
330 enemies (Boiteau and Osborn, 1997; Jung et al., 2018; Lee et al., 2013; Silva Barros et al.,
331 2020). For example, doses between LC_{10} and LC_{30} of the neurotoxic insecticides carbaryl,
332 chlorpyrifos and thiacloprid led to a significant decrease in the mobility of *Halyomorpha halys*
333 (Hemiptera: Pentatomidae) (Lee et al., 2013). In some rare cases, mobility however increased
334 but only for a short time after an acute sublethal exposure to insecticides such as dianizon and
335 phosmet (Lee et al., 2013).

336 In the last steps of host/prey selection by both phytophages and natural enemies, contact cues,
337 mostly linked to cuticle texture and composition, determine whether or not the host/prey is
338 suitable (Lang and Menzel, 2011; Ramaswamy, 1988; Sauvion et al., 2013). Sublethal doses of
339 pesticides were shown to deeply modify both chemical and structural patterns of plant and
340 insect cuticle, yet the importance of such alteration on trophic interactions remain to be
341 assessed. For example, texture of eucalyptus' leaf cuticle was damaged by drift exposure to
342 commercial formulations of glyphosate, and field rates of the herbicide EPTC altered the
343 composition of epicuticular waxes in *Brassica oleacea* (Brassicaceae) (Flore and Bukovac,
344 1978; Tuffi Santos et al., 2009). The insecticide diflubenzuron, led to an alteration of cuticle
345 elasticity and firmness by inhibiting chitin synthesis and deposition, even at low doses (Ishaaya,
346 2001; Wei et al., 2013). Sublethal doses of a pyrethroid insecticide also induced shifts in the
347 hydrocarbon composition of adult leaf beetles' cuticle (Müller, 2017).

348 In summary, visual and contact cues used by insects for host/prey selection are broadly altered
349 by sublethal doses of pesticides (Figure 1). While target pesticides mainly lead to decreased
350 attractivity, other pesticides often have opposite effects. However, these non-target effects are
351 far less studied (Figure 4), less consistent among the current literature, and the underlying
352 mechanisms are still unknown. Overall, sublethal effects of pesticides on visual and contact
353 cues are likely to disturb trophic interactions by interfering with host/prey recognition/selection,
354 mostly by making exposed organisms less appealing (Figure 1, 3).

355 **4.3. Pesticide effects on cue perception and signal integration**

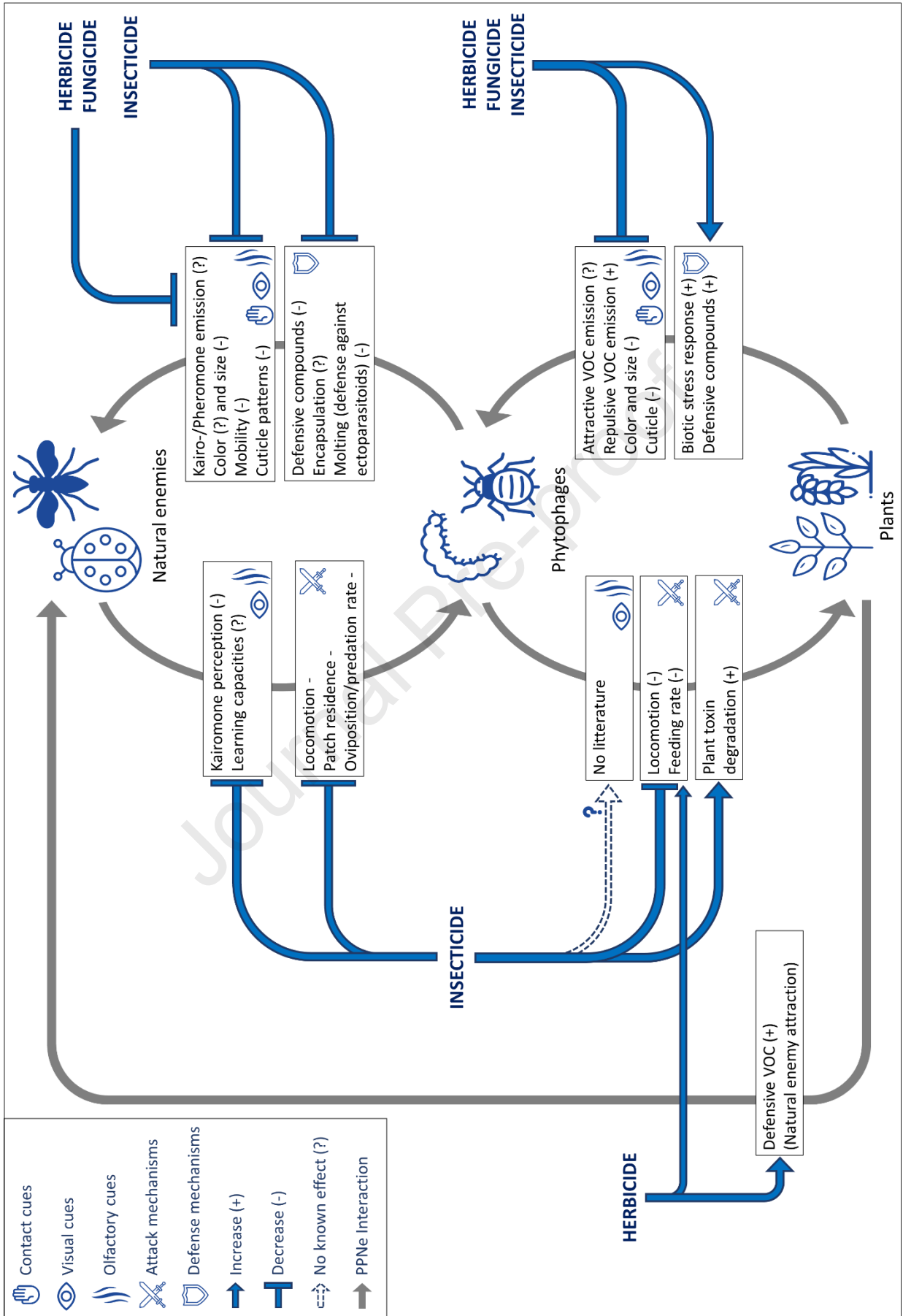
356 The effects of pesticides on the responses of natural enemies to various cues (mostly olfactory)
357 have been thoroughly studied (Figure 1, Table S1). For example, nearly non-lethal doses (<
358 LC₅) of the neonicotinoid imidacloprid significantly reduced the ability of the parasitoid
359 *Nasonia vitripennis* (Hymenoptera: Pteromalidae) to locate its host through olfactory cues
360 (Tappert et al., 2017). Higher sublethal doses however have contrasted outcomes, with exposure
361 to deltamethrin decreasing the time spent on a kairomone patch while chlorpyrifos increased it
362 (Delpuech et al., 2005; Komeza et al., 2001; Salerno et al., 2002). The ability of natural enemies
363 to perceive VOC signals emitted by plants can also be impaired by sublethal doses of pesticides
364 (Liu et al., 2012, 2010; Teodoro et al., 2009). For example, the predatory mite *Iphiseiodes*
365 *zuluagai* (Arachnida: Phytoseiidae) is unable to recognize a plant previously infested by its prey
366 after an exposure to sublethal doses of the acaricide febutatin oxide (Teodoro et al., 2009).
367 Concerning behaviors related to other cue perception, the pyrethroid lambda-cyhalothrin
368 reduced the occurrence of host-tapping behavior by *Neochrysocharis formosa* (Hymenoptera:
369 Eulophidae) and thus its ability to assess host size (Tran et al., 2004).

370 While studies on phytophage olfaction are scarce, insecticides were often shown to reduce
371 pheromone perception, which could underline a general impairment of olfactory faculties
372 (Wang et al., 2011; Zhou et al., 2005). By contrast, the only study investigating the effects of

373 sublethal doses of pesticides on plant VOC perception by phytophages did not report any
374 modification of insect responses to plant odors (Lalouette et al., 2016).

375 Altogether, the results presented in this section underlined that the responses of natural enemies
376 to host/prey signals could be impaired by sublethal exposure to at least insecticides (Table S1,
377 Figure 1, Figure 3). Moreover, since detrimental effects on cue emission (making hosts/preys
378 less appealing) and perception tend to have synergistic outcomes, it seems that sublethal doses
379 of pesticides could effectively alter trophic interactions.

