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## ► To cite this version:

Séverin Yvoz, Stéphane Cordeau, Alexandre Ploteau, Sandrine Petit. A framework to estimate the contribution of weeds to the delivery of ecosystem (dis)services in agricultural landscapes. *Ecological Indicators*, 2021, 132, pp.108321. 10.1016/j.ecolind.2021.108321 . hal-03483120

**HAL Id: hal-03483120**

**<https://hal.inrae.fr/hal-03483120>**

Submitted on 5 Jan 2024

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# 1 **A framework to estimate the contribution of weeds to the delivery** 2 **of ecosystem (dis)services in agricultural landscapes**

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## 7 **Abstract**

8 There is a pressing need for indicators and methods to quantify the provision of ecosystem  
9 services as a prerequisite to identify management options that optimize trade-offs between  
10 services. Arable weeds provide multiple services and are thus a good model to evaluate such  
11 trade-offs. This flora provides trophic resources (flowers or seeds) that support pollinators and  
12 pest natural enemies (pollination and pest control services) but can also be harmful for crop  
13 production (disservice). To date, few indicators are available to quantify the contribution of  
14 weeds to ecosystem services or their harmfulness, and no indicators account for intraspecific  
15 variability in weed traits that result from contrasting growing conditions, notably the location  
16 of weeds within fields (field edge vs field core) and crop type. Here, we developed nine proxies  
17 for potential weed harmfulness (competition, harvest difficulties and future weed infestations)  
18 and weed contributions to resources provision to pollinators (bees, bumblebees and hoverflies)  
19 and pest natural enemies (carabid beetles, birds and parasitoid wasps). These nine proxies  
20 accounted for individual weed plant response to growing conditions (combination of within-  
21 field location by crop type) for 155 weed species, resulting in 967 unique situations  
22 (combinations of species by within-field locations by crop types). Apart from harvest  
23 difficulties, all proxies were positively correlated, i.e. harmfulness increased when services  
24 increased. Weed plants located on field edges had greater contributions to all proxies than those  
25 located in field cores, especially in cereal crops. We identified that small weed species with  
26 short life cycles and low competitiveness, presented the optimum proxy combination, i.e. high  
27 services and low harmfulness. The development of these proxies and the proposed framework  
28 provide new avenues for assessing trade-offs between multiple ecosystem services at different  
29 temporal (crop sequence) and spatial scales (landscape).

30 **Keywords:** indicator, ecosystem function, biological control, pollination, disservice,  
31 multifunctionality, functional traits, crop edge

## 32 1. Introduction

33 The intensification of human activities has led to a general decline of biodiversity worldwide  
34 (Vitousek, 1997) and has shed light on the role of biodiversity in the functioning of ecosystems  
35 and the maintenance of human well-being (Duru et al., 2015). Research on ecosystem services  
36 has developed considerably over the past decades and their quantification is often identified as  
37 a priority because it is a prerequisite to planning that enhances ecosystem multifunctionality  
38 (Kremen and Ostfeld, 2005). However, the assessment of ecosystem services still presents  
39 many methodological challenges (Reyers et al., 2013), a situation that calls for the development  
40 of indicators quantifying services and their response to land management (van Oudenhoven et  
41 al., 2012).

42 While often considered as pests in agricultural landscapes, weeds interact with many organisms  
43 and are often associated with the provision of multiple ecosystem services (Blaix et al., 2018;  
44 Gaba et al., 2020). Weeds can be harmful to crop production if they outcompete crops for  
45 resources (Adeux et al., 2019). Weed seeds can also affect the quality of the harvest and/or  
46 replenish weed seedbank (Walsh et al., 2013), leading to potential crop yield loss in the future.  
47 Weeds are however also key providers of trophic resources in agroecosystems (Marshall et al.,  
48 2003; Pocock et al., 2012). The role of weed seeds for farmland birds (Holland et al., 2006) and  
49 carabid beetles (Honek et al., 2003) is well established. Weed flowers are an important trophic  
50 resource for bees (Requier et al., 2015) and can asynchronously supplement provisions made  
51 by mass flowering crops (Bretagnolle and Gaba, 2015). Functional approaches offer a robust  
52 framework to quantify and understand the mechanisms underlying the delivery of weed  
53 functions in agroecosystems (Navas, 2012). There have been substantial advances in the  
54 identification of weed traits that are key to specific functions (Cordeau et al., 2017; Gaba et al.,  
55 2017), and weed mean trait values (*i.e.* average value of a trait for a species, across a wide range  
56 of growing conditions) have become increasingly accessible in databases (*e.g.* TRY: (Kattge,  
57 2012); LEDA: (Kleyer et al., 2008)). Functional approaches accounting for the pattern of weed  
58 competitive ability and the resulting impact on crop yield have been the focus of several studies  
59 (Adeux et al., 2019; Storkey, 2006). Similarly, quantification of weed traits have helped  
60 decipher the complex interactions between weeds and other trophic groups, for example floral  
61 traits and pollinators (Rosas-Guerrero et al., 2014) or seed traits and pest natural enemies  
62 (Storkey et al., 2013). In some rare instances, this knowledge has been mobilised to derive trait-  
63 based indicators of weed functions, for example valuations of weed species for different  
64 pollinator groups (Ricou et al., 2014), or index of ecological value (Fanfarillo and Kasperski,  
65 2021; Hyvönen and Huusela-Veistola, 2008). One important limitation has been the assumption

66 that weed traits values are constant across a large range of environmental situations. Indeed,  
67 trait values can vary according to the growing conditions of individual plants, with important  
68 implications for the outcome of ecological interactions (Bolnick et al., 2011).

69 Intraspecific variability in weed trait values remains poorly documented and can be quite large  
70 for some traits (Kazakou et al., 2014) as weeds in arable agriculture grow in different  
71 environments. First, many species are both found in the interior and in the edge of fields, an  
72 area potentially less impacted by farming practices and crop competition (Dutoit et al., 1999).  
73 Several studies have demonstrated significant intraspecific differences in trait values in  
74 common weed species between the edge and the core of the field (Perronne et al., 2014).  
75 Second, the crop type and the agricultural practices that are implemented to grow each type of  
76 crop are substantial causes of variations in the growing environment of weed plants. For  
77 example, Borgy et al. (2016) demonstrated a high intraspecific variability in specific leaf area  
78 (SLA) of several common weed species between crop types, possibly due to differences in crop  
79 canopy closure. This suggests a variation of the plant growth and thus in the timing and amount  
80 of flower and seed production. Crop management (tillage and sowing date, level of fertilisation,  
81 type and frequency of weeding operations) can also strongly modulate weed growth/phenology  
82 and hence their capacity to compete with the crop (Blackshaw et al., 2004) or to provide floral  
83 or seed resources throughout the season (Perron and Legere, 2000).

