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Understanding plant–arthropod interactions in multitrophic communities to improve conservation biological control: useful traits and metrics

Antoine Gardarin, Manuel Plantegenest, Armin Bischoff, Muriel Valantin-Morison

► To cite this version:

Antoine Gardarin, Manuel Plantegenest, Armin Bischoff, Muriel Valantin-Morison. Understanding plant–arthropod interactions in multitrophic communities to improve conservation biological control: useful traits and metrics. *Journal of Pest Science*, 2018, 91 (3), pp.943-955. 10.1007/s10340-018-0958-0 . hal-01778315

HAL Id: hal-01778315

<https://univ-avignon.hal.science/hal-01778315>

Submitted on 14 May 2018

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1 **Understanding plant-arthropod interactions in multitrophic** 2 **communities to improve conservation biological control:** 3 **useful traits and metrics**

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6 Antoine Gardarin ¹, Manuel Plantegenest ², Armin Bischoff ³ and Muriel Valantin-Morison ¹

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10 Corresponding author: Antoine.Gardarin@inra.fr. +33 1 30 81 54 40.11 ¹UMR Agronomie, INRA, AgroParisTech, Université Paris-Saclay, 78850 Thiverval-Grignon, France12 ²UMR1349 IGEPP, Agrocampus Ouest, 65 rue de Saint-Brieuc, CS 84215, 35042 Rennes Cedex,

13 France

14 ³UMR Mediterranean Institute of Biodiversity and Ecology (IMBE), Aix-Marseille University-CNRS-

15 IRD-University of Avignon, IUT Agroparc, 84911 Avignon, France

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17

18 **Acknowledgements**

19 This work was partly supported by the *Agence Nationale de la Recherche* PEERLESS project (ANR-

20 12-AGRO-0006). We thank the reviewers for their helpful comments on the manuscript.

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24 **Summary**

25 The role of biodiversity in the delivery of ecosystem services is increasingly being studied by trait-
26 based functional approaches. Here, we review and discuss the contribution of a trait-based approach to
27 understanding plant-arthropod interactions and improving conservation biological control. The stable
28 biological control of multispecies herbivore communities requires functional diversity and a
29 redundancy of natural enemies, including specialists and generalists, with minimal antagonistic
30 interactions. The management of arthropod communities through plant community requires the plant
31 community to perform several functions, including the provision of diversified trophic resources and
32 appropriate physical habitats. Many studies have investigated the ability of plants to provide these
33 functions, but many of the results obtained were limited to single species. The description of
34 communities in terms of traits underlying trophic and non-trophic interactions between plants and
35 animals would make it possible to extrapolate findings to other species. Studies on plant-herbivore and
36 plant-pollinator interactions have identified several traits as important for trophic resource provision,
37 in terms of resource quantity, accessibility, quality and temporal availability. By contrast, traits
38 relating to physical habitat provision and microclimate modification have been little explored. Several
39 metrics describing the functional composition and diversity of communities have been proposed, to
40 extend the trait-based approach to plant community level, but the extent to which multitrophic
41 communities are affected by plant traits remains largely unexplored. The next step will be to identify
42 the combinations of these plant community metrics best explaining their impact on arthropod
43 communities and disentangling the roles of plant functional composition and diversity.

44

45

46 **Keywords:** entomophagous arthropods; flower strip; functional diversity; functional trait; interaction
47 trait; natural enemy

48

49

50 **Key message**

51 • The management of arthropod communities for conservation biological control requires plant
52 communities to provide diversified trophic resources and physical habitats.

53 • A trait-based approach would provide more generic knowledge.

54 • Several interaction traits relating to resource provision have been identified, but traits relating to
55 physical habitat provision have been little identified.

56 • At community level, it remains unclear how multitrophic communities are affected by plant traits.

57 • A functional description of plant communities might facilitate the management of semi-natural
58 habitats to enhance biological control.

59

60

61 **Author contribution statement**

62 AG, AB and MP wrote the paper. MVM provided comments on the manuscript.

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66

67 **Introduction**

68 There is increasing evidence that semi-natural habitats provide a wide range of services (Wratten et al.
69 2012) dependent on ecosystem functioning and on its interactions with the management of these
70 habitats. The role of biodiversity in ecosystem service provisioning is increasingly being studied by
71 trait-based functional approaches investigating the relationships between environmental variables,
72 including habitat management, and ecosystem functioning, community assembly and structure. Trait-
73 based approaches are widely used in plant ecology (e.g. Lavorel et al. 2011) and have been extended
74 to studies of other taxonomic groups, such as soil invertebrates (Birkhofer et al. 2017; Pey et al. 2014),
75 but studies connecting different trophic levels on the basis of their traits remain rare (Boukal 2014; but
76 see Moretti et al. 2013).

77

78 Several ecosystem services, such as herbivore regulation, pollination and biogeochemical cycles, are
79 dependent on multitrophic interactions, and there is an urgent need to improve our understanding of
80 the relationships between plant and animal communities (Wood et al. 2015). The functioning of
81 species-rich assemblages involved in interaction networks has been little studied to date and the
82 mechanisms underlying the functioning of such assemblages remain poorly understood and quantified
83 (Violle et al. 2014). Correlations have recently been found between the functional composition of
84 vegetation and the abundance of phytophagous invertebrates in agroecosystems (Storkey et al. 2013)
85 and natural habitats (Frenette-Dussault et al. 2013). Here, we extend the trait-based framework of
86 Lavorel et al. (2013), which focused on trophic interactions, to non-trophic interactions, and we
87 explain how it applies to conservation biological control in agroecosystems.