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381 **Figure 1:** Main effects of sublethal doses of pesticides on host/prey recognition mechanisms
382 and attack/defense mechanisms in land plants, phytophages and natural enemies. While grey
383 arrows represent interactions within PPNe networks, blue arrows represent the effects of
384 sublethal doses of pesticides on traits involved in those interactions. Flat-head arrows indicate
385 an overall decrease of the trait, while point-head arrows indicate an increase. Dashed white
386 arrows indicate a lack of knowledge on the effects. The effects of pesticides on each trait,
387 represented by the different pictograms, are indicated in the associated inserts, with (+), (-) and
388 (?) depending on the effect (increase, decrease, no known effect respectively).

389 **5. How sublethal doses of pesticides alter attack and defense mechanisms in organisms** 390 **within trophic networks**

391 **5.1. Pesticide effects on insect attack behaviors**

392 **5.1.1. Phytophage feeding behaviors**

393 Feeding mechanisms in phytophages are well known to be impaired by insecticides, which
394 primary role is to limit phytophagy (Table S1). Whereas some insecticides are specifically
395 designed to prevent feeding (Ishaaya, 2001), neuroactive insecticides, mainly represented by
396 neonicotinoids, generally impair behavior in phytophagous insects (Table S1). For instance,
397 wheat seed treatment with neonicotinoid insecticides reduced both probing and feeding in
398 *Sitobion avenae* (Hemiptera: Aphididae) (Miao et al., 2014). Even at low doses, this decrease
399 in feeding behavior has been observed in many phytophagous insects exposed to a variety of
400 insecticides (Chen et al., 2017; He et al., 2013; Jacobson and Kennedy, 2014; Li et al., 2010;
401 Okano, 2009; Seo, Mi Ja et al., 2009; Stamm et al., 2013; Wolz et al., 2021; Yuan et al., 2017).
402 Moreover, sublethal rates of insecticides can simply affect insect mobility, and therefore their
403 ability to colonize new plants (Boiteau and Osborn, 1997; Lee et al., 2013; Silva Barros et al.,
404 2020). Without impairing nervous activities, pesticides can also have non-target effects on
405 phytophage attack behaviors, even at low doses. For example, the herbicide atrazine induced
406 gut lesions in insects that are thought to increase feeding behavior by a decrease in satiety
407 (Behmer, 2009; Ganassi et al., 1996). Therefore, the non-target effects of other types of
408 pesticides on feeding mechanisms remain to be studied more extensively since they may lead
409 to unexpected increases in feeding behaviors.

410 **5.1.2. Attack and foraging behaviors of natural enemies**

411 Low doses of pesticides can decrease the attack behaviors of predators and parasitoids.
412 Insecticides, by affecting nervous activity, impact prey capture in predators and oviposition
413 rates in parasitoids (Claver et al., 2003; Desneux et al., 2004; Longley and Jepson, 1996;

414 Martinou and Stavrinides, 2015; Shang et al., 2021; Singh et al., 2004; Tooming et al., 2017;
415 Tran et al., 2004; Yao, 2015). For instance, , the predation rate of coccinellid, carabid and mite
416 predators decreased after being sprayed with sublethal levels of neuroactive insecticides
417 (Martinou and Stavrinides, 2015) but also after consuming contaminated preys (Singh et al.,
418 2004; Tooming et al., 2017; Yao, 2015). Sublethal doses of neuroactive insecticides also
419 decrease host parasitism rates of several parasitic wasps (Desneux et al., 2007; Sheng et al.,
420 2021; Stapel et al., 2000; Tran et al., 2004). Despite such effects of neuroactive insecticides
421 could be expected, these results highlight the extent of the action spectrum of these molecules,
422 which goes far beyond the targeted phytophagous species, with significant consequences on
423 trophic interactions (Figure 1). However, to our knowledge, the effects of other pesticides such
424 as fungicides, herbicides, or non-neuroactive insecticides on attack behaviors in natural enemies
425 remain unknown.

426 **5.2. Pesticide effects on host physiological defense mechanisms and enemy virulence**

427 **5.2.1. Plant defenses against phytophages and phytophage counter-attack**

428 Action of phytophagous insects being usually deleterious to plants, plant species evolved
429 mechanisms in order to defend themselves against these negative biotic interactions (War et al.,
430 2012). To counter-attack these mechanisms, phytophages in return can avoid or deter many
431 plant defenses through physiological alteration processes. For instance, several phytophages are
432 able to either degrade or sequestrate plant toxins, therefore suppressing one of the main defenses
433 of their host (Heckel, 2014). Here we review how pesticides can alter herbivore-induced plant
434 defenses and the responses of phytophages to these defense mechanisms.

435 **5.2.1.1. Plant defense mechanisms against phytophages**

436 Constitutive plant defenses include various mechanisms leading to non-preference by
437 phytophages. These mechanisms include physical barriers but also constitutively emitted

438 repellent chemicals. Indeed, some plants emit specific, unappealing VOCs to reduce
439 phytophage attraction, especially among Solanaceae (Unsicker et al., 2009). This mechanism
440 is affected by sublethal doses of herbicides. For example, the herbicide chlorosulfuron
441 decreased the constitutive biosynthesis of unappealing sucrose esters by secretory cells within
442 tobacco trichomes (Kandra and Wagner, 1990). Moreover, sublethal rates of herbicides may
443 alter the efficiency of physical barriers such as trichome density (Levin, 1973). Sublethal doses
444 of carbamate herbicides thus disrupted microtubule formation in *Allium cepa* (Liliaceae), which
445 can lead to reduced trichome growth, as shown in *Arabidopsis thaliana* (Brassicaceae)
446 (Giménez-Albian, 1997; Mathur and Chua, 2000).

447 Antibiosis is an inducible, post-contact or post-consumption defense during which plants alter
448 their chemical and nutritional content in order to affect insect physiology, behavior and survival
449 (Sauvion et al., 2013). Because it requires the production of secondary metabolites not only
450 useless for growth and reproduction but potentially toxic for the plant, this strategy is highly
451 energy consuming, and not constitutive (Prasad, 2022; Ramarosan et al., 2022; Sauvion et al.,
452 2013). Antibiosis mechanisms are generally triggered by molecules called elicitors that are
453 found in the saliva of phytophages, or by signal molecules coming from damaged cell walls.
454 These signals activate two different signaling pathways, either the jasmonate/ethylene pathway
455 or the salicylate pathway, depending on the type of aggressor (chewing insects and sap-sucking
456 insects respectively) (De Vos and Jander, 2009; Thaler et al., 2012). Each response pathway
457 leads to the production of a large array of secondary metabolites and proteins.

458 Salicylate production can be activated by sublethal doses of herbicides (Alberto et al., 2018; Lu
459 et al., 2018) but also by insecticides and fungicides (Bian et al., 2020; Ford et al., 2010). For
460 example, in *Arabidopsis thaliana* (Brassicaceae), several genes involved in plant defense
461 against phytophagy were upregulated under exposure to low doses of the herbicide atrazine
462 (Alberto et al., 2018). Pesticide exposure could therefore act as a defense priming mechanism

463 that may lead to stronger defenses against phytophages, and especially sap-sucking insects
464 (Figure 1). Another argument supporting this hypothesis is that sublethal doses of pesticides
465 increase the emission of defensive VOCs known to be part of the salicylate and
466 jasmonate/ethylene response pathways (Figure 1, Aljbory and Chen, 2018). However, these
467 studies being focused on plants in absence of phytophagy, it remains to be determined if
468 pesticide exposure could increase antibiosis defenses against phytophagous insects and actually
469 reduce phytophagy.