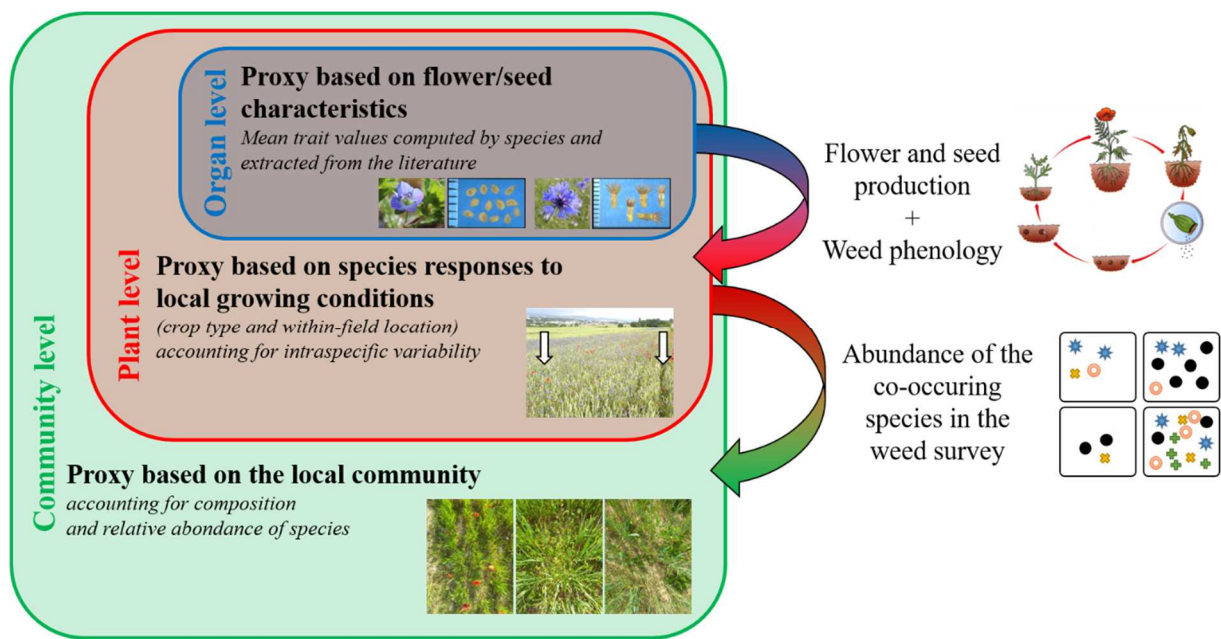
84 Here, we address the impact of intraspecific variability found in weed species on the estimation  
85 of several ecosystem services provided by weeds. We first present a framework and a set of  
86 nine proxies that were developed in order to account for the combined effect of within-field  
87 location (field edge *vs* field core) and crop type (six crop types) on plant contribution to  
88 ecosystem services and harmfulness. We applied these proxies to 155 weed species observed  
89 in various growing conditions. We then used these proxies to identify and characterise (response  
90 trait values and growing conditions) groups of species expressing similar proxy bundles. We  
91 hypothesised that traits and/or growing conditions of certain weed species may solve  
92 antagonisms between services and harmfulness. Specifically, we expected that species located  
93 in field edges have a higher contribution to ecosystem services due to the possibly lower crop  
94 competition and intensity of farming practices.

95 **2. Materials and methods**

96 Our framework transforms weed surveys, *i.e.* lists of weed species described by their abundance  
97 in a particular within-field location (field core or edge) and crop type into values representing  
98 their potential contribution to ecosystem services and harmfulness.

99 **2.1. Framework to develop proxies of weed contribution to ecosystem**  
100 **services and harmfulness**

101 In our framework, the computation of a proxy considered three levels of organisation  
102 (Figure 1): the organ level, describing the invariant characteristics of species, the plant level  
103 accounting for the species response to the growing conditions, and the community level  
104 accounting for the species composition and relative abundance observed in weed surveys. In  
105 the present paper, we focus on the account for plant growing conditions on the provision of  
106 (dis)services and do not address the community level.



107  
108 **Figure 1:** Methodological scheme presenting the three levels of organisation involved in the construction of  
109 proxies of ecosystem services and harmfulness provided by weeds.

110 Nine proxies were developed to estimate the delivery of ecosystem (dis)services by weeds.  
111 Three proxies evaluate the production of resources for pollinators (namely bees (Pol1),  
112 bumblebees (Pol2) and hoverflies (Pol3)). Three other proxies assess the production of  
113 resources for pest natural enemies (namely farmland birds (PCont1), carabids (PCont2) and  
114 parasitoid wasps (PCont3)). Finally, three harmfulness proxies assess the direct competition  
115 between weeds and the crop for resources (Harm1), harvest difficulties caused by weeds  
116 (Harm2) and future weed infestations (Harm3).

117 Based on a literature review, we identified the main traits impacting the quality of a flower or  
118 a seed for pollinators or pest natural enemies. The resource provision for pollinators (*i.e.* Pol1,  
119 Pol2, Pol3) and pest natural enemies (*i.e.* PCont1, PCont2, PCont3) and the future weed  
120 infestations (*i.e.* Harm3) are linked to characteristics of weed species organs which are  
121 relatively stable over the growing conditions. We then extracted values from the literature or  
122 online databases when available. The values at the organ level were then multiplied by the  
123 number of flowers or seeds produced by an individual weed plant. This step accounted for the  
124 effect of the within-field location and the crop type on the number of flowers and seeds per  
125 plant through the season (Yvoz et al., 2020a). Some potential weed contributions to ecosystem  
126 services and harmfulness are associated with characteristics of the plant not associated with a  
127 specific organ (*e.g.* maximum height at flowering being related to the competitive ability) but  
128 still varying with growing conditions. Thus, competition for resources (Harm1) and harvest  
129 difficulties (Harm2) were characterised at the plant level, based on traits and indicators  
130 describing the weed development in interaction with the growing conditions.

## 131 **2.2. Application of the proxies to weed survey data**

### 132 **2.2.1. Data collection**

133 We used weed data collected within the Fénay platform located near Dijon in eastern France  
134 (47°13 N, 5°03 E) and composed of 950 ha of contiguous fields subject to homogeneous  
135 continental climatic conditions. The area is mostly cultivated with winter crops (54% of winter  
136 cereals and 28% of winter mustard and oilseed rape) in rotation with spring and summer crops  
137 (*e.g.* spring barley and soybean).

138 Between 2008 and 2013, the weed flora in the core and edge of 97 fields was surveyed once a  
139 year (Yvoz et al., 2020b). Weed surveys were carried out in March for winter crops, in April  
140 for spring crops and in June for summer crops. In both locations, weed species were identified  
141 to the species level when possible, named according to Jauzein (1995) and their abundance  
142 visually estimated using the scale developed by Barralis (1976). Based on the records of  
143 farming operations (Yvoz et al., 2020b), weed surveys conducted less than one week after the  
144 last in-crop weeding practices (chemical or mechanical) were discarded. This resulted in three  
145 to six annual records per field across the six years, leading to a total of 826 weed records. (*i.e.*  
146 413 in both field cores and field edges) associated with six crop types (winter oilseed rape,  
147 winter mustard, winter wheat, winter barley, spring barley and soybean). Altogether, this  
148 dataset contained a total of 155 weed species observed in 12 combinations of crop type by  
149 within-field location (Table 1), resulting in a dataset of 967 unique situations (*i.e.* an individual  
150 plant of a weed species observed in a within-field location of a particular crop type).

151 **Table 1:** Occurrence of the 155 studied weed species in each of the 12 combinations of within-field location by  
 152 crop type (*i.e.* 967 unique situations of species by within-field location and crop type), based on weed surveys  
 153 conducted over the 2008-2013 period on the Fényay platform (Dijon, France).