88

89 Our understanding of interactions between plant and animal communities and their effect on the
90 biological control of pests remains limited. Conservation biological control aims to increase the
91 abundance, diversity and efficacy of natural enemies through environmental management and the
92 adoption of particular agricultural practices. Species-rich habitats, such as linear field margins between
93 crop fields, support populations of the natural enemies of pests, and therefore help to improve the
94 biological control of crop herbivores (Bischoff et al. 2016). Their effects are thought to be mediated by

95 plant species composition (Haaland et al. 2011). The plant species found in these habitats provide
96 functions not supplied by crop plants. This is obvious in natural enemies of crop herbivores that
97 depend on specific plant resources at particular stages of their life cycle, such as hoverflies and
98 parasitic wasps do. The role of plant species composition is less obvious for groups of natural enemies
99 that do not feed on plants. For ground beetles, spiders and ground-dwelling arthropods, vegetation
100 cover via structure-mediated effects is as important, or more, than resource-mediated effects (Balzan
101 et al. 2016; Diehl et al. 2012).

102

103 If the implementation or the management of habitats to enhance functional biodiversity increases
104 natural enemy populations, this does not necessarily result in a significant reduction of crop
105 herbivores. The performance of these populations, in terms of biological control, depends on many
106 other factors and interactions (Jonsson et al. 2008), and we are often unable to understand why some
107 plant species mixtures perform better than other ones. There is also currently no methodology for
108 knowledge transfer concerning the biological control efficiency of a given plant mixture to facilitate
109 the choice of new sets of species adapted to other agronomic and climatic situations. Previous studies
110 on trophic and non-trophic interactions within and between plant and animal communities focused
111 principally on analyses of biological diversity through taxonomic approaches or on the global
112 relationship between species diversity and community functioning (Snyder et al. 2006). Their results
113 depended strongly on the species composition of the plant community studied (Wilby et al. 2013). A
114 functional description of plant and arthropod communities is therefore required, to render findings
115 more general and for the development of predictive agroecology.

116

117 Here, we review and discuss the contribution of a trait-based approach to improving our understanding
118 of plant-arthropod interactions in agroecosystems, focusing on both trophic (e.g. arthropods feeding on
119 plants, predators feeding on alternative prey) and non-trophic interactions. We address the following
120 questions: (1) What characteristics of entomophagous arthropod communities are related to the
121 regulation of crop herbivore populations? (2) Which functions and plants traits are involved in plant-
122 arthropod interactions? (3) How could the effects of plants on arthropod assemblages at community
123 and landscape levels be scaled up, and what issues would this raise?

124
125 For the preparation of this review, we searched the Web of Science literature database
126 (<http://apps.webofknowledge.com>) with two search strings in the “topic” search field. The first was
127 [*(arthropod* or insect* or pest* or prey* or "natural ennem*" or predator* or parasitoid*) and*
128 *("biological control" or biocontrol) and diversity and communit*]*, to target scientific articles
129 investigating the role of arthropod community structure in biological control. The second search string
130 was [*("food web*" or "trophic network*" or "interaction network*") and (multitrophic or*
131 *interaction*) and (trait* or morpholog* or characteristic*) and (plant* or arthropod* or insect* or*
132 *flower*)]*, to target articles identifying traits involved in plant-arthropod interactions. Limiting our
133 search to articles published between 2005 and 2017 (last updated 29th November 2017), the two search
134 strings identified 507 and 528 articles, respectively. This first set of articles was analysed, and
135 additional relevant articles cited by these articles were added to the working set, whereas articles
136 considered to be outside the scope of the study were removed. We retained 515 articles for the final
137 analysis (Online Resource 1).

138

139 **1. The role of natural enemy diversity in controlling crop**

140 **herbivore communities**

141 The main properties of biological control and their relationship to the characteristics of
142 entomophagous arthropod communities emerging from the selected studies are summarized in Fig. 1
143 (first two columns). Crops harbour many herbivore species differing in terms of their taxonomic
144 identity and relative importance between years and between crop species. Interannual pest dynamics
145 and crop rotations make it necessary to consider interactions of herbivores and natural enemies at
146 community level. In general, control efficiency, for a large range of herbivore species, increases with
147 the diversity of natural enemies (Jonsson et al. 2017). Studies on predator and prey communities in
148 mesocosms have shown that the niche complementarity of predators is the principal mechanism
149 underlying the higher levels of predation in more diverse predator communities (Northfield et al.
150 2010; Wilby et al. 2005). The number and complementarity of functional groups of natural enemies,
151 rather than their taxonomic richness, thus appears to be the major determinant of the effect of

152 diversity, when it exists.

153

154 By contrast, the stability of biological control for multispecies herbivore communities requires
155 functional diversity (i.e. diversity in the functions provided) and redundancy of natural enemies, which
156 should include both specialists and generalists (Gontijo et al. 2015), with no antagonistic interactions
157 (Fig. 1). Most relationships between community structure and functioning have been inferred from
158 experiments carried out in mesocosms, and their extrapolation to more complex communities under
159 field conditions is problematic. In croplands, habitat management is often used as a tool to support
160 beneficial insects (conservation biological control). It has been suggested that high levels of plant
161 diversity in non-crop habitats favour the amount of natural enemies, leading to a decrease in herbivore
162 abundance (Letourneau et al. 2011). However, little is known about the plant traits favouring effective
163 biological control and their interactions with arthropod communities. Below, we will review and
164 discuss current knowledge.

165

166 **2. A trait-based approach to understanding plant–arthropod** 167 **interactions**

168 ***2.1 What functions must plant communities provide to promote herbivore*** 169 ***regulation within arthropod communities?***

170 Plant community management to improve the efficiency of herbivore control by natural enemy
171 communities should have several objectives (third column in Fig. 1). Here, we focus on the case of the
172 neighbouring environment of the field, but our analysis also applies to within-field plant diversity. The
173 surrounding non-crop vegetation fulfils two main functions for the natural enemies of pests (detailed
174 in Fig. 1): it provides both trophic resources and shelter (Griffiths et al. 2008).