470 Pesticides, and more particularly herbicides, may disrupt plant inducible defenses by affecting
471 the synthesis of secondary metabolites involved in antibiosis. On the one hand, several
472 herbicides such as glyphosate specifically target key metabolic steps, synthesizing precursors
473 of plant defensive compounds, such as flavonoids, alkaloids, phenols or gallic acids (Canal et
474 al., 1987; Deng, 2005; Lydon and Duke, 1988), thus leading to a reduction of defensive
475 compounds such as phenylpropanoids (Hollander and Amrhein, 1980). On the other hand, it
476 seems that defensive compounds such as isoflavones and phenylpropanoids are overproduced
477 in response to generic pesticide stress (i.e. photosynthesis inhibitors, phytohormone analogs,
478 insecticides and fungicides not targeting plant defensive compound metabolic pathways),
479 probably due to the oxidative stress it generates and/or the activation of salicylate/jasmonate
480 signaling pathways as explained above (Dixon and Paiva, 1995; Kömives and Casida, 1982;
481 Landini et al., 2003; Mahdavi et al., 2015; Ramel et al., 2009). For example, the herbicide
482 lactofen, targeting chlorophyll biosynthesis pathway and leading to oxidative stress, increased
483 the levels of defensive isoflavones in soybean (Landini et al., 2003).

484 **5.2.1.2. Phytophage responses to overcome plant defenses**

485 Most phytophagous insects have the ability to cope with toxins secreted by plants, either
486 through sequestration or degradation (Heckel, 2014). Transcriptomic studies analyzing insect's
487 responses to pesticides allow understanding how pesticide exposure and the overcoming of

488 plant defenses interact. For example, in *Sogatella furcifera* (Hemiptera: Delphacidae), an LC₁₅
489 of the insecticide imidacloprid induced an overexpression of several Cytochrome P450
490 monooxygenase genes from the CYP6 subfamily, as part of a pesticide degrading process (Yang
491 et al., 2018). As some of these CYP6 subfamily genes were previously identified in other insect
492 species to be involved in plant toxin detoxification (Rix et al., 2016; Schuler, 1996), pesticide
493 exposure may also allow insects to better cope with plant toxins. From an evolutionary point of
494 view, pesticide detoxication mechanisms observed in phytophages are thought to derive from
495 plant toxin detoxication mechanisms, which could explain the tight links between responses to
496 pesticides and plant toxins (Alyokhin and Chen, 2017).

497 This review underlined both antagonisms and synergisms between responses to pesticides and
498 responses to biotic interactions in plants and insects. However, due to the overlap between some
499 biotic and pesticide stress responses, and with the exception of specific plant metabolism
500 disruptors, it seems that pesticides induce chemical stress response pathways, which may
501 promote at least plant antibiosis and phytophage detoxification processes. Nevertheless, the
502 outcome of plant-insect interactions in this context remains unpredictable and largely
503 undescribed (Figure 1). It is thus crucial to focus more on the effects of pesticides at the scale
504 of defense/counter-attack mechanisms to better understand how sublethal pesticide exposures
505 may reshape plant-phytophage interactions.

506 **5.2.2. Phytophage defenses against natural enemies**

507 Defense mechanisms of phytophagous insects against their natural enemies are slightly
508 different depending on the type of enemy. While defense against parasitoids mainly rely on
509 insect immunity, defense against predators generally mobilizes toxicity or escape strategies
510 (Greeney et al., 2012; Gross, 1993).

511 In most phytophagous insect species, defense against parasitoids is feasible through two
512 different mechanisms depending on the type of parasitism. Immune cells within the
513 hemolymph, called hemocytes, kill the eggs and larvae of endoparasitoids through nodulation
514 or encapsulation (Greeney et al., 2012; Salt, 1970) while defensive behaviors and molting allow
515 phytophages to get rid of the eggs and larvae of ectoparasitoids (Gross, 1993). To our
516 knowledge, no data has been published on the effects of pesticides on the nodulation or
517 encapsulation processes in phytophagous species. However, in non-phytophagous insects,
518 exposure to sublethal doses of insecticides usually reduces the encapsulation/nodulation
519 success (Delpuech et al., 1996; James and Xu, 2012). Furthermore, sublethal doses of toxic
520 plant extracts negatively affected nodulation against a pathogen in the phytophage *Eurygaster*
521 *integriceps* (Heteroptera: Scutellaridae) (Zibae and Bandani, 2010). More data are available
522 concerning molting, which is impaired by growth regulator insecticides (Jia et al., 2022; Meng
523 et al., 2020; W. Zhang et al., 2021). For example, expression of genes involved in ecdysis were
524 repressed by an LC₁₀ of the insecticide broflanilide the, which led to a decreased biosynthesis
525 of molting hormone and, eventually, to failed molting (Jia et al., 2022). While the impact of
526 such impairment on defense against ectoparasitoids was never assessed, failed molting is likely
527 to increase phytophage sensitivity to these natural enemies.

528 In aphids, several facultative endosymbionts are of particular importance in insect defense
529 against various biotic stressors (Baumann, 2005; Engel and Moran, 2013). For example, the
530 bacteria *Hamiltonella defensa* protects the pea aphid *Acyrtosiphon pisum* (Hemiptera:
531 Aphididae) against its main parasitoid *Aphidius ervi* (Hymenoptera: Braconidae) (Oliver et al.,
532 2003). This bacteria is also known to help aphids to cope with insecticides (Li et al., 2021).
533 Thus, despite endosymbiotic communities being deeply altered by pesticides (Shang et al.,
534 2021; Zeng et al., 2020), it is likely that *H. defensa* populations are selected and maintained in
535 aphids under parasitoid pressure and pesticide contaminated environments.

536 The synthesis of secondary metabolites involved in defense against predators might also be
537 affected by pesticides. For example, exposure of larvae of the leaf beetle *Phaedon cochleariae*
538 (Coleoptera: Chrysomelidae) to sublethal doses of lambda-cyhalothrin led to an increased
539 attraction of their ant predator *Myrmica rubra* (Hymenoptera: Formicidae) to their secretions
540 (Müller et al., 2019). The authors hypothesized that it may be due to a reduction in the synthesis
541 of defensive repellent compounds within larval secretions.

542 Altogether, insect defenses, both against parasitoids and predators, seem to be reduced under
543 exposure to sublethal doses of insecticides (Figure 1, Figure 3), yet the effects of other
544 pesticides on this process remain unknown. Moreover, studies on the impact of pesticides on
545 parasitoid virulence (i.e. ability to overcome hosts' defenses) are lacking in order to assess
546 precisely their effects on phytophage-natural enemy interactions.

547

548 **6. How sublethal doses of pesticides alter host nutritional quality and impact the upper** 549 **trophic levels**

550 **6.1. Pesticide effects on plant nutritional quality and impacts on phytophages**

551 From the perspective of phytophagous insects, plant quality is mostly driven by soluble sugar
552 and amino acid contents as well as their bigger counterparts (polysaccharides and proteins). A
553 high-quality plant is usually characterized by a high nitrogen content (i.e. high protein/amino-
554 acid contents) and easily accessible carbon resources (i.e. soluble sugars or storage
555 polysaccharides such as starch). In addition, their contents in essential amino-acids to
556 phytophages (i.e. that they cannot synthesize ; Brodbeck et al., 1987) also condition their quality
557 as host plants. High quality plants may thus attract more phytophages and therefore suffer more
558 damages than low quality plants (Awmack and Leather, 2002; Couture et al., 2010; Lindroth,
559 2010; Sarfraz et al., 2006). However, phytophages may also consume more plant material when
560 poor quality plants fail to provide adequate nutrients, which could be increased by a lower

561 ability of these plants to cope with phytophages' attack (Berner et al., 2005; Lindroth, 2010;
562 Lou and Baldwin, 2004). In this section we review how low doses of pesticides can induce
563 metabolic shifts and modify host quality, and how these changes may affect the upper trophic
564 levels.

565 Host plant quality can be altered by low doses of pesticides (Table S1; Tafoya-Razo et al.,
566 2019). Indeed, whether herbicides, insecticides and fungicides, pesticides induce profound
567 modifications of plant physiology, alter their metabolism, and activate stress responses (Serra
568 et al., 2015; Sulmon et al., 2015).

569 Firstly, plant quality is strongly affected by herbicides disrupting amino-acid biosynthesis.
570 Sublethal doses of glyphosate thus disturb the synthesis of aromatic amino acids in plants
571 (through inhibition of the shikimate pathway), which can consequently alter the acquisition of
572 essential amino acids by phytophages such as phenylalanine, tryptophan and tyrosine (Antonio
573 Carbonari et al., 2014; Brodbeck et al., 1987; Serra et al., 2015, 2013; Vivancos et al., 2011).
574 However, these effects seem to depend on the considered species and timing of exposure. For
575 example, a sublethal dose of glyphosate (10 times below field rates) induced a short-term
576 increase of phenylalanine and tyrosine contents in sugarcane plants (*Saccharum officinarum* :
577 Poaceae), followed by a decrease of these shikimate derivatives after seven days (Antonio
578 Carbonari et al., 2014). In contrast, after seven days, similar glyphosate exposures strongly
579 increased tryptophan contents, another shikimate derivative, in *Cyperus rotundus* (Cyperaceae)
580 (Wang, 2001). Contents in other non-aromatic essential amino-acids also increased in response
581 to glyphosate (Vivancos et al., 2011).