Crop type Within-field location	Winter oilseed rape	Winter mustard	Winter wheat	Winter barley	Spring barley	Soybean	<b>Total</b>
Field edge	111	114	126	99	94	83	<b>627</b>
Field core	70	66	65	44	41	54	<b>340</b>
<b>Total</b>	<b>181</b>	<b>180</b>	<b>191</b>	<b>143</b>	<b>135</b>	<b>137</b>	<b>967</b>

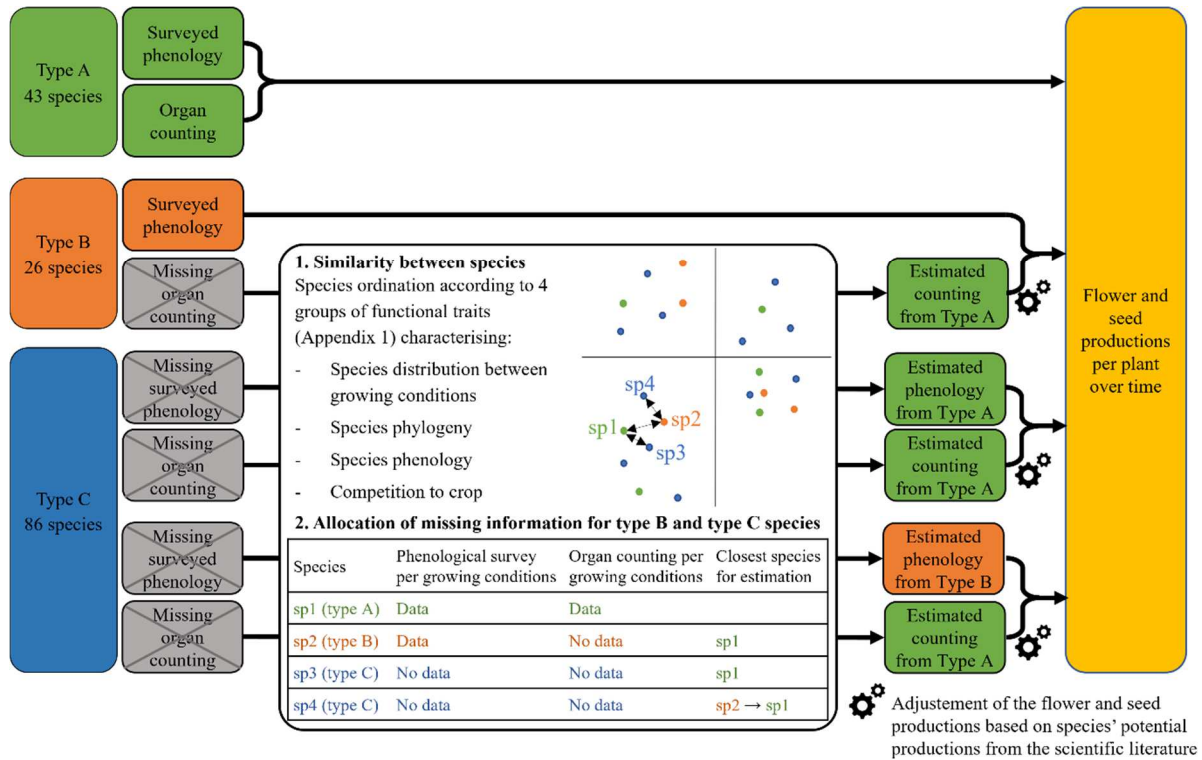
154

### 155 **2.2.2. Proxy calculation**

156 To integrate weed plant responses to the local growing conditions (*i.e.* intraspecific variability)  
 157 for the 155 weed species, we divided species into 3 categories (Type A, B and C, Figure 2)  
 158 based on available phenological data (Yvoz et al., 2020a): phenology and flower/seed  
 159 production were known for Type A species (N=43 species, Figure 2), only phenology was  
 160 known for Type B species (N=26) and none of this information was collected for the Type C  
 161 species (N=86). A procedure was thus developed to allocate missing information (grey boxes  
 162 in Figure 2), based on the proximity between species in terms of their occurrence in and  
 163 response to the set of growing conditions studied. Proximity was estimated through  
 164 multidimensional distance between Type B or C species and Type A or B species, accounting  
 165 for 27 variables, *i.e.* 12 variables describing the occurrence of plants in the 12 growing  
 166 conditions and 15 plant traits describing their response to growing conditions. The whole  
 167 procedure, including traits description and selection, clustering methodology, identification of  
 168 the closest species observed in the same growing conditions (within-field location by crop type),  
 169 is presented in Appendix A. For Type A species, the production of flowers and seeds over time  
 170 (*i.e.* every two-weeks) was calculated for each growing condition, based on the phenological  
 171 surveys and organ counting (Figure 2). For Type B species, the production of flowers and seeds  
 172 were estimated for each species (sp2 in Figure 2) across all growing conditions from the closest  
 173 species observed in the same growing condition (*i.e.* sp1 in Figure 2, see details in Appendix  
 174 A: Table A3). Production of flowers and seeds of sp2 (Type B) were then adjusted by the known  
 175 differences of potential organ production (Eq. 1) with sp1 (Type A), based on a literature  
 176 review. Finally, like Type A species, production of flowers and seeds were estimated over time  
 177 based on the phenological surveys of sp2.

$$178 \text{ Adjustment} = \frac{\text{Potential organ production of sp2,3 or 4}}{\text{Potential organ production of sp1}} \quad (\text{Eq. 1})$$

179



181

182 **Figure 2:** Methodology used to estimate phenological development and production of flowers and seeds of weed  
 183 species when data were present (Type A) or missing (Type B and C species). When data were missing, the known  
 184 data from the closest species (*i.e.* multivariate trait-based distance) observed in the same growing condition  
 185 (within-field location-by-crop type) were attributed to the species (see Appendix A for the detailed procedure and  
 186 traits' description). Flower and seed numbers attributed to sp2, sp3 or sp4 were adjusted by considering the  
 187 differential ratio of the potential organ production derived from the literature between species with missing (sp2,  
 188 sp3, sp4) and counted (sp1) data. Adjustment = Potential production of the estimated species (sp2, 3 or 4)/Potential  
 189 production of the counted species (sp1).

190

191 For Type C species, we attributed both the phenological profile and production of flowers and  
 192 seeds from the closest species (see details in Appendix A: Table A3) when these data were  
 193 known. If the closest species was a Type A species, we attributed the phenology and organ  
 194 counting of sp1 (Type A) to sp3 (Type C) and then adjusted it (Eq. 1). If the closest species was  
 195 a Type B, we attributed the surveyed phenology and estimated organ productions of sp2 (Type  
 196 B) to sp4 (Type C), then adjusted (Eq. 1).



## 197 **2.3. Data analyses**

### 198 **2.3.1. Correlations between proxies at the plant level**

199 All statistical analyses were implemented with the R software version 4.0.4 (R Core Team,  
200 2021). To identify antagonisms or synergisms between proxies at the plant level, a Principal  
201 Component Analysis (PCA) using the *PCA* function from the [FactoMineR] package was  
202 implemented on the proxy values of the 967 unique situations. As proxies showed few extreme  
203 values (Supp. Figure 1), they were rescaled prior to the grouping analysis. For each proxy, we  
204 calculated the log10 ratio of the observed value to the maximum value, then rescaled it from 0  
205 to 10 using the *rescale* function from the [scales] package (Eq. 2).

$$206 \text{ Scaled proxy} = \text{rescale}\left[\text{Log}_{10}\left(\frac{\text{proxy}+1}{\max(\text{proxy})+1}\right), \text{to} = c(0,10)\right] \quad (\text{Eq. 2})$$