175

176 The abundance of several insect groups (e.g. Heteroptera, Syrphidae: Pfiffner and Wyss 2004)
177 increases with the total amount of resources available, whereas other groups of insects also respond to

178 the diversity of these resources (Carabidae, Harwood et al. 2009). The resources supplied by plant
179 communities and required for completion of the life cycles of several natural enemies include nectar
180 and pollen for adults herbivores (hoverflies, parasitoids), and alternative prey for larval or adult
181 predators. The provision of trophic resources, such as floral nectar, increases the fecundity of some
182 parasitoids and, thus, the parasitism rates (Heimpel and Jervis 2005). Food resources must be
183 abundant, but also accessible and available at different times. Accessibility, such as the matching of
184 nectar depth in the corolla to the size of arthropod mouthparts, can be used as a criterion for targeting
185 specific arthropod natural enemies (Baggen et al. 1999). Plant communities could be designed to
186 improve the regulation of a large range of herbivores through the support of diverse groups of natural
187 enemies. The duration of the resource provisioning period is also crucial for both the maintenance of
188 entomophagous communities throughout the year, and to increase the growth rates of specialists
189 during pest outbreaks (Welch and Harwood 2014).

190 The role of vegetation in providing shelter has been little studied. Perennial plant communities, such
191 as beetle banks, provide refuges to protect populations of natural enemies against disturbances in the
192 vicinity of cropped habitats (MacLeod et al. 2004; Porcel et al. 2017). The density and complexity of
193 vegetation architecture and litter are important drivers of microclimate affecting vulnerable stages in
194 the life cycles of arthropods (oviposition, estivation, hibernation, Griffiths et al. 2008). Vegetation
195 provides attachment points for spider webs (MacLeod et al. 2004). Vegetation structure also
196 determines habitat complexity, thereby modifying interactions between natural enemies. It may reduce
197 intraguild predation by providing refuges and shelter, and reduce competition between natural enemies
198 from the same guild (Finke and Denno 2006; Wilby et al. 2013). However, studies investigating
199 resource- and structure-mediated effects have suggested that the provision of shelter and a favourable
200 microclimate affect the activity-density of arthropod generalist predators indirectly, by increasing
201 weed-borne resources or alternative prey (Birkhofer et al. 2008; Diehl et al. 2012).

202

203 Increases in the quantity and diversity of trophic resources may also affect crop pests, as demonstrated
204 for several lepidopteran herbivores (Balzan et al. 2016; Winkler et al. 2010). Plant communities
205 designed to enhance natural enemies should provide these populations with specific resources and
206 other habitat features not favourable to crop herbivores.

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Overall, plant communities can promote herbivore regulation by supplying diversified trophic resources accessible to various arthropod species with mouthparts of different shapes and sizes. These trophic resources should be available over a long period and should not be exploitable by unwanted herbivores (Fig. 1). Many studies have been performed to investigate the provision, by plants, of floral resources for parasitoids (e.g. Sivinski et al. 2011; Winkler et al. 2009) and hoverflies (van Rijn and Wäckers 2010), and of overwintering habitats (Bürki and Hausammann 1992). A few of these studies have shown that arthropod groups tend to be associated with particular functional traits of plant resources (e.g. Wäckers and van Rijn 2012). Most of the studies cited above focused specifically on particular species, and their results cannot be directly extrapolated to other plant-arthropod pairs. Given the large number of possible interactions within and between arthropod communities, alternative approaches are required to predict the functioning of these communities.

220 ***2.2. Use of interaction traits to analyse relationships between plant and*** 221 ***arthropod communities***

222 The mechanisms underlying community assembly processes involve morphological, physiological,
223 phenological and behavioural traits (sensu Pey et al. 2014; Violle et al. 2007). A role for
224 morphological traits has been demonstrated in several plant-insect studies. For instance, pollination
225 depends on the existence of a good match between insect proboscis length and the nectar holder depth
226 of the corolla (Ibanez 2012; Stang et al. 2006). Grasshopper herbivory is mediated by a match between
227 the toughness of plant leaves and insect mandibular strength (Ibanez et al. 2013).

228 Pairs of response-and-effect traits must be identified, to improve resource provisioning to beneficial
229 arthropods (Lavorel et al. 2013): plants modify arthropod performance via their effect traits, and the
230 response of arthropods to the vegetation depends on their response traits. We will use the term
231 “interaction traits” to denote all traits mediating interactions between plants and animals.

232

233 Interaction traits include not only trophic (Lavorel et al. 2013), but also non-trophic interactions, such
234 as shelter functions, with all of them having an effect on overall performance. Non-trophic interactions

235 can modify feeding parameters (escape from predation), non-feeding parameters (mortality,
236 reproduction) and dispersal. A well-known example of a non-trophic interaction is the presence of
237 domatia in some plant species, providing specific habitats for arthropods, such as ants, to increase
238 predation on herbivores and enhance plant defences (Agrawal and Karban 1997).

239
240 A trait-based approach, such as that recently used to predict the effect of various flower strips on
241 hoverflies (van Rijn and Wäckers 2016), might improve the understanding and prediction of
242 assemblages of invertebrate communities as a function of plant community composition (weed
243 communities, semi-natural habitats, flower strips). Many studies have assessed the attractiveness of
244 individual plant species to insects, but the identification of plant and animal interaction traits would
245 make it possible to extrapolate findings to untested plant species. Despite the known effects of traits in
246 mediating interactions, most ecological networks are still built on a taxonomic basis. Improvements in
247 our understanding of interaction traits should facilitate the prediction of the role of these traits in
248 structuring ecological networks and communities (Kissling and Schleuning 2015).

249
250 The mechanisms by which invertebrates affect other components of the ecosystem involve several
251 interaction traits (Moretti et al. 2013). This is of great practical importance when the studied
252 organisms are predators or parasitoids of agricultural pests. The relevant effect traits may be related to
253 diet, foraging behaviour, dispersal ability, shelter requirement and longevity.

254

255 ***2.3. What are the key plant traits involved in plant-arthropod interactions?***

256 We will focus here on some key arthropod functional groups involved in biological control (soil
257 dwellers, nectar and pollen feeders, leaf feeders, vegetation dwelling and flying predators).