582 Some herbicides do not directly target amino acid biosynthesis pathways but inhibit key steps
583 of primary metabolism, such as photosynthesis and fatty acid biosynthesis, with consequences
584 on metabolite contents (Nemat Alla et al., 2008; Singh et al., 1972; Tafoya-Razo et al., 2019).
585 For example, herbicides inhibiting acetyl-coA carboxylase were found to deeply alter plant

586 metabolite contents, even at doses 10,000 times below the recommended field rate (Tafoya-
587 Razo et al., 2019). More generally, sublethal rates of these herbicides increase soluble amino-
588 acid contents (Hjorth et al., 2006; Nemat Alla et al., 2008; Singh et al., 1972). Some essential
589 amino-acids (i.e. valine, leucine, isoleucine) were however found less abundant in chlorimuron-
590 ethyl treated wheat and maize shoots, underlining the occurrence of herbicide-specific patterns
591 (Nemat Alla et al., 2008). Finally, sublethal levels of dicamba decreased plant global nitrogen
592 contents while, as an auxin analog, this herbicide does not specifically target metabolic
593 processes (Bohnenblust et al., 2013).

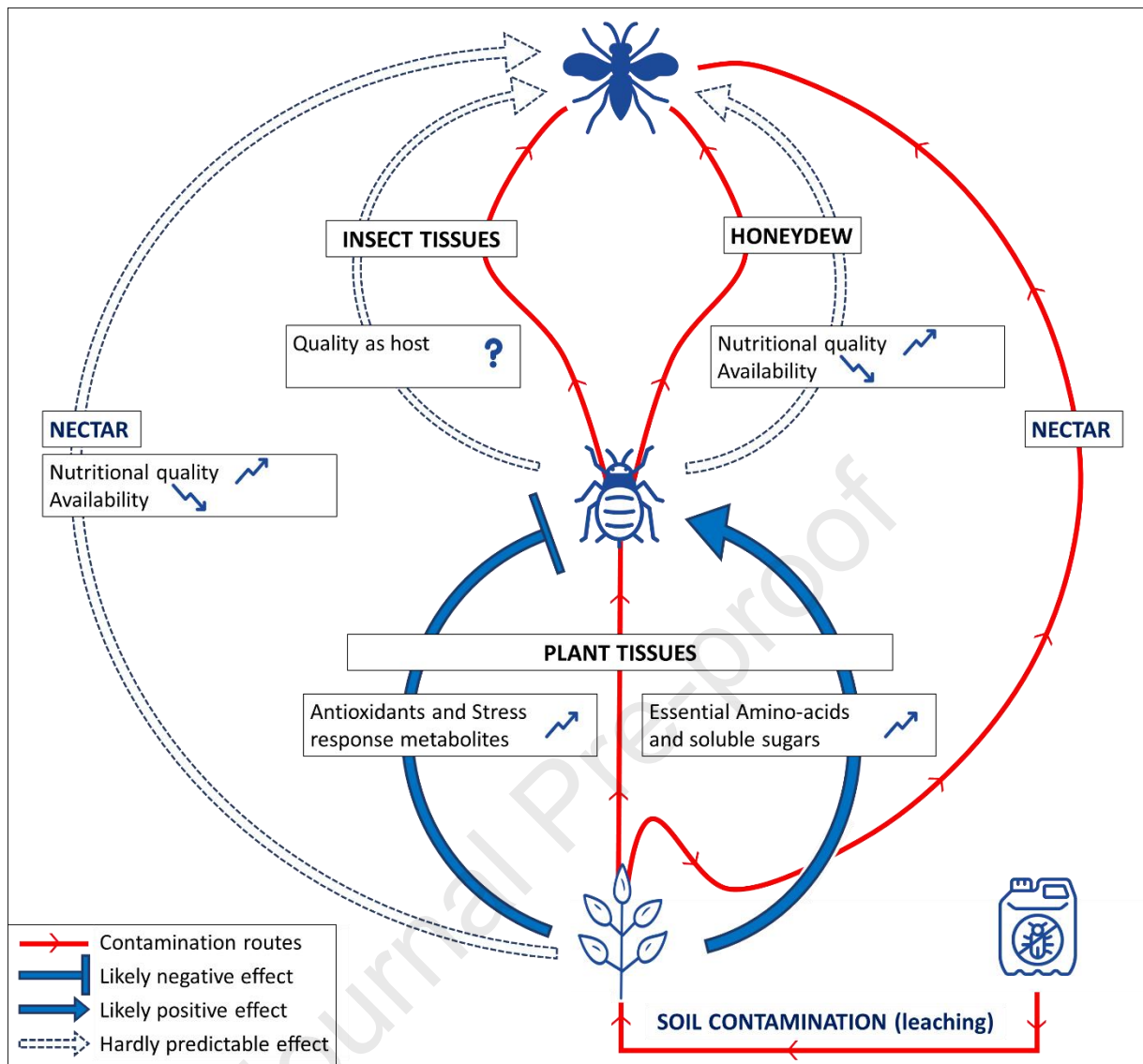
594 Pesticides other than herbicides can also affect plant quality in a subtler way. For example,
595 sublethal doses of the fungicide tebuconazole, equivalent to levels found in peri-agricultural
596 systems, modified metabolic profiles of plant leaves and roots, especially sugar and amino-acid
597 contents but also led to an accumulation of anti-oxidants (Serra et al., 2015, 2013). Insecticides
598 also alter plant metabolism through non-target effects, leading in some cases to increases in
599 amino-acid contents (Cesco et al., 2021; Mahdavi et al., 2015; Nemat Alla et al., 2008). For
600 example, field rates of the insecticide diazinon, while being totally non-lethal to plants, induced
601 shifts in sugar and amino-acid contents but also increased phenylpropanoid contents (secondary
602 metabolites involved in stress response) (Mahdavi et al., 2015).

603 Plant quality is strongly driven by plant interactions with micro-organisms, and especially
604 symbionts (Babalola, 2010; Igiehon and Babalola, 2017; Turan et al., 2014). The effects of
605 pesticides on plant-interacting micro-organisms, such as mycorrhizae and beneficial
606 rhizobacteria, have been extensively studied and reviewed (Aloo et al., 2021; Chowdhury et al.,
607 2008; Hage-Ahmed et al., 2019; Hussain et al., 2009). There is no particular tendency towards
608 beneficial or deleterious effects on mycorrhizae and there is a strong variation depending on
609 the type of molecule, dose and soil characteristics (Hage-Ahmed et al., 2019). However,
610 reviews concerning soil bacterial communities and especially beneficial bacteria underline clear

611 detrimental effects of pesticides and their degradation byproducts (Aloo et al., 2021;
612 Chowdhury et al., 2008; Hussain et al., 2009), such as the inhibition of nitrogen fixation and
613 phosphorus solubilization, which are essential metabolic processes in plant nutrient uptake (Das
614 and Debnath, 2006; Das et al., 2016; Fox et al., 2007; Sannino and Gianfreda, 2001). Such
615 effects on bacteria, alongside with the detrimental effects of pesticides on mycorrhizae, could
616 have drastic consequences on plant quality and therefore on trophic networks they support.

617 Altogether, sublethal doses of pesticides induce shifts in amino-acid and sugar contents in
618 plants. While these changes generally seem to increase plant quality, predicting a detrimental
619 or beneficial outcome for phytophagous insects is challenging (Figure 2). Indeed, most
620 pesticides induce accumulation of secondary metabolites involved in generic stress responses,
621 such as phenylpropanoids and antioxidants (Mahdavi et al., 2016; Serra et al., 2015, 2013),
622 which is likely to be stressful to insects and could therefore compensate beneficial shifts in
623 primary metabolite contents (Ramaroson et al., 2022).