207

### 208 **2.3.2. Identification and characterisation of unique situations delivering similar proxy** 209 **bundles**

210 Groups of unique situations that exhibited similar values for multiple proxies, (called proxy  
211 bundles) were identified using the method proposed by Raudsepp-Hearne et al. (2010). The  
212 unique situations-by-proxies database was submitted to a PCA followed by a Hierarchical  
213 Clustering Analysis (HCA) based on the Ward's method, using the *HCPC* function from the  
214 [FactoMineR] package. Clear and non-redundant groups were identified through examination  
215 of the dendrogram and confirmed the grouping using the Elbow method computing the gain of  
216 explained variance when increasing the number of clusters. Groups were then characterised in  
217 terms of average proxy values using a one-way analysis of variance using the *catdes* function  
218 from the [FactoMineR] package. Radar charts were implemented to represent the distribution  
219 of all proxy values for each of the identified groups of plants using the *radarchart* function  
220 from the [fmsb] package. Here, proxies for harmfulness (*i.e.* Harm1, Harm2 and Harm3) were  
221 reversed so that they had the same directionality as service proxies, *i.e.* the highest, the best.  
222 Groups of unique situations were then characterised, first, by the proportion of situations  
223 associated with the different crop types and within-field locations and, second, by the six  
224 functional response traits (maximum height at flowering, SLA, leaf dry matter content  
225 (LDMC), Ellenberg.N and .L values, and seed mass) and five descriptors of weed phenology  
226 (germination onset and end, flowering onset and end, and leaf type) (traits description in Supp.  
227 Table. 1).

## 228 **3. Results**

### 229 **3.1. Proxies of potential weed contribution to services and harmfulness**

230 The equations of the nine proxies we developed to quantify potential weed contribution to  
231 ecosystem services and harmfulness are detailed in Table 2. The description, references and  
232 data sources used in the equations are detailed in Supp. Table 1.

#### 233 **3.1.1. Resources for pollinators (Pol1, Pol2, Pol3)**

234 Pollinators include a diversity of organisms such as bees, bumblebees and hoverflies  
235 contributing largely to the pollination of crops in agricultural landscapes (Eilers et al., 2011).  
236 Weeds contribute to the conservation of pollinator populations by the provision of nectar and  
237 pollen before and after crop flowering, and by providing more diverse resources otherwise  
238 (Carvalho et al., 2011). The benefits of a particular weed species depend on its attractiveness  
239 (*e.g.* associated with the flower colour (Backhaus, 1992), ultra-violet (UV) reflectance (Horth  
240 et al., 2014) or flower symmetry (Wignall et al., 2006)), its accessibility (*e.g.* determined by the  
241 form and size of the corolla (Lehrer, 2005)) and the quantity and quality of the floral rewards  
242 (*e.g.* pollen (Hass et al., 2019) and/or nectar (Pamminger et al., 2019)).  
243 Ricou et al. (2014) listed and integrated these aspects to develop an indicator of pollination  
244 value of a large number of weed species for three groups of pollinators: bees (wild and honey  
245 bees), bumblebees and hoverflies. Based on their work, we developed three proxies estimating  
246 the contribution of individual weed plants to bees (Pol1), bumblebees (Pol2) and hoverflies  
247 (Pol3). We used pollination values from Ricou et al. (2014) and exponentialized them as authors  
248 showed a linear regression between pollination values and the natural logarithm of pollinator  
249 visits. As they recommended, we multiplied these indicators by flower diameter, thus  
250 accounting for the differences between species in flower size and resources quantity per flower  
251 (Table 2). As pollinator values were missing for 34 of our 155 weed species, we computed the  
252 mean value of the species belonging to the same genus for 12 species. For the 22 other species,  
253 we imputed the values of the closest species among the 133 others, based on the 12 variables  
254 describing flowers (*i.e.* nectar quantity and quality, pollen quantity, protein content of pollen,  
255 flower symmetry, colour, size and shape, flower class, flower type and UV reflectance in the  
256 centre and the petals, see details in Supp. Table 1), using the *imputeMFA* function from the  
257 [missMDA] package.

#### 258 **3.1.2. Resources for pest natural enemies (PCont1, PCont2, PCont3)**

259 Many studies highlighted that weed species may impact the longevity and fecundity of pest  
260 natural enemies such as farmland birds (Holland et al., 2006), carabid beetles (Honek et al.,

261 2003) and parasitoid wasps (Wäckers et al., 2005). Thus, we developed three proxies  
262 highlighting the contribution of individual weed plants to sustain farmland birds (PCont1),  
263 carabids (PCont2) and parasitoids (PCont3).

264 Although farmland birds' diet is mainly composed of invertebrates (Barré et al., 2018), seeds  
265 represent most of their diet in autumn and winter when arthropods become scarce (Holland et  
266 al., 2006). In spring and summer, adult birds complete their diet with seeds (Holmes and Froud-  
267 Williams, 2005). Gibbons et al. (2006) showed a positive correlation between seed preference  
268 and their energy concentration, somehow related to the seed lipid content (Greig-Smith and  
269 Wilson, 1985). Carabids can consume a third of their weight of seeds daily in spring and  
270 summer (Honek et al., 2003). Carabid preferences are also linked to the seed lipid content (Gaba  
271 et al., 2019), however the seed size is a limiting factor for their consumption, *i.e.* seeds heavier  
272 than 3 mg are rarely consumed by carabids (Petit et al., 2014). For birds (PCont1) and carabids  
273 (PCont2), we thus considered the quantity of lipids per seed as a proxy of the energy resources  
274 (Table 2). For carabids only, we added an accessibility coefficient accounting for seed mass  
275 thresholds (3 and 35 mg, Table 2). The seed lipid content was extracted from the literature  
276 (Supp. Table 1). For 13 weed species where data were missing in the literature, we computed  
277 the average of the species belonging to the same genus.

278

279 Most parasitoid wasps rely on carbohydrate resources, provided by honeydew or by crop and  
280 weed floral and extra-floral nectar, to increase their longevity and fecundity (Leatemala et al.,  
281 1995). Beneficial effects of nectar could depend on the type of carbohydrate (Vattala et al.,  
282 2006), despite no consensus emerges on the best type. Baker and Baker (1983) showed  
283 preferences for nectar rich in saccharose, whereas recent studies showed no differences between  
284 saccharose, fructose and glucose effects on parasitoid longevity (Hausmann et al., 2005;  
285 Winkler et al., 2005). The contribution of weed species to parasitoidosis however restricted by  
286 the accessibility to the floral nectar, which depends on the flower morphology (Jervis, 1998).  
287 Parasitoids generally have short mouthparts avoiding them to exploit nectar from tubular  
288 flowers longer than 4.5 mm (Orr and Pleasants, 1996; Vattala et al., 2006). Olfactive and visual  
289 attractivity also influence nectar consumption (Wäckers, 2004). In addition, Zhu et al. (2020)  
290 showed, through a trait-based approach, the importance of flower colour and shape, and nectar  
291 position. Nevertheless, the inflorescence type and the corolla depth emerge as the most  
292 important aspects. Rogers (1985) also highlighted the importance of the extra-floral nectar,  
293 easily accessible for parasitoids.

294 As a result, our proxy for weed contribution to the maintenance of parasitoid wasps (PCont3)  
295 was the sum of the contribution of the floral and the extra-floral nectars. To evaluate the

296 contribution of the floral nectar at the organ level (here flower), we developed an equation  
297 multiplying the flower diameter by three coefficients (between 0 and 1) representing the interest  
298 in terms of nectar quantity, flower shape and corolla depth (Table 2). This equation allows the  
299 computation of null values, as soon as at least one aspect is not favourable. The nectar quantity  
300 was extracted from the literature (Supp. Table 1) or computed as the average value of species  
301 belonging to the same genus for 17 species. At the plant level, we added a bonus rewarding the  
302 six weed species producing extra-floral nectar (Table 2), namely *Cyanus segetum* Hill,  
303 *Centaurea jacea* L., *Centaurea scabiosa* L., *Fallopia convolvulus* (L.), *Sambucus ebulus* L. and  
304 *Vicia sativa* L. (Jayanthi et al., 2019; Keeler, 1979; Salisbury, 1909; Weber et al., 2015). The  
305 bonus (REN in Table 2) was computed as a proportion (from 0 to 1) of the floral nectar part  
306 (QEN in Table 2), determined by the position of the extra-floral nectar on the plant (*i.e.* on  
307 vegetative or reproductive tissues), the bonus increasing with the phenological stage of plants  
308 until flowering. As adult parasitoids have a short life cycle and their prey are mainly associated  
309 with cereal crops, oilseed rape and mustard, we computed this proxy from March to June, the  
310 value being null otherwise.