258

259 *2.3.1. Plant traits associated with trophic interactions*

260 Studies on plant-herbivore and plant-pollinator interactions have identified several plant traits implied
261 in these interactions related to resource type, attractiveness, accessibility, quality and availability (Fig.
262 2).

263

264 *Resource type*: Plants provide various food resources, such as leaves, stems, roots, fruits and seeds,
265 sap, floral and extrafloral nectar and pollen. They also indirectly provide honeydew and alternative
266 hosts and prey. Nectar and pollen have been studied mostly as resources for parasitoids, but these
267 resources are also consumed by various other insects and spiders (Chen et al. 2010). The availability
268 over time, quality and quantity of these resources constitute interaction traits that vary broadly among
269 plant species (Kühn et al. 2004). The carbohydrate and protein resources provided by plants increase
270 the longevity, reproduction and dispersal of their consumers (Wäckers et al. 2005). Fitness effects vary
271 considerably with the diet, sex and stage in the lifecycle of the arthropod consumer (Wäckers et al.
272 2007). Plants may act as occasional and supplementary food sources, but the resources they supply
273 may also be of crucial importance, in synovigenic species of parasitoids for instance (Jervis et al.
274 2004), with nectar and pollen proteins have strong effects on adult performance and egg maturation.

275

276 *Attractiveness of the resource*: The presence of trophic resources does not necessarily imply that they
277 are consumed. Olfactory, gustatory and visual signals facilitate the recognition and detection of
278 resources, but may also be repellent, depending on the preferences of arthropod groups. Flowers emit
279 olfactory signals and different species are not equally attractive to parasitoids (Belz et al. 2013).
280 Visual signals, such as plant height, flower height, inflorescence size and colour, are involved in
281 resource detection and a high degree of visual attractiveness increases the abundance of natural
282 enemies (Fiedler and Landis 2007).

283 For phytophagous insects feeding on plant tissues, secondary metabolites have a deterrent effect,
284 defending the plant against attack. In the Brassicaceae, glucosinolates act as defence compounds
285 against generalist herbivores, but may attract specialists (Fahey et al. 2001). This attractiveness to
286 specialists increases with specific glucosinolate content (Kos et al. 2014). Chemical traits are often
287 used to predict the relative attractiveness or repellent effects of plant species and genotypes, although
288 the effect of secondary metabolites on phytophagous insects varies considerably, and their role as
289 defence compounds has been called into question (Carmona et al. 2011).

290 *Resource accessibility*: Flower morphology, including corolla shape in particular, plays a crucial role

291 in determining the accessibility of floral nectar and pollen (Heimpel and Jervis 2005). In flower-
292 visiting arthropods, head or body size may physically restrict access to floral resources in flowers with
293 a small corolla diameter. In such cases, the plant-arthropod interaction depends on the length of the
294 mouthparts. A correlation between nectar holder depth and the proboscis length of the flower visitor
295 has been observed in several insect groups, especially in pollinators. Short corolla flowers favour
296 hoverflies, whereas bumblebees prefer long corollas (Campbell et al. 2012). As a result, flower size is
297 one of the most important variables determining the abundance and diversity of flower visitors and
298 their size (Ibanez 2012; Stang et al. 2006; van Rijn and Wäckers 2016). By contrast, extrafloral nectar
299 is generally produced on exposed nectaries, with no size constraints on its accessibility. However,
300 extrafloral nectar has a higher sugar content than floral nectar, rendering it more viscous. This high
301 viscosity facilitates the feeding of hymenopteran parasitoids, which have adapted mouthparts, but
302 limits the accessibility of this resource to lepidopterans, which feed only on dilute nectar (Géneau et
303 al. 2012).

304

305 In the herbivores serving as alternative prey for the natural enemies of pests, resource provisioning is
306 dependent on plant palatability, which in turn depends on various morphological (e.g. presence of
307 trichomes, Carmona et al. 2011), biomechanical and chemical traits (e.g. silica content, Massey et al.
308 2006). Plant resistance to chewing insects is positively related to leaf punch strength, work to shear
309 and work to tear (Peeters et al. 2007). The incisor strength of insect mandibles is thus related to the
310 traits of the leaves consumed (like leaf dry matter content and carbon:nitrogen ratio, Deraison et al.
311 2015). Biomechanical properties are associated with several leaf structure traits, such as cuticle
312 thickness, lignin content, specific leaf area and leaf dry matter content (Pérez-Harguindeguy et al.
313 2003; Schädler et al. 2003). However, the effect of biomechanical properties may be partly
314 confounded with leaf nutrient quality (nitrogen content, carbon:nitrogen ratio, assimilate content),
315 which is negatively correlated with mechanical resistance (Peeters et al. 2007).

316

317 *Nutritional characteristics of the resource:* Floral nectar, extrafloral nectar and honeydew are
318 composed of sugars, whereas pollen is a source of proteins and free amino acids. The sugar, protein
319 and amino acid composition of these resources varies considerably between plant species (Heimpel

320 and Jervis 2005). Floral nectar contains mostly sucrose, fructose and glucose (Baker and Baker 1983).
321 The sugar composition of nectar affects pollinator preferences. Parasitoids prefer floral nectar
322 composed predominantly of sucrose (Vattala et al. 2006), partly due to a gustatory response (Cocco
323 and Glendinning 2012). Extrafloral nectar generally has a higher sugar concentration, whereas
324 honeydew has a lower nutritional quality than nectar (Lee et al. 2004).

325

326 *Temporal availability of resources:* The synchrony between the plant and arthropod cycles determines
327 the likelihood of interaction (Welch and Harwood 2014). The circadian rhythm of nectar production
328 must coincide with the timing of flower and extrafloral nectaries visitors. The seasonal availability of
329 resources depends on plant phenology. The phenological match between flowering period and
330 arthropod floral resource requirements is crucial for completion of the life cycles of both herbivores
331 and their natural enemies.