624 While metabolic studies on the effects of low doses of insecticides on plant-insect interactions
625 are still lacking, previously mentioned plant metabolic changes due to sublethal doses of
626 herbicides could explain detrimental developmental effects in phytophagous insects. For
627 instance, the caterpillar *Mamestra brassicae* (Lepidoptera: Noctuidae) had a slower
628 development when feeding on exposed *Ranunculus acris* (Ranunculaceae) plants with
629 sulfonyleurea at 10% of the recommended field rate (Hahn et al., 2014). Moreover, *Gastrophysa*
630 *polygoni* (Coleoptera: Chrysomelidae) larvae feeding on chlorsulfuron-treated *Fallopia*
631 *convolvulus* (Polygonaceae) displayed lower survival rates (Kjaer and Heimbach, 2001).
632 However, such bottom-up effects of herbicides highly depend on the considered species and
633 molecule, and could involve, in addition to a decrease in plant nutritional value, the induction
634 of plant defenses, leading to either toxicity and/or repellence towards phytophages (Figure 1,
635 see sections 4.1 and 5.2.1).



636

637 **Figure 2:** Main effects of sublethal doses of pesticides on the quality of plants, phytophages
 638 and related secondary food sources and potential cascading effects on natural enemies.
 639 Pesticide-induced changes in nutritional quality (inserts with arrow/question mark pictograms)
 640 and their potential effect on the upper trophic level (blue arrows) as well as pesticide
 641 contamination routes (red lines) are summarized here. Flat-head arrows indicate an overall
 642 negative effect on the upper trophic level, while point-head arrows indicate an overall positive
 643 effect. Dashed white arrows indicate a lack of knowledge on the effects of quality changes.

644

6.2. Effects of pesticides on natural enemies through their effect on plant and phytophage quality

Overall, stress alter plant quality which results in a shift in phytophage fitness, which can either increase or decrease (see section 6.1). Moreover, plant quality conditions the quality of phytophage excretion products that can be consumed by natural enemies as secondary food sources (Crafts-Brandner, 2002). Some natural enemies also feed on plant resources such as nectar and pollen, which quality is linked to general plant quality (Pirotte et al., 2018; Silva et al., 2011). Therefore, low doses of pesticides are likely to affect the fitness of natural enemies through various bottom-up effects (Calvo-Agudo et al., 2022; Stapel et al., 2000).

Absence of toxicity is a major part of plant and phytophage quality, as primary and/or secondary food sources for natural enemies. Exposure to pesticides, either direct or through the resource, generally leads to pesticide contamination of tissues and products of plants and phytophagous insects, that can decrease the fitness of natural enemies (Figure 2). For example, spraying aphids with a combination of thiacloprid and deltamethrin insecticides at sublethal rates (lethal concentration of 10%) led to a significant decrease in population growth rates and parasitism rates in the parasitoid *Aphidius flaviventris* (Hemiptera: Aphididae) (Majidpour et al., 2020). Similar results were observed in predatory arthropods feeding on contaminated prey, with effects ranging from behavioral changes to fitness decreases (Schneider et al., 2009; Singh et al., 2004; Wanumen et al., 2016; Yao, 2015). Other studies remain nonetheless necessary, especially on the non-target effects of herbicides and fungicides, known to be deleterious to various natural enemies through direct exposure (Yokoyama and Pritchard, 1984; Youn et al., 2003).

Honeydew and feces produced by phytophagous insects, together with plant nectar, are important food subsidies for many natural enemies (Araj et al., 2011; Rahat et al., 2005; Tena et al., 2013; Wäckers et al., 2008). Exposure to herbicides can decrease and delay flowering,

670 even when used at less than 5% of field rate, therefore reducing the availability of floral nectar
671 for natural enemies. Nevertheless, chronic exposure to sublethal doses of herbicides such as
672 glyphosate induced an increase in soluble sugar contents in the floral nectar of several wild
673 plants, meaning that the quality of plant nectar may increase after pesticide exposure (Russo et
674 al., 2022). In addition, the nutritive quality and amount of honeydew and feces excreted by
675 phytophages usually correlates positively with plant quality (Fischer et al., 2005; Fischer and
676 Shingleton, 2001; Whitaker et al., 2014). This means that an increase in plant quality in
677 response to sublethal doses of herbicides (see section 6.1) could lead to an increase in honeydew
678 and feces quality for natural enemies. However, He et al. (2013) and Chen et al. (2017) showed
679 that exposure of hemipteran phytophages to sublethal doses of insecticides such as
680 imidacloprid, bifenthrin and flupyradifurone led to a decrease in honeydew production.
681 Therefore, despite a potential increase in quality, pesticide exposure of plant-phytophage
682 systems may reduce secondary food source availability for parasitoids and consequently
683 decrease their fitness (Damien et al., 2020, 2019).

684 Food subsidies can also represent an additional source of toxicity for natural enemies. Indeed,
685 soil application of pesticides leads to a significant contamination of plant nectar (Botías et al.,
686 2015; Cowles and Eitzer, 2017; Stoner and Eitzer, 2012), and is often shown to impair natural
687 enemies, both in plant-natural enemy systems (Stapel et al., 2000) and in simulated interaction
688 systems (i.e. feeding natural enemies with contaminated sucrose solution; Gao et al., 2021). For
689 example, the treatment of cotton plants with different systemic insecticides led to disturbed
690 foraging ability and reduced lifespan in the parasitoid *Microplitis croceipes* (Hymenoptera:
691 Braconidae) after it fed on contaminated extrafloral nectar (Stapel et al., 2000). Moreover,
692 quantifiable levels of neonicotinoids were present in the honeydew of the mealybug
693 *Planococcus citri* (Hemiptera: Pseudococcidae) following rearing on plants either exposed
694 through spraying or soil application (Calvo-Agudo et al., 2019; Quesada et al., 2020). This

695 honeydew contamination led to high mortality rates of parasitic wasps feeding on it (Calvo-
696 Agudo et al., 2019). Despite those studies were conducted using field application rates, it is
697 likely that honeydew remains a source of exposure to residual levels of pesticides for non-target
698 beneficial insects, even in non-crop systems (Calvo-Agudo et al., 2022).

699 In summary, pesticides induce changes in plant metabolism and, while these changes depend
700 on plant species, pesticides and doses, they can still affect upper trophic levels. Whereas the
701 observed shifts in plant nutritive metabolite contents suggest an increase in plant quality for
702 phytophages, the associated increase in secondary metabolites and plant defenses may counter
703 this benefit (Figure 2). Concerning natural enemies, pesticide exposure of plants can lead to an
704 increase in the quality of food subsidies (i.e. nectar, honeydew and feces), but also a decrease
705 in their availability. Moreover, it is clear that the consumption of host/prey contaminated with
706 pesticides, but also of contaminated food subsidies, leads to deleterious effects on natural
707 enemies (Figure 3).

708 **7. A short note on sublethal pesticide effects at the population scale, with potential**
709 **impact on trophic networks**

710 The different impacts of pesticides on plants previously reviewed are likely to affect plant
711 populations and especially plant density and plant community structure, which, in plant-
712 phytophage interactions, usually define the carrying capacity of insect populations (Friess et
713 al., 2017). Moreover, the impact of phytophagy on plants depends on the capacity of the
714 phytophage to access food sources (location, choice, feeding behavior and resistance to plant
715 defense), but also on the density of phytophages. Pesticides are designed to kill and therefore
716 reduce population density. However, sublethal exposures have more complex and context-
717 dependent effects on populations as they can either be deleterious, neutral or induce hormesis.
718 Hormesis consists in the biphasic response that some organisms display after exposure to stress,
719 pesticides in our case, and that is characterized by a stimulation of the trait under sublethal
720 doses, and an inhibition at higher doses. (Calabrese, 2018; Cutler et al., 2022; Guedes, 2022).
721 Since these aspects of sublethal pesticide exposure have been extensively studied and reviewed,
722 we will only quickly summarize them here.