311 **Table 2:** The nine proxies assessing the potential contribution of weeds to ecosystem services and harmfulness. In all equations, *i* refers to one of the 155 studied weed species.  
 312 The colours refer to the level of organisation (Figure 1): blue is the weed species' organ level, depending only on the weed species; red: plant level, thus influenced by the  
 313 growing conditions (*e.g.* crop type and within-field location); green: community level, influenced by the weed community composition and abundance recorded in the weed  
 314 survey. Traits used in the equations are detailed in Supp. Table 1.

Proxies	Equations
Potential weed contribution to pollinators: - bees ( <b>Pol1</b> ) - bumblebees ( <b>Pol2</b> ) - hoverflies ( <b>Pol3</b> )	$Polj = \sum_{i=1}^{155} (exp \exp (PV_j(i)) \times FD(i) \times FN(i) \times A(i))$ <ul style="list-style-type: none"> <li>- <b>PV<sub>j</sub></b>: Pollinator value from Ricou et al. (2014), j in {1, 2, 3}</li> <li>- <b>FD</b>: Flower diameter</li> <li>- <b>FN</b>: Average flower number per plant</li> <li>- <b>A</b>: Abundance of the species in the survey</li> </ul>
Potential weed contribution to pest natural enemies - farmland birds ( <b>PCont1</b> )	$PCont1 = \sum_{i=1}^{155} (SL(i) \times SM(i) \times SN(i) \times A(i))$ <ul style="list-style-type: none"> <li>- <b>SL</b>: Seed lipid content</li> <li>- <b>SM</b>: Seed mass</li> <li>- <b>SN</b>: Average seed number per plant</li> <li>- <b>A</b>: Abundance of the species in the survey</li> </ul>
Potential weed contribution to pest natural enemies - carabids ( <b>PCont2</b> )	$PCont2 = \sum_{i=1}^{155} (SL(i) \times SM(i) \times SA(i) \times SN(i) \times A(i))$ <ul style="list-style-type: none"> <li>- <b>SL</b>: Seed lipid content</li> <li>- <b>SM</b>: Seed mass</li> <li>- <b>SA</b>: Seed availability (1 if SM &lt; 3mg; Linear decrease from 1 to 0 for SM=3 to 35mg; 0 if SM &gt; 35mg)</li> <li>- <b>SN</b>: Average seed number per plant</li> <li>- <b>A</b>: Abundance of the species in the survey</li> </ul>

Proxies	Equations																											
Potential weed contribution to pest natural enemies - parasitoid wasps ( <b>PCont3</b> )	$PCont3 = \sum_{i=1}^{155} (NQ(i) \times FF(i) \times CD(i) \times FN(i) \times A(i)) + \sum_{k=1}^9 (QEN(i) \times P(ki) \times REN(ki) \times A(i))$ <ul style="list-style-type: none"> <li>- <b>NQ</b>: Nectar quantity (none = 0; little = 0.4; present = 0.8; plenty = 1)</li> <li>- <b>FF</b>: Flower form (funnel shaped = 1; disc-bowl shaped = 0.7; bell shaped = 0.6; head shaped = 0.5; flag shaped = 0.2; other = 0)</li> <li>- <b>CD</b>: Corolla depth (&lt;4.5 mm = 1; &gt;4.5 mm but nectar available = 0.5; no nectar or unavailable = 0)</li> <li>- <b>FN</b>: Average flower number per plant</li> <li>- <b>A</b>: Abundance of the species in the survey</li> <li>- <b>QEN</b>: Quantity of extra-floral nectar estimated as the maximum value of PCont3 per half month for the floral nectar part</li> <li>- <b>P</b>: Proportion of plants at the stage k; k phenological stage in {A, B, C1, C2, D1, D2, D3, E1, E2} (Yvoz et al., 2020a)</li> <li>- <b>REN</b>: Rate of the maximum extra-floral nectar production depending of the phenological stage k</li> </ul> <hr/> <table border="1" style="width: 100%; border-collapse: collapse;"> <thead> <tr> <th style="text-align: left;">Phenological stage (Yvoz et al., 2020a)</th> <th style="text-align: center;"><b>REN</b> for <i>Fallopia convolvulus</i> (L.), <i>Sambucus ebulus</i> L. and <i>Vicia sativa</i> L. Extra-floral nectar on vegetative parts</th> <th style="text-align: center;"><b>REN</b> for <i>Cyanus segetum</i> Hill, <i>Centaurea jacea</i> L. and <i>Centaurea</i> <i>scabiosa</i> L. Extra-floral nectar on flower parts</th> </tr> </thead> <tbody> <tr> <td>Seedling: A, B</td> <td style="text-align: center;">0</td> <td style="text-align: center;">0</td> </tr> <tr> <td>Adult: C1</td> <td style="text-align: center;">0.5</td> <td style="text-align: center;">0</td> </tr> <tr> <td>Adult: C2</td> <td style="text-align: center;">0.7</td> <td style="text-align: center;">0.5</td> </tr> <tr> <td>Flowering: D1</td> <td style="text-align: center;">0.8</td> <td style="text-align: center;">0.8</td> </tr> <tr> <td>Flowering: D2</td> <td style="text-align: center;">1</td> <td style="text-align: center;">1</td> </tr> <tr> <td>Flowering: D3</td> <td style="text-align: center;">1</td> <td style="text-align: center;">1</td> </tr> <tr> <td>Maturity: E1</td> <td style="text-align: center;">0.7</td> <td style="text-align: center;">0</td> </tr> <tr> <td>Maturity: E2</td> <td style="text-align: center;">0</td> <td style="text-align: center;">0</td> </tr> </tbody> </table>	Phenological stage (Yvoz et al., 2020a)	<b>REN</b> for <i>Fallopia convolvulus</i> (L.), <i>Sambucus ebulus</i> L. and <i>Vicia sativa</i> L. Extra-floral nectar on vegetative parts	<b>REN</b> for <i>Cyanus segetum</i> Hill, <i>Centaurea jacea</i> L. and <i>Centaurea</i> <i>scabiosa</i> L. Extra-floral nectar on flower parts	Seedling: A, B	0	0	Adult: C1	0.5	0	Adult: C2	0.7	0.5	Flowering: D1	0.8	0.8	Flowering: D2	1	1	Flowering: D3	1	1	Maturity: E1	0.7	0	Maturity: E2	0	0
Phenological stage (Yvoz et al., 2020a)	<b>REN</b> for <i>Fallopia convolvulus</i> (L.), <i>Sambucus ebulus</i> L. and <i>Vicia sativa</i> L. Extra-floral nectar on vegetative parts	<b>REN</b> for <i>Cyanus segetum</i> Hill, <i>Centaurea jacea</i> L. and <i>Centaurea</i> <i>scabiosa</i> L. Extra-floral nectar on flower parts																										
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Flowering: D2	1	1																										
Flowering: D3	1	1																										
Maturity: E1	0.7	0																										
Maturity: E2	0	0																										