332 A number of trophic interaction traits have, thus, been clearly identified (Fig. 2), and several traits
333 must be considered simultaneously in the evaluation of trophic interactions between plants and
334 arthropods.

335

336 *2.3.2. Plant traits associated with the non-resource functions of the habitat*

337 Plants have a number of other effects on invertebrates in addition to providing food (Fig. 2): physical
338 habitat provision, microclimate modification and habitat provision for all life stages, including the
339 most critical, such as reproduction.

340

341 The structural properties of non-crop vegetation, such as density, height and litter quantity, are known
342 to influence the distribution of soil-dwelling arthropods (Griffiths et al. 2008). Plant structural traits,
343 such as growth form, height, architecture (density and orientation of branches and leaves, leaf
344 morphology) and the presence of domatia shape arthropod habitats (Parolin et al. 2012). For example,
345 plant morphology influences small-scale invertebrate distribution: plants with a complex morphology
346 have higher invertebrate abundances and biomasses than plants with a simple morphology (Hansen et
347 al. 2010). At a smaller scale, the properties of plant surfaces, such as leaf toughness, epicuticular
348 waxes, pubescence and trichomes, affect the attachment and movement of arthropods, with contrasting

349 effects on herbivores and predators, either enhancing or impairing biological control (Mitchell 2016;
350 Petersen 2016).

351

352 Plants also provide epigeic invertebrates with shelter, particularly during the periods outside the crop
353 growing season. The plant canopy maintains a moist microclimate and reduces wind speed (Norris and
354 Kogan 2005), protecting invertebrates from desiccation and providing favourable sites for aestivation.
355 Conversely, relatively dry sites with little temperature variation, such as grass tussocks, are favourable
356 sites for the overwintering of ground beetles (MacLeod et al. 2004). The role of plants in providing
357 suitable overwintering sites has been evaluated for a large range of plant and soil invertebrate species
358 (Bürki and Hausammann 1992), but the corresponding traits have yet to be identified, making it
359 difficult to draw general conclusions.

360

361 Habitat provision for reproduction, such as the choice of oviposition sites, has been analysed
362 principally in relation to adult and larval food distribution in the framework of optimal oviposition
363 theory (Wäckers et al. 2007). The olfactory stimuli emitted by plants, such as kairomones and
364 allomones, seem to predominate in the long-distance attraction or repulsion of gravid female
365 herbivores, whereas visual stimuli drive the choice of specific oviposition sites, limiting oviposition on
366 non-host plants (Hooks and Johnson 2003). Plants associated with higher egg survival rates are
367 suitable oviposition sites for phytophagous and predatory insects, and may be different from the plants
368 on which these insects feed (Norris and Kogan 2005). The physical characteristics of the plant are also
369 important. For example, hollow tree and shrub stems are selected as nesting sites for sphecid wasps
370 (Bitsch and Leclercq 1993). Nentwig (1992) recorded the oviposition preferences of lacewings on a
371 large range of plant species and found that oviposition rates were particularly high on plants of the
372 Papaveraceae and Boraginaceae species, possibly due to the pilosity of these species. However, it
373 remains unclear how plant traits, such as architecture or surface features (wax, pilosity etc.) affect the
374 oviposition behaviour of arthropods.

375

376 **3. Scaling up to the community and landscape levels**

377 ***3.1. Overcoming the limitations of single-species approaches***

378 Most studies on conservation biological control have focused on one or a few plant species and their
379 role in the regulation of one or a few herbivore groups by one or a few natural enemies (e.g. Langoya
380 and van Rijn 2008; Laubertie et al. 2012). Several of these studies have involved the screening of
381 plants in controlled conditions to identify the most appropriate species for increasing the biocontrol
382 performance of a particular natural enemy. The most frequently tested species are *Phacelia*
383 *tanacetifolia*, *Fagopyrum esculentum* Moench and *Lobularia maritima* (L.) Desv.

384

385 However, crops are generally susceptible to attacks from several herbivore species. Moreover, in
386 arable fields used for the cultivation of annual crops in rotation, a diverse community of natural
387 enemies is required to regulate the associated communities of herbivores. The surrounding non-crop
388 vegetation must, therefore, also consist of a mixture of plant species if it is to support a diverse
389 community of natural enemies. However, plant effects on arthropod behaviour have been analysed
390 mostly in pure stands, and little is known about the effect of plant assemblages (Pontin et al. 2006). In
391 plant communities, attractive plant species may divert herbivores from less attractive species, resulting
392 in lower visiting rates than for single-species stands. Interactions may also occur within arthropod
393 communities, such as competition between an aggressive species and a less aggressive species (bee vs.
394 hoverflies, Hogg et al. 2011). A greater diversity of plant resources and plant habitats may result in
395 lower levels of competition and other negative interactions between arthropods, promoting a greater
396 diversity of arthropods than would be expected from experimental results obtained for single-species
397 stands. The occurrence of interactions makes it necessary to develop community-level approaches, to
398 identify the characteristics of plant communities most likely to improve conservation biological
399 control. Most studies to date have focused on a particular mixture (e.g. Gillespie et al. 2011; Pfiffner et
400 al. 2009), but a small proportion of studies have compared different mixtures (eight studies out of 40
401 synthesized in Haaland et al. 2011).

402

403 However, there is strong evidence for functional relationships between plant and arthropod

404 communities. The abundance of phytophagous invertebrates is positively correlated with plant traits
405 related to resistance to community-level disturbances (e.g. low leaf dry matter content), suggesting a
406 functional link between the two communities (Storkey et al. 2013). In addition to the mean trait values
407 for plant communities, trait diversity may also be important. Potts et al. (2004) showed that the
408 diversity of nectar resources was positively related to bee species richness.

409

410 ***3.2. Which metrics provide information about the effects of plant community*** 411 ***structure on arthropod assemblages, and what are their limitations?***

412 In this section, we review the characteristics of plant communities relating to arthropod assemblages
413 and their functioning in terms of herbivore regulation.