723 Sublethal doses of pesticides, mostly herbicides, are known to negatively affect plant population
724 features, such as flowering intensity, seed production and seed quality, or even the efficiency
725 of asexual reproduction (Albrecht et al., 2014; Andersson, 1996; Boutin et al., 2004; Egan et
726 al., 2014; Melton et al., 1988; Pokhrel and Karsai, 2015; Riemens et al., 2009; Schmitz et al.,
727 2013). This generally leads to the decline in plant abundance observed in field studies
728 investigating herbicide drift (Egan et al., 2014; Johnson et al., 2023; Schmitz et al., 2013). While
729 hormetic effects have been observed frequently on plant growth, very few studies to this date
730 showed that sublethal rates of pesticides could increase plant reproduction and therefore
731 abundances (Pokhrel and Karsai, 2015).

732 In phytophages, sublethal pesticide exposure leads to a wide range of responses when it comes
733 to fitness traits such as fecundity, longevity, development time and birth rate, which all
734 modulate population size. While several studies underlined deleterious effects of pesticides on
735 insect pests' fitness traits (Table S1, Deng et al., 2019; Lashkari et al., 2007; Lutz et al., 2018;
736 Mahmoodi et al., 2020; Saska et al., 2016), several studies reported hormetic effects of sublethal
737 doses of pesticides, mostly insecticides (Table S1, Chelliah et al., 1980; Morse and Zareh, 1991;
738 Christopher Cutler et al., 2005; Yu et al., 2010; Cho et al., 2011; Cordeiro et al., 2013; Ayyanath
739 et al., 2015; Tang et al., 2015; Lu et al., 2016; Rix et al., 2016; Chen et al., 2017; Cao et al.,
740 2019; Deng et al., 2019; Ullah et al., 2020). Very few studies focused on non-target effects of
741 pesticides on the fitness of phytophages and, while they seem usually deleterious (Bohnenblust
742 et al., 2013; Clements et al., 2018; Saska et al., 2016), further work is required to know if these
743 effects are consistent.

744 Population features of natural enemies are negatively affected by pesticides, even at low doses
745 through direct exposure or through the consumption of contaminated host/prey (Table S1,
746 Yokoyama and Pritchard, 1984; Schneider et al., 2009; Rahmani and Bandani, 2013; Abedi et
747 al., 2014; Maia et al., 2016; de Morais et al., 2016; Majidpour et al., 2020; Ricupero et al.,
748 2020). Cases of hormetic effects of sublethal doses of pesticides, mostly non-target, were often
749 reported on natural enemies (Basana Gowda et al., 2021; Hou et al., 2023; Leite et al., 2015;
750 Pratissoli et al., 2010; Ray et al., 2022; Wang et al., 2022). These short-term effects range from
751 increased longevity and fecundity to higher parasitism and emergence rates, without
752 demonstrated positive impact on their population growth rate and survival over generations.

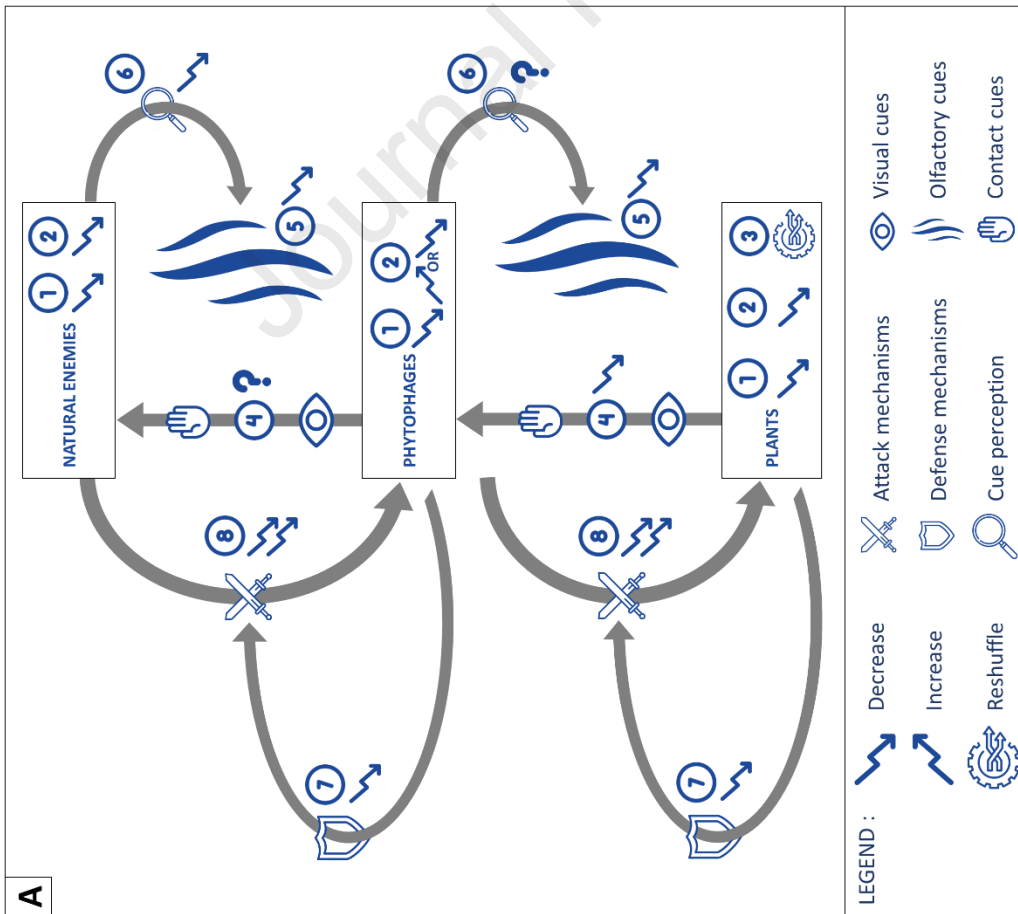
753 In summary, pesticide effects on land plants and insects go far beyond effects at the scale of the
754 organism. Fitness traits are negatively affected by sublethal doses of pesticides in most
755 organisms whether or not they are targeted by the molecule, leading to populations' declines.
756 However, some organisms, mostly phytophages and natural enemies to a lesser extent,

757 displayed an increase of their fitness in response to sublethal rates of pesticides, due to hormetic
758 mechanisms. This phenomenon, alongside with the fact that species display different tolerance
759 levels to pesticides, may have consequences on species dominance and abundance and therefore
760 disturb plant and arthropod communities.

761 **Figure 3: (A)** Summary of sublethal effects of pesticides on traits involved in interactions (grey
762 arrows associated to their pictograms) between land plants (bottom), phytophages (middle) and
763 natural enemies (top). Effects are synthesized by blue arrows/question mark pictograms and are
764 detailed in the associated table **(B)**. Each effect can be linked to the scheme and the
765 corresponding traits thanks to circled blue digits. Capital letters between brackets refer to the
766 type of pesticide concerned (H=Herbicide, I=Insecticide, F=Fungicide)

B

Trait affected	Effect(s) observed on plants	Effect(s) observed on phytophagous insects	Effect(s) observed on natural enemies
① Size and development	Decrease in biomass, more consistent concerning roots (increase observed once under F) (H, I, F)	Decrease in size, increase in development time (slight hormetic increases also observed) (I)	Increased development time, reduced biomass (H,I,F)
② Population features	Decrease in seed production, seed quality and asexual reproduction (H)	Decrease or Increase in various population features (Fecundity, Lifespan, Intrinsic rate of increase) depending on the dose (Hormetic effects) (H,I)	Decrease or Increase in various population features (Fecundity, Lifespan, Intrinsic rate of increase) Observed population decrease in treated fields (H,I)
③ Nutritional quality and metabolism	Increase in essential Amino-acid contents, Metabolic reshuffle, Decrease in nitrogen content (H,I)	X	X
④ Visual / contact cues	Color modification through changes in pigment contents (less chlorophyll mostly) Architectural modifications (H,I,F)	Potential color and cuticle structure modification (I)	X
⑤ Olfactory cues	Modification of the emitted VOC spectrum with both decrease and increase in the emitted amount reported (H)	Decrease of pheromone emission (I)	X
⑥ Cue perception	X	X	Impairment of responses to Kairimones and Volatiles (I)
⑦ Defense mechanisms	Activation of defense genes and increase in phytohormones involved in defense Higher attraction of natural enemies (H,I,F)	Impairments of the immune response, potential increase of defensive bacteria in aphids (I)	X
⑧ Attack mechanisms	X	Decrease in feeding behaviors and feeding intensity (I)	Decrease in predation and mobility for predators, Decrease in foraging behaviors and oviposition rates for parasitoids (I)