Proxies	Equations
Potential weed competition against crop ( <b>Harm1</b> )	$Harm1 = \sum_{i=1}^{155} (GP(i) \times FP(i) \times RH(i) \times EN(i) \times SLA(i) \times GS(i) \times A(i))$ <ul style="list-style-type: none"> <li>- <b>GP</b>: Germination period synchrony (details in Supp. Table 2)</li> <li>- <b>FP</b>: Flowering period synchrony (details in Supp. Table 3)</li> <li>- <b>RH</b>: Relative height = height(weed)/height(crop)</li> <li>- <b>EN</b>: Relative Ellenberg.N = Ellenberg.N(weed)/Ellenberg.N(crop)</li> <li>- <b>SLA</b>: Relative SLA = SLA(weed)/SLA(crop)</li> <li>- <b>GS</b>: Growing success = 1-proportion of plant dead without reaching the stage C1, <i>i.e.</i> adult plant (Yvoz et al., 2020a)</li> <li>- <b>A</b>: Abundance of the species in the survey</li> </ul>
Potential weed contribution to harvest difficulties ( <b>Harm2</b> )	$Harm2 = \sum_{i=1}^{155} ((H(i) \times S(i)) - 15) \times PG(i) \times A(i)$ <ul style="list-style-type: none"> <li>- <b>H</b>: Maximum height (cm)</li> <li>- <b>PG</b>: Proportion of plants still green at harvest</li> <li>- <b>S</b>: Synchrony between weed flowering period and crop harvest</li> <li>- <b>A</b>: Abundance of the species in the survey</li> </ul>
Potential weed contribution to future infestations ( <b>Harm3</b> )	$Harm3 = \sum_{i=1}^{155} (SP(i) \times SN(i) \times A(i))$ <ul style="list-style-type: none"> <li>- <b>SP</b>: Seed longevity</li> <li>- <b>SN</b>: Average seed number per plant</li> <li>- <b>A</b>: Abundance of the species in the survey</li> </ul>

317

318

319           **3.1.3. Competition with crop (Harm1)**

320 Weeds compete with crops for resources, such as nitrogen, light and water (Blackshaw et al.,  
321 2004; Swanton et al., 2015). Weeds outcompete crops when they share the same space at the  
322 same time and highlight a higher efficiency to uptake a limiting resource. Moreau et al. (2013)  
323 showed that the Ellenberg's indicator value N (Ellenberg et al., 1992), a simple ordinal  
324 classification of plants according to the position of their realized ecological niche along an  
325 environmental gradient (here soil nitrogen), is a reliable proxy of the ability of weeds to  
326 compete for nitrogen. Synchrony between weed and crop for germination and flowering  
327 increases the intensity of competition (Fried et al., 2015), the outcome being dictated by the  
328 species able to germinate earlier and grow faster. In addition, Swanton et al. (2015) highlighted  
329 the importance of a high leaf area development, light absorption efficiency and height in weed  
330 competitiveness. Fried et al. (2019) also showed that a high SLA is generally associated with a  
331 high ability of weed to compete with crop by intercepting more of the incident radiations for a  
332 given leaf biomass unit.

333 The proxy for the potential weed competition with crop (Harm1) was thus based on similarities  
334 between the weed and crop species traits listed above, the intensity of the competition being  
335 maximum when weeds express similar or higher trait values than the crop. Five ratios were  
336 computed and then multiplied (Table 2), comparing the synchrony of the germination and  
337 flowering periods (Supp. Table 2), the maximum height at flowering, the Ellenberg.N value  
338 and SLA (Supp. Table 1). For instance, germination and flowering synchrony ratios reach 1  
339 when the weed growth is synchronic with the crop. Since certain weed plants die without  
340 reaching the vegetative stage (Yvoz et al., 2020a), we subtracted a proportion of plants (GS in  
341 Table 2), hypothesizing they do not cause significant yield loss in their early growth (Adeux et  
342 al., 2019).

343           **3.1.4. Harvest difficulties (Harm2)**

344 Even if weed species emerging late in season are generally low competitors, they may remain  
345 green at harvest and cause harvest difficulties for farmers (Swanton et al., 2015). They can also  
346 reduce the quality and the value of the grain harvest if the weed green biomass is located above  
347 the combine cutting bar and exported with crop seeds (Mézière et al., 2015).

348 The proxy for the potential weed contribution to harvest difficulties (Harm2) was estimated by  
349 the estimated height of green biomass located above the cutting bar at harvest. Since weed  
350 species reach their maximum green biomass at flowering, we multiplied the maximum height  
351 of weed species found in the literature by a coefficient of synchrony between the weed



352 flowering period and the crop harvest period, for each weed:crop couples, to account for weed  
353 growth (Supp. Table 3). For instance, the height of green tissues was equal to the maximum  
354 weed height for a weed plant flowering at crop harvest (*i.e.* high synchrony) when it was  
355 decreased by the synchrony coefficient if the weed plant flowers later than crop harvest (*i.e.*  
356 being smaller than its maximum height). We then subtracted 15 cm, the average cutting height,  
357 from the weed height, *i.e.* only the green tissues located above contributing to harvest  
358 difficulties. Finally, we multiplied these values by the proportion of individual weed plants still  
359 green at harvest (*i.e.* phenological stages between C1 (adult plants) and E1 (end of flowering)  
360 assessed in Yvoz et al. (2020a)) (Table 2).

### 361 **3.1.5. Future weed infestations (Harm3)**

362 Weeds can shed seeds at maturity and regenerate the soil seedbank, with some species capable  
363 of remaining viable for several years in the soil (Mahé et al., 2020), increasing the probability  
364 of high abundance and weed:crop competition in the following years (Jabbour et al., 2014).  
365 Our proxy for the potential weed contribution to future weed infestations (Harm3, Table 2) was  
366 based on the seed production and persistence in the soil (as categories, *i.e.* 1, 3, 5 and 10 years  
367 or more) extracted from the literature and databases (Table 2, Supp. Table 1).

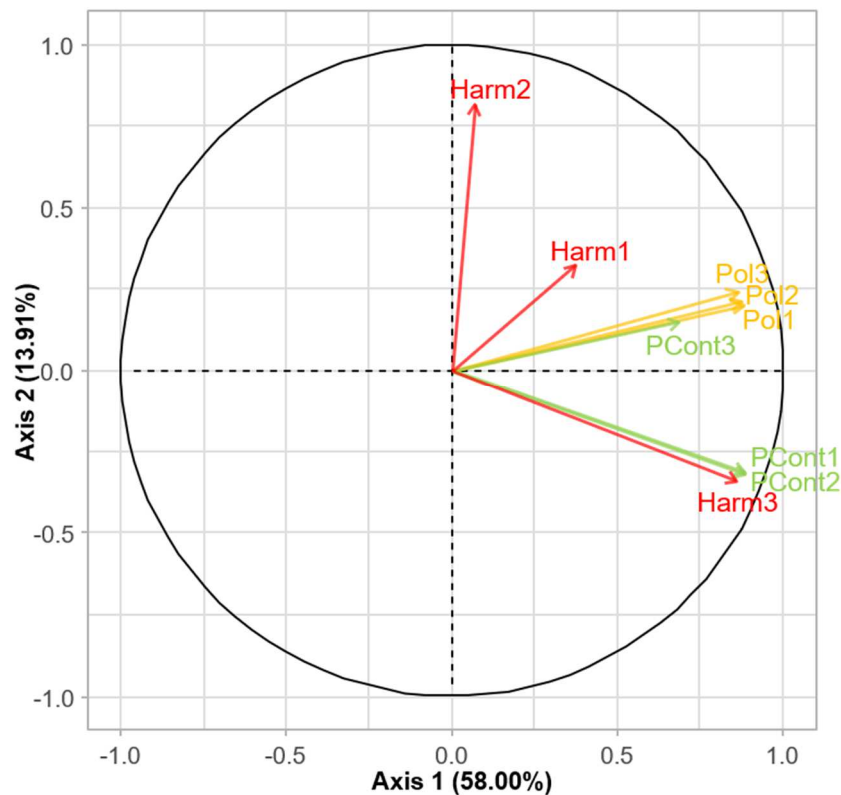
## 368 **3.2. Identification of plant groups expressing similar proxy bundles.**

369 Proxy values calculated at the organ and plant levels are detailed in Appendix B. The  
370 distributions of the proxy values of the 967 unique situations showed a non-symmetric  
371 distribution with few high values (Supp. Figure 1), highlighting that most of the situations  
372 contribute to low levels of proxies compared to the maximum observed value.