414

415 Several descriptors can be used to characterise communities. The first is species identity. This
416 approach assumes that each species has an idiosyncratic role and that the functioning of the
417 community depends on the particular species it contains. This view may reflect insufficient knowledge
418 or an inadequate description of the mechanisms underlying the processes studied.

419

420 The second type of descriptor is based on the functional composition of the community. According to
421 the biomass-ratio hypothesis, ‘the extent to which the traits of a species affect ecosystem properties is
422 likely to be strongly related to the contributions of the species [...]’ to community biomass (Grime
423 1998). This suggests that the effects of plants on ecosystem functions are determined primarily by
424 mean trait values at community level, weighted by the relative importance of each species. For
425 example, in subalpine grasslands, the mean body mass of grasshoppers responds to the community
426 weighted mean of leaf dry matter content (Moretti et al. 2013). The abundance of nectar- and pollen-
427 feeding arthropods would be expected to increase with the amount of accessible resources provided by
428 the whole plant community, possibly modulated by their nutritional value.

429

430 However, interactions between the functional components of the community may result in a
431 community functioning that could not be inferred simply by adding together the effects of individual

432 species. The ecosystem impact of organisms from higher trophic levels may be less related to
433 abundance or biomass (Grime 1998) as in plants. Non-additive diversity effects can result from
434 functional complementarity, which facilitates niche partitioning, or from synergistic or antagonistic
435 interactions. Functional diversity is often measured as the diversity of functional traits and can be
436 described by functional trait richness, evenness and divergence (Dias et al. 2013). In plant-invertebrate
437 communities, a high diversity of plant resources and microhabitats would be expected to support a
438 high diversity of invertebrates. Podgaiski et al. (2013) found a positive correlation between functional
439 diversity in plant communities (in terms of size and architecture) and functional diversity in spiders
440 (morphology and web-building type). However, this finding was not supported by those of other
441 recent studies analysing the effects of the functional diversity of flower resources on natural enemies
442 (Balzan et al. 2014; Uyttenbroeck et al. 2017). Due to the long generation times of several natural
443 enemies, particularly for generalists, the temporal diversity of resource provisioning (e.g. flowering
444 date and duration) may play an important role than the instantaneous diversity of flower resources.

445

446 There is no consensus concerning the relative importance of community species composition and
447 functional structure (Costanzo and Barberi 2014), and the contribution of functional diversity effects
448 to ecosystem functioning remains unclear (Gagic et al. 2015; Garibaldi et al. 2015; Garnier et al.
449 2016).

450

451 Recent meta-analyses have provided evidence that plant species diversity and functional diversity
452 favour generalist predators (Dassou and Tixier 2016), thereby increasing herbivore regulation by
453 natural enemies (Iverson et al. 2014). Several unanswered questions remain concerning the type of
454 functional diversity (i.e. which traits?) and the degree of diversity optimising herbivore regulation.

455

456 ***3.3. How is plant functional diversity related to herbivore regulation?***

457 It is not easy to determine the level of functional diversity required to optimise herbivore control at
458 community level. The biological control of a single herbivore species might be expected to depend
459 principally on the amounts of trophic resources and habitats supporting its main natural enemies

460 (dominance effects). The plants traits supporting the natural enemies of additional herbivore species
461 may differ, resulting in a need for diverse plant functions to support the entire natural enemy
462 community required to regulate a community of herbivores. As shown by Isbell et al. (2011), the
463 larger the number of ecosystem services required of plant communities, the larger the number of plants
464 with different functions is needed to provide those services. However, in a plant community of fixed
465 size, plant functional diversity cannot be increased in isolation, without modifying other community
466 properties.

467

468 First, the generally hump-shaped relationship between the community weighted mean of traits (CWM)
469 and functional diversity (Dias et al. 2013) implies that, for any given trait, functional diversity tends to
470 be lowest at extreme values of CWM. Thus, depending on the plant trait values related to biological
471 control, this interdependence may constrain increases in functional diversity.

472

473 Second, evenness, which is a component of functional diversity, reduces dominance effects by diluting
474 the relative contribution of dominant species within the community. For example, combining plant
475 species according to their flowering period, so as to ensure that nectar and pollen are supplied
476 throughout the year, decreases the density of plants flowering at the same time. At peak flowering,
477 more resources are available in communities with a homogeneous phenology than in communities
478 with a heterogeneous phenology, resulting in a trade-off between the diversity of resources and their
479 instantaneous availability. Thus, increasing the diversity of plant traits to increase the diversity of
480 arthropods may result in a lower density of each type of arthropod.

481

482 This trade-off between evenness and dominance effects suggests that the functional diversity-
483 biological control relationship may not be monotonous. Provided that plant functional diversity
484 promotes complementarity and positive interactions with natural enemies, this should counterbalance
485 the decrease in plant dominance effects. Thus, the functional diversity-herbivore regulation
486 relationship may not always be positive, and may reach a plateau or an optimum value, depending on
487 the strength of the synergistic interactions at high levels of plant functional diversity. The deciphering
488 of this relationship will require experiments in which the functional composition and diversity of plant

489 communities are varied, for the simultaneous testing of the two effects, and for quantitative analyses
490 of the relationships between functional trait diversity, composition and ecosystem functions.

491

492 Several traits (Fig. 2) and metrics have been proposed to account for the interactions between species
493 or between restricted taxonomic groups. The next step is the identification of combinations of plant
494 community metrics accounting for the effects of the plant community on arthropod communities, and
495 taking into account the effects of functional composition, functional diversity and species identity
496 (when effects cannot be related to functional traits). The level of functional redundancy is another
497 important aspect.