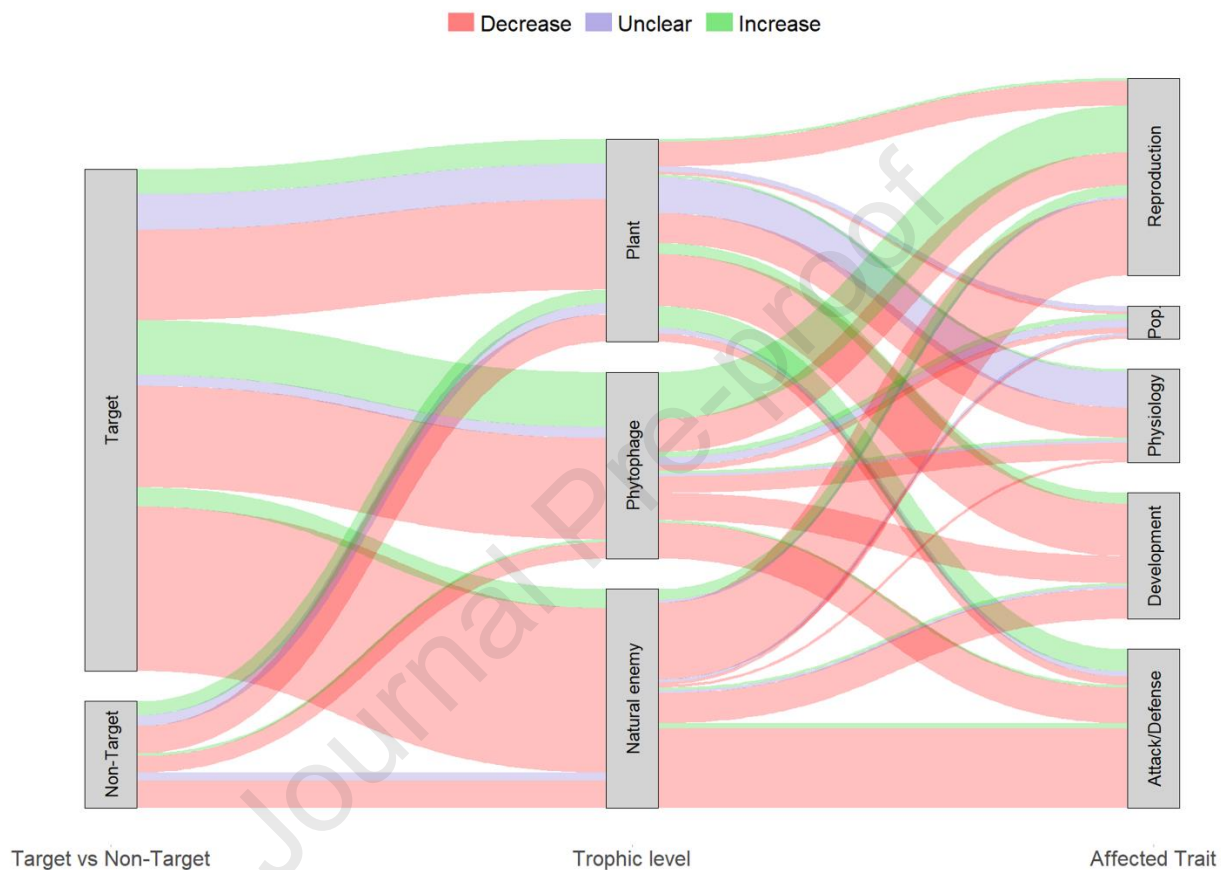
768 **8. Conclusions and recommendations**

769 **8.1. Conclusions**

770 Throughout this review, we highlighted that sublethal doses of pesticides induce a wide
771 diversity of effects, mostly deleterious, on land plants and arthropods and on their interactions.
772 Even at sublethal doses, pesticides disturb direct interaction mechanisms and behaviors (i.e.
773 host/prey recognition, attack/defense; Figure 1, 3), as well as matter fluxes within trophic
774 networks (Figure 2, 3). They decrease fitness and population size of interacting organisms and
775 may further contribute to biodiversity losses in agricultural landscapes (Figure 3). Pesticide
776 effects highly depend on the considered molecule, with target effects being usually more
777 deleterious (Figure 4). However, because non-target effects have received less attention,
778 especially concerning phytophages, it is hard to assess their impact on trophic networks, (Figure
779 4, Table S1). Finally, this review showed that interactions between pesticide effects observed
780 at each trophic level remain unknown and seem hardly predictable in terms of compensation,
781 additivity or antagonisms. For example, the outcome of sublethal pesticide exposures increasing
782 both phytophage reproduction (thus phytophagy pressure on plants) and plant defenses against
783 phytophages remains to be described (Figure 4).

784 Sublethal rates of pesticides are likely to strongly disturb PPNe terrestrial trophic systems, and
785 especially impair natural enemies (Figure 3, 4). A decrease in the effectiveness of phytophage
786 control by natural enemies, even at low doses, could thus represent a significant cause of pest
787 outbreaks, in addition to pesticide adaptations (resistance or tolerance). Therefore, while
788 pesticides are currently the predominant mean for controlling pests in the short term (Clapp,
789 2021; Popp et al., 2013), their effects on adjacent systems may have considerable feedback
790 impacts on agricultural production in the longer run (Dutcher, 2007; Mironidis et al., 2013;
791 Schmidt et al., 2004). Moreover, these results question recent pest management strategies
792 aiming at developing insecticides compatible with biocontrol (i.e. affecting pests but not

793 parasitoids; Torres and Bueno, 2018). Indeed, in addition to potential cryptic negative effects
 794 of such compounds on natural enemies, this review showed that pesticide effects were more
 795 generic and involved not only insecticides but also herbicides and fungicides. These two latter
 796 categories of pesticides also act as non-target and may impair biocontrol services.



797

798 **Figure 4:** Sankey diagram summarizing the publications assessing sublethal effects of
 799 pesticides on plants, phytophages and natural enemies (191 publications listed in Table S1).
 800 When studies investigated different traits, different trophic levels or different types of
 801 pesticides, they were counted once for each, reaching a total of 222 occurrences. From left to
 802 right, publications are distributed across the type of pesticide (Target: n=183 or Non-target:
 803 n=39), the studied organism (Plant: n=74; Phytophage: n=68; Natural enemy: n=80), and the
 804 type of trait studied (Reproduction: n=72; Pop. = Population metrics: n=12; Physiology: n=34;
 805 Development: n=46; Attack/Defense: n=58). Path color roughly represents the effect, in terms

806 of decrease, increase, or unclear variation, of sublethal pesticide exposure on the considered
807 trait.

808 **8.2. Recommendations**

809 As seen throughout this review, dose strongly influences the effects of pesticides on organisms,
810 ranging from strong deleterious effects at sublethal yet high doses, to cryptic (e.g., metabolic
811 shifts) or increases in their fitness generally occurring at low sublethal or non-lethal doses.
812 While high sublethal doses (i.e. LC₂₀₋₃₀) are quite well studied in the current literature, there is
813 a lessened interest for lower doses (Table S1). It is therefore essential to consider a wider range
814 of doses when studying sublethal effects of target and non-target pesticides on organisms, in
815 order to investigate the complete range of responses organisms can display and to identify
816 unexpected effects. Furthermore, while pesticide responses have frequently been undertaken at
817 various scales (i.e. gene expression, metabolomics, macroscopic traits, and population features)
818 in plants, insects deserve more attention to offer deeper insights into sublethal effects of
819 pesticides, especially cryptic ones (Figure 4).

820 A major challenge when reviewing sublethal pesticide effects on terrestrial organisms is the
821 exposure method, which strongly differs between studied organisms (Figure S1). Natural
822 enemies are generally exposed through direct application or by being reared on contaminated
823 artificial surfaces, while phytophages are more generally exposed by being reared on
824 contaminated plants and, for some studies, through an artificial food source (Figure S1). For
825 plants, direct application is also the main exposure method (Figure S1). While direct application
826 allows to control the dose of exposure, it lacks ecological relevance. Indeed, sublethal pesticide
827 exposures mostly happen in peri-agricultural systems, where pesticides are located in the soil
828 and in the atmosphere due to leaching and drift and then in PPNe due to trophic transfer.
829 Therefore, soil and aerial exposures for plants as well as through the food chain for phytophages
830 and natural enemies appear more relevant to understand how pesticides can affect trophic

831 interactions. To fill the knowledge gap on the real and precise dose to which organisms are
832 exposed *in vivo*, quantifications of pesticides and of their degradation products in the organism
833 tissues need to be carried out and linked to the observed effects.