### 373 **3.2.1. Correlations between proxies**

374 The first PCA axis (representing 58% of the variability, Figure 3) was positively correlated with  
375 the six proxies of services (*i.e.* Pol1, Pol2, Pol3, PCont1, PCont2, PCont3) and negatively  
376 correlated with Harm3 and Harm1, separating weed plants by their ability to produce flowers  
377 and seeds. Proxies representing the contribution of weeds to pollination and pest control were  
378 highly positively correlated at the plant level, as their computation was related to the same  
379 organs (flowers for Pol1, Pol2, Pol3, PCont3, and seeds for PCont1, PCont2, Table 2). The  
380 second PCA axis (13.9% of the variability, Figure 3) was correlated with Harm2, which was  
381 not correlated with the six proxies of services. There was a general antagonism between high

382 provision of services and low harmfulness, except for Harm2 (Figure 3).. However, the negative  
 383 correlation between Harm1 and the six services was low, suggesting the existence of trade-offs.

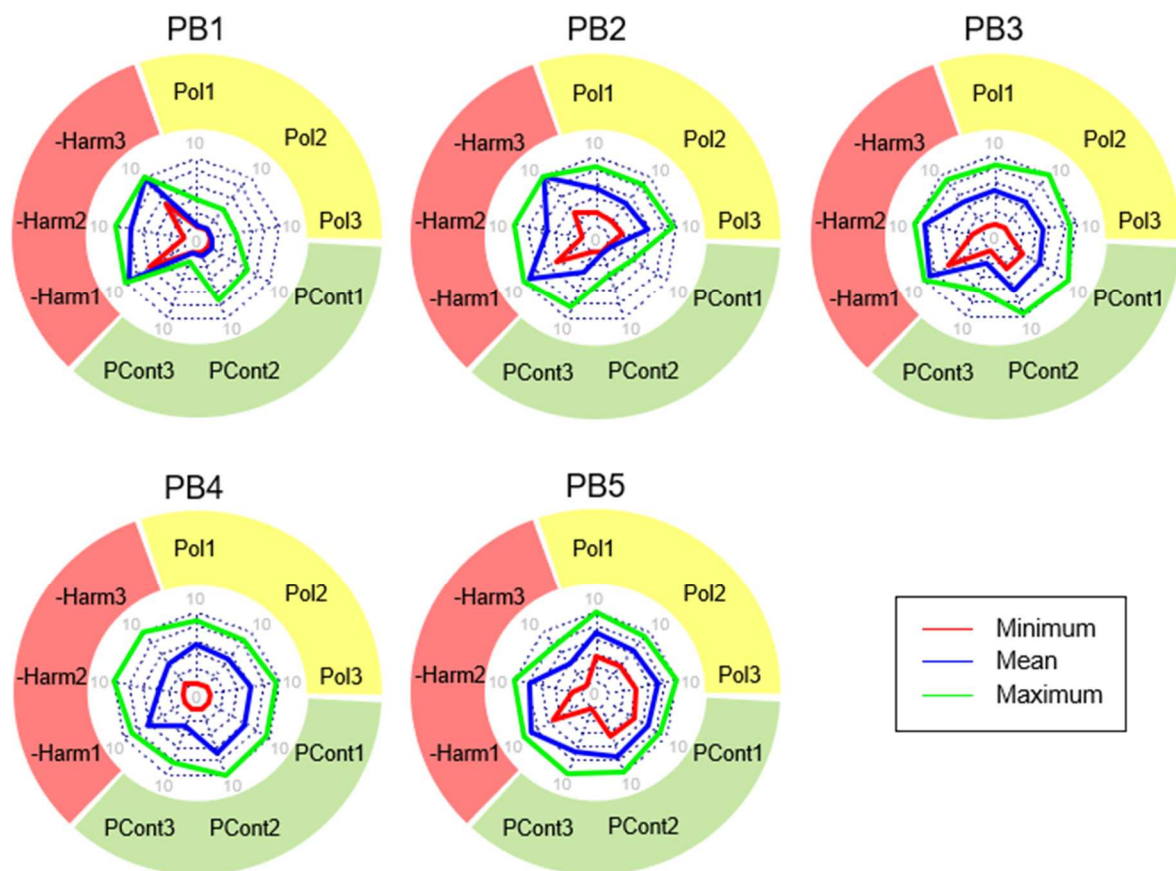


384  
 385 **Figure 3:** Correlations between the nine proxies (detailed in Table 2) and the two first dimensions of the principal  
 386 component analysis. Potential weed contribution to pollinators (bees: Pol1, bumblebees: Pol2, hoverflies: Pol3),  
 387 Potential weed contribution to pest natural enemies (farmland birds: PCont1, carabids: PCont2, parasitoids:  
 388 PCont3), Potential weed competition with crop (Harm1), Potential weed contribution to harvest difficulties  
 389 (Harm2), Potential weed contribution to future weed infestations (Harm3).

### 390 3.2.2. Identification of proxy bundles

391 Five PB were identified by the clustering analysis. PB1 (196 unique situations) had low  
 392 contribution values to both ecosystem service and harmfulness proxies (Figure 4). PB2 (162  
 393 unique situations) had low values of harmfulness (except for Harm2) and PCont1/PCont2  
 394 services, but an intermediate contribution to pollinators (Pol1, Pol2, Pol3) and parasitoids  
 395 (PCont3). PB3 (256 unique situations) showed an intermediate contribution to pollinators and  
 396 pest natural enemies (except for PCont3), a low weed:crop competition, but a high contribution  
 397 to future weed infestations (Harm3). PB4 (115 unique situations) was similar to PB3, but with  
 398 higher values of services and harmfulness (especially for Harm2 and Harm3). Finally, PB5 (238  
 399 unique situations) showed high contribution to ecosystem services, with low contribution to

400 harmfulness (except for Harm3) (Figure 4). In decreasing order of significance, PB5 and PB3  
 401 showed the best trade-offs with high values of services and limited values of harmfulness.