498

499 ***3.4. Taking interactions with surrounding landscapes into account***

500 The management of a given habitat for conservation biological control must be adapted to the
501 characteristics of the neighbouring habitats, such as crop fields and other non-crop structures
502 (Tschamtkke et al. 2016). The creation of a new habitat, such as a wildflower strip, provides additional
503 resources and habitats. Plant community management or establishment should therefore be based on i)
504 assessments of the requirements of natural enemies and ii) assessments of the resources already
505 provided in the surroundings, in locally limiting resources or habitats. For instance, the effect of
506 wildflower strips on pollinators depends strongly on their complementarity with the resources already
507 available at landscape scale (Scheper et al. 2015), particularly as concerns synchrony between
508 flowering period and pollinator requirements. Plant traits must be adapted to abiotic conditions, such
509 as climate and soil conditions. In arid climates, arthropods may search for moist shelters protecting
510 them from drought stress (tussocks and creeping plants providing shade and higher levels of
511 humidity), whereas, in humid climates, open habitats with rapid warming may result in higher levels
512 of arthropod activity. A functional characterisation of the surrounding landscape (functional landscape
513 ecology) is therefore required, with an improvement of the metrics of landscape description beyond
514 land use (Vialatte 2017; landscape ecology). Simplified vegetation relevés, stratified by habitat type,
515 can be used to calculate the landscape-wide floral resource availability (Scheper 2015). This approach
516 could be extended to other plant properties, including habitat-related traits, and other metrics, such as

517 the spatial diversity of plant trait values. In the future, such descriptions of the properties of plant
518 communities at the landscape scale should make it possible to adapt habitat creation and management,
519 to improve spatial functional supplementation and complementation rather than making use of
520 standardised greening infrastructures.

521

522 **Conclusions and implications for conservation biological**

523 **control**

524 A trait-based approach opens up exciting new possibilities for improving our understanding of the
525 relationships between plant assemblages and conservation biological control. The well-known
526 influence of morphological and biochemical traits on the interaction between plants and pollinators
527 (Stang et al. 2009) suggests that this approach may also be useful for dealing with other biotic
528 interactions.

529

530 We also need to identify the characteristics of arthropod communities associated with efficient
531 biological control. Despite the general finding that the stable biological control of multispecies
532 herbivore communities requires functional diversity and a redundancy of natural enemies, the
533 development of appropriate management practices remains limited by our poor understanding of the
534 functioning of arthropod communities, and of their trophic interaction network, in particular.

535

536 We also propose the identification of “interaction traits” specifically involved in plant-arthropod
537 interactions, including the effect traits of plants (traits with an impact on arthropods) and the response
538 traits of arthropods (traits associated with the arthropod response to plants). Interaction traits are
539 correlated with plant features relating to the provision of trophic resources (amount of resource,
540 phenology of production, corolla shape etc.) and habitat (plant architecture) affecting arthropods (Fig.
541 2). Important interaction traits, such as nectar composition, extrafloral nectar availability, presence of
542 domatia and plant pilosity, are currently poorly documented in botanical databases. The use of such
543 traits would improve our mechanistic understanding of interactions at community level. It might also

544 make it possible to quantify the diversity and redundancy of interaction traits in plant communities and
545 to determine their relationship to the abundance of natural enemies or herbivore regulation.

546

547 We need to scale up our knowledge of plant-arthropod interactions, from the population to the
548 community level. The extent to which arthropod communities are affected by plant traits at
549 community level remains largely unexplored. An intermediate level of plant functional diversity might
550 be expected to maximise the service of herbivore regulation, but experimental designs facilitating the
551 comparison of contrasting plant communities (such as Hatt et al. 2017) will be useful for disentangling
552 the respective roles of plant functional composition and diversity.

553

554 The identification of relevant community characteristics should not be limited to additive species
555 traits. It should also take into account the structure of the interaction network, species complementarity
556 and the generalist/specialist ratio.

557

558 Over and above the identification of relevant plant traits, the high specificity of certain plant-insect
559 and insect-insect interactions may weaken the trait-based approach. Aphid-parasitoid and plant-aphid
560 interactions are usually species-specific. Consequently, aphid regulation often requires the targeting of
561 a particular aphid species by promoting a particular parasitoid species. Trade-offs may occur between
562 the positive effects of plant traits on one group of natural enemies and negative effects on another. It
563 therefore seems likely that some sets of traits are related to herbivore regulation in general, but we
564 cannot exclude the possibility that these combinations are highly specific and that a trait-based
565 approach is not necessarily more straightforward than a species-based approach. We do not, therefore,
566 recommend the exclusive use of trait-based approaches, and advances in food-web ecology will
567 undoubtedly also improve the understanding and management of trophic interactions. If interactions
568 are idiosyncratic or poorly understood, and if trait attributes are phylogenetically conserved, then
569 phylogenetic parameters may be better predictors of ecosystem functioning than functional traits or
570 groups (Cadotte et al. 2008). However, interaction specificity usually includes a single dimension of a
571 niche, and a trait-based approach may still be straightforward for the other dimensions. For generalist
572 predators, a trait-based approach would remain relevant, but difficulties may arise due to the number

573 of traits and their interactions to be considered in each situation to predict their functioning. If patterns
574 become too complex and difficult to generalize, then the trait-based approach may be impractical.

575

576 In practice, interaction traits may be used to decide on the combinations of plant properties required to
577 guide the formulation of seed mixtures for creating or restoring semi-natural habitats, rather than using
578 standard species lists applied to several biogeographical zones. The identification of plant species from
579 the local flora with the desired trait criteria would make it possible to design seed mixtures with
580 similar functional characteristics based on species adapted to local climatic conditions.

581

582 The use of functional traits as proxies for community and ecosystem functioning should not
583 completely supplant other drivers of plant arthropod interactions, such as environmental conditions
584 and habitat management. In addition, the use of plant communities to support biological control must
585 also take into account a diversity of ecological, technical and socio-economic criteria, such as a
586 potential loss of diversity during plant succession.

587

588 Problematic weed species cannot be included in the mixtures sown, even if they present ideal trait
589 combinations. Plant species of local origin should be preferred whenever possible, to select locally
590 adapted populations and to prevent genetic pollution. Finally, trade-offs with other ecosystem services
591 should be considered from a multifunctional standpoint, including pollination, species conservation
592 and landscape aesthetics.