834 Another aspect lacking consideration when studying the sublethal effects of pesticides in the
835 scope of trophic interactions or biocontrol, is that animals and plants are holobionts (Engel and
836 Moran, 2013; Vandenkoornhuyse et al., 2015). Symbionts strongly drive indeed both PPNe
837 trophic interactions and responses to pesticides (Frago et al., 2012; Hackett et al., 2013; Kikuchi
838 et al., 2012; Oliver et al., 2012). Many studies focused on how bacterial and fungal symbionts
839 may help plants and arthropods to cope with pesticides, but the consequences on processes such
840 as metabolism and defense mechanisms remain uninvestigated, as the impacts on bottom-up /
841 top-down species interactions (Kikuchi et al., 2012; Ramya et al., 2016). Therefore, future
842 research on sublethal pesticide effects needs to broaden the range of considered species
843 interactions, including microorganisms.

844 This review highlighted that focusing on the responses of single organisms to single molecules,
845 led to a current incapacity to understand how pesticides really disrupt ecosystem functioning,
846 especially through their impact on biotic/trophic interactions (Calow and Forbes, 2003; Relyea
847 and Hoverman, 2006). Our understanding of the impact of sublethal exposure to pesticides,
848 both target and non-target, on trophic networks therefore remain superficial, both from an
849 ecological and evolutionary point of view. Works on sublethal pesticide effects now need to be
850 focused on biotic/trophic interactions within PPNe systems to acquire experimental and field
851 data, and understand how biotic interactions are shaped by the expression of traits under
852 pesticide exposure. Moreover, associating these works to modeling approaches could allow
853 testing and improving current models in order to develop better prediction for pesticide risk
854 assessment. Finally, sublethal pesticide effects on PPNe systems and biocontrol services now
855 need to be considered at the landscape scale. Pesticide contaminations resulting from

856 conventional agriculture may indeed strongly impact biocontrol efficiency of organic farming
857 systems together with the functioning of trophic networks unexploited by humans, also hosting
858 beneficial organisms for many other ecosystem services: water quality, carbon and nitrogen
859 recycling, pollination, etc. (Bloom et al., 2021; Knapp et al., 2023; Ricci et al., 2019).

860

Journal Pre-proof

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869 **Author contributions**

870 **Axel Beringue:** Investigation, Writing - Original Draft, Visualization **Joséphine Queffelec:**
871 Writing - Review & Editing **Cécile Le Lann:** Conceptualization, Writing - Review & Editing,
872 Supervision **Cécile Sulmon:** Conceptualization, Writing - Review & Editing, Supervision

873 **Figure legends**

874 **Figure 1:** Main effects of sublethal doses of pesticides on host/prey recognition mechanisms
 875 and attack/defense mechanisms in land plants, phytophages and natural enemies. While grey
 876 arrows represent interactions within PPNe networks, blue arrows represent the effects of
 877 sublethal doses of pesticides on traits involved in those interactions. Flat-head arrows indicate
 878 an overall decrease of the trait, while point-head arrows indicate an increase. Dashed white
 879 arrows indicate a lack of knowledge on the effects. The effects of pesticides on each trait,
 880 represented by the different pictograms, are indicated in the associated inserts, with (+), (-) and
 881 (?) depending on the effect (increase, decrease, no known effect respectively).

882

883 **Figure 2:** Main effects of sublethal doses of pesticides on the quality of plants, phytophages
 884 and related secondary food sources and potential cascading effects on natural enemies.
 885 Pesticide-induced changes in nutritional quality (inserts with arrow/question mark pictograms)
 886 and their potential effect on the upper trophic level (blue arrows) as well as pesticide
 887 contamination routes (red lines) are summarized here. Flat-head arrows indicate an overall
 888 negative effect on the upper trophic level, while point-head arrows indicate an overall positive
 889 effect. Dashed white arrows indicate a lack of knowledge on the effects of quality changes.

890

891 **Figure 3: (A)** Summary of sublethal effects of pesticides on traits involved in interactions (grey
 892 arrows associated to their pictograms) between land plants (bottom), phytophages (middle) and
 893 natural enemies (top). Effects are synthesized by blue arrows/question mark pictograms and are
 894 detailed in the associated table **(B)**. Each effect can be linked to the scheme and the
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897

898 **Figure 4:** Sankey diagram summarizing the publications assessing sublethal effects of
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904 type of trait studied (Reproduction: n=72; Pop. = Population metrics: n=12; Physiology: n=34;
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906 of decrease, increase, or unclear variation, of sublethal pesticide exposure on the considered
907 trait.

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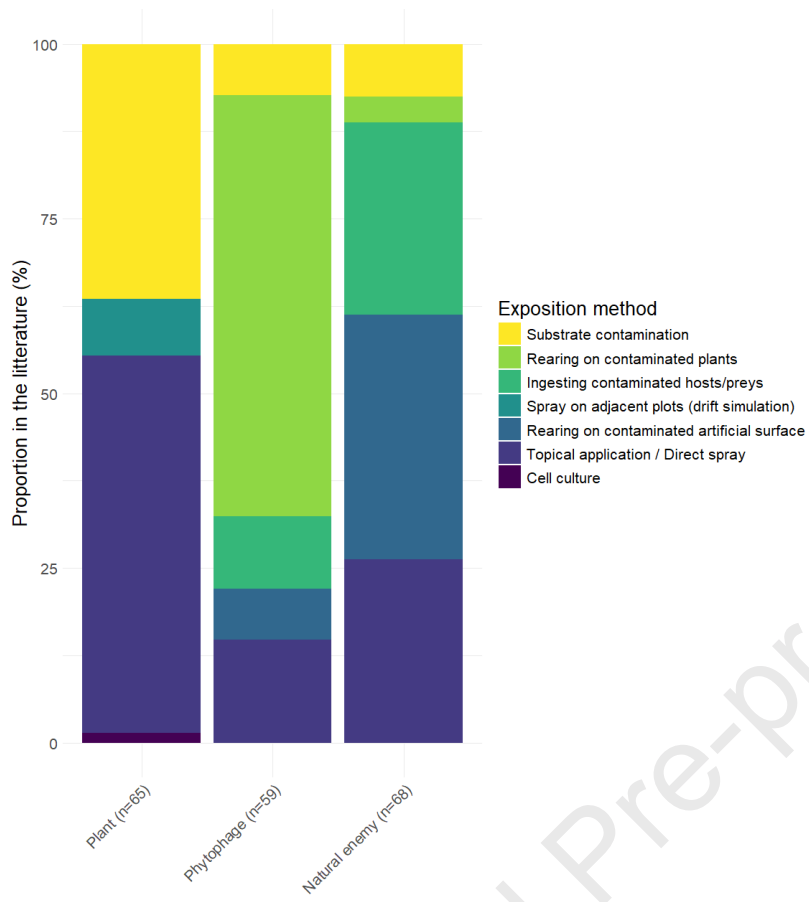
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 1813

1814 **Supplementary Materials**

1815 Table S1: Summary of publications relevant in the scope of trophic interactions that assess the
 1816 effects of pesticides on terrestrial organisms (publications cited in this table are all listed in the
 1817 Bibliography section of the manuscript) with detailed information on the species studied, the
 1818 pesticide(s) tested, alongside with its effect and its effect dose, the way the organisms were
 1819 exposed and a brief summary of the observed effects. While two organisms are studied but
 1820 tested separately thus not in interaction, the “Number of interacting trophic networks” generally
 1821 indicates 1

1822 Figure S1: Proportion in the current literature (191 publications listed in Table S1) of the
 1823 different types of exposure routes to pesticides for the three types of organisms considered in
 1824 this review. Color gradient roughly represents the ecological relevance of the exposure route,
 1825 yellow shades corresponding to methods closer to contaminations occurring within terrestrial
 1826 non-target trophic networks.



1827

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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