593

594

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597 Conflict of interest: The authors have no conflict of interest to declare.

598

599

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843 **Figures and online resource**

844

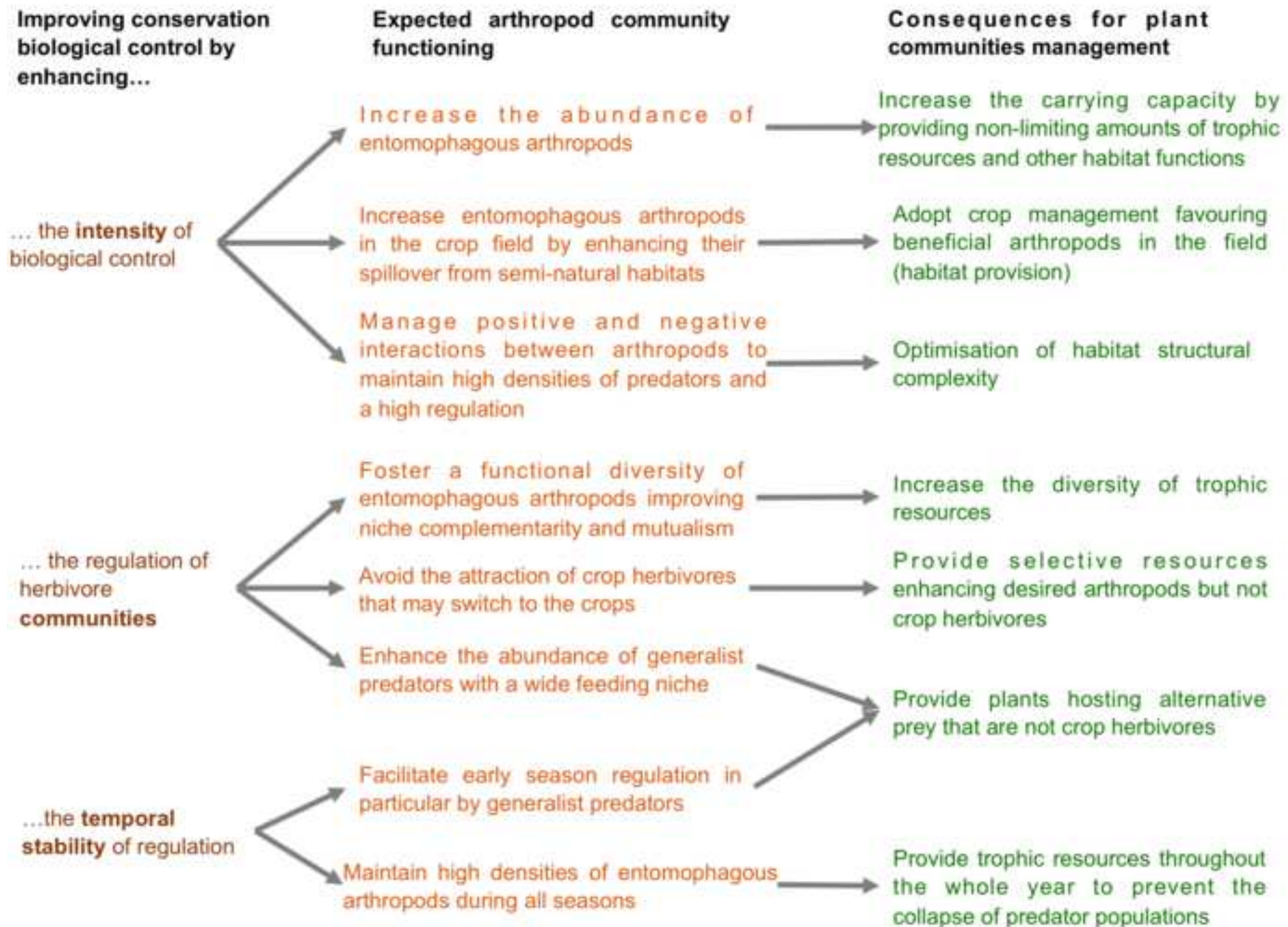
845 **Fig. 1** Outline of the main objectives targeted for efficient conservation biological control (first
846 column), their effects on arthropod community functioning (second column) and on plant community
847 and habitat management (third column), synthesised from published findings.

848

849 **Fig. 2** Overview of the main plant-arthropod interaction traits recorded in published studies and
850 relevant for managing arthropod communities by conservation biological control. *Heracleum*
851 *sphondylium* image © Pierre Déom – www.lahulotte.fr

852

853 **Online Resource 1.** List of the articles selected with the search equation in the Web of Science
854 literature database and used for the review.



Plant traits***Traits associated with trophic interactions***

Resource type (nectar, pollen, seeds, leaves) and quantity

Attractiveness: odour, taste, inflorescence size and colour, secondary metabolites

Accessibility: flower shape

Nutritional quality : sugar composition, leaf structural traits

Phenology: flowering date, duration, timing of resource production

Traits associated with non-resource habitat functions

Physical habitat provision: domatia, hollow stems, pilosity

Architecture: height, growth form, vertical leaf distribution

**Arthropod traits*****Traits associated with trophic interactions***

Trophic level, diet and specific food requirements at different life-cycle stages

Food preferences, ovigeny, mouthparts structure

Body size, head width

Phenology: voltinism, breeding season, emergence season

Traits associated with non-resource habitat functions

Mobility, body size, dispersal mode, hunting strategy, sociality

Ecological preferences for overwintering, aestivation, oviposition

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Understanding plant-arthropod interactions in multitrophic communities to improve conservation biological control: useful traits and metrics

Journal of Pest Science

Antoine Gardarin, Manuel Plantegenest, Armin Bischoff and Muriel Valantin-Morison

Corresponding author: UMR Agronomie, INRA, AgroParisTech, Université Paris-Saclay, 78850 Thiverval-Grignon, France. Antoine.Gardarin@inra.fr.

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