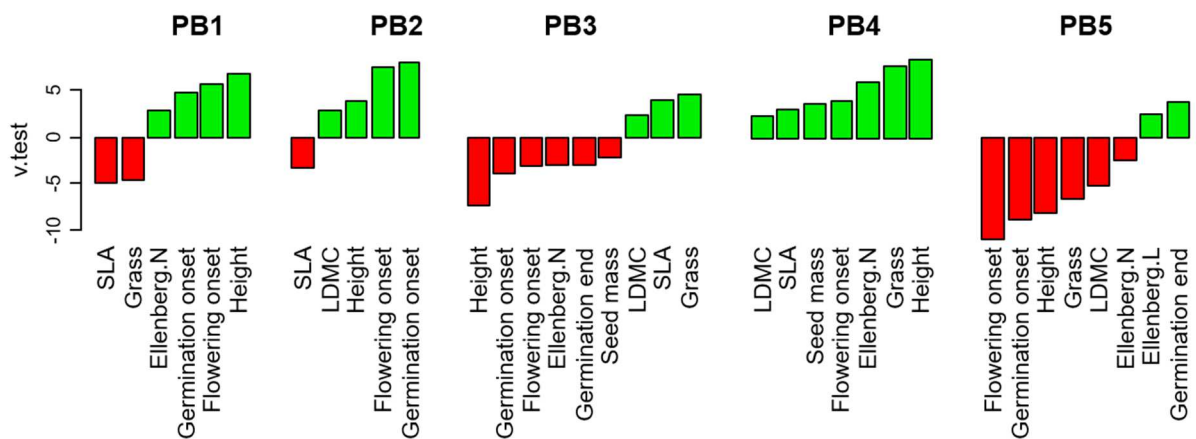


402  
 403 **Figure 4:** Radar plots of the minimum (red line), mean (blue line) and maximum (green line) values of the nine  
 404 proxies (detailed in Table 2) calculated for the five identified proxy bundles (PB). Values were log<sub>10</sub>-transformed  
 405 and scaled from 0 to 10. Harm1, Harm2 and Harm3 were reversed before plotting the radar plot so that 0 indicates  
 406 high harmfulness (-Harm) or low services (PCont and Pol) and 10 indicates low harmfulness or high services.

407 **3.2.3. Characterisation of the proxy bundles: plant functional profile and main**  
 408 **growing conditions**

409 PB1 was significantly associated with tall forb species (Figure 5, 1 m on average), with high  
 410 Ellenberg.N values (6.6), low SLA (23.0 mm<sup>2</sup>/mg), and late germination and flowering onsets  
 411 (on average in December and mid-May, respectively), as *Aethusa cynapium* L. and *Atriplex*  
 412 *patula* L. Besides, unique situations in PB1 mainly occurred in field cores of cereal crops  
 413 (Table 3). PB2 was associated with tall species (93 cm) with low SLA (23.5 mm<sup>2</sup>/mg), high  
 414 LDMC (190.8 mg/g) and late germination and flowering onsets (in January and end of May,  
 415 respectively), as *Fallopia convolvulus* (L.) and *Convolvulus arvensis* L. Unique situations in  
 416 PB2 mainly occurred in field edges of winter mustard and oilseed rape but rarely in soybean.  
 417 PB3 was associated with small (63 cm on average) grasses (20 % of the species) with low

418 Ellenberg.N values (6.2) and seed mass (2.2 mg), high LDMC (186 mg/g) and SLA  
 419 (27.1 mm<sup>2</sup>/mg) and early germination and flowering onsets and end of the germination period  
 420 (in October, end of April and April, respectively), as *Poa annua* L. and *Viola arvensis* Murray.  
 421 Unique situations in PB3 occurred mostly in field edges of winter oilseed rape. PB4 was  
 422 associated with tall (113 cm) grasses (a third of the species) with high Ellenberg.N values (7.1),  
 423 seed mass (4.3 mg), SLA (27.5 mm<sup>2</sup>/mg) and LDMC (190 mg/g) and with late flowering onset  
 424 (in Mid-May), as *Echinochloa crus-galli* (L.) and *Chenopodium album* L. Unique situations in  
 425 PB4 mostly occurred in the field cores and field edges of soybean. Finally, PB5 was associated  
 426 with species having a high Ellenberg.L (7.2) and low Ellenberg.N (6.2) values, low LDMC  
 427 (165 mg/g) and height (60 cm), early germination and flowering onsets and late end of  
 428 germination (in September, beginning of April and in June, respectively), as *Veronica persica*  
 429 Poir. and *Geranium dissectum* L. Unique situations in PB5 mainly occurred in the field cores  
 430 and field edges of winter oilseed rape and in the field edges of winter mustard.  
 431 Within the 12 growing conditions (within-field location-by-crop type), a weed species was  
 432 found to be associated with one to all identified PB (Table 3, Supp. Table 4): 39 weed species  
 433 were associated with a unique PB in all the growing conditions, and 48, 44, 19 and 5 species  
 434 were associated with 2, 3, 4 or 5 PB, respectively.  
 435



436  
 437 **Figure 5:** Response traits associated with each of the five proxy bundles (PB). Associations between traits and PB  
 438 were estimated by a one-way analysis of variance implemented with the *catdes* function from the [FactoMineR]  
 439 package. Only significant (p-value < 0.05) traits were presented, green and red bars indicating traits that were  
 440 positively (v.test values > 0, unitless) and negatively (v.test values < 0, unitless) correlated with each PB,  
 441 respectively. SLA: specific leaf area, LDMC: leaf dry matter content.

442

443 **Table 3:** Number of weed species associated with each of the 12 combinations of crop type by within-field location  
 444 for the five identified proxy bundles (PB1 to PB5). Situations coloured in green and red were significantly over-  
 445 and under-represented in the proxy bundle, respectively.

Crop type	Winter oilseed rape		Winter mustard		Winter barley		Winter wheat		Spring barley		Soybean	
	Field core	Field edge	Field core	Field edge	Field core	Field edge	Field core	Field edge	Field core	Field edge	Field core	Field edge
PB1	9	11	18	9	22	12	33	16	29	24	6	7
PB2	13	19	10	35	7	27	3	24	5	14	0	5
PB3	20	40	20	27	11	24	21	39	5	21	10	18
PB4	2	3	0	5	2	13	1	15	1	11	27	35
PB5	26	38	18	38	2	23	7	32	1	24	11	18

446

## 447 4. Discussion

448 The rationale of the study was to propose a generic framework to quantify the potential  
 449 contribution of weed species to multiple ecosystem services and harmfulness and develop a set  
 450 of trait-based proxies that could translate weed surveys into values of their contribution to these  
 451 services. Our approach was novel in that it integrated the intraspecific variability of weed plant  
 452 development in response to its growing conditions (*i.e.* within-field location and crop type). In  
 453 addition to the development of nine proxies of services and harmfulness, we provided a  
 454 database documenting weed plants multifunctionality for 155 species observed across 12  
 455 growing conditions, *i.e.* 967 unique situations. The analysis of these situations revealed a  
 456 general antagonism between the delivery of ecosystem services and the degree of harmfulness  
 457 at the plant level. It also enabled the identification of sets of weed species (and their dominant  
 458 functional profiles) that express interesting bundles of services in some growing conditions.

### 459 4.1. Validation of the proxies of ecosystem services and harmfulness

460 The equations that estimate weed contribution to different services and harmfulness have not  
 461 all been validated with external data as it is often recommended (Girardin et al., 1999), either  
 462 originating from field observations (Gaba et al., 2020) or outputs of model simulations (Mézière  
 463 et al., 2015). The proxies we developed for pollination, for a large number of species, were  
 464 similar to those developed by Ricou et al. (2014), these latter being validated with flower visits  
 465 by pollinators. However, alternative approaches have been identified to evaluate indicators.  
 466 Bockstaller and Girardin (2003) highlighted that the most important aspect to validation is to

467 design indicators according to a scientific approach, and then evaluate if the indicators are  
468 scientifically robust, what they call the “design validation”.

469 Our proxies were based on a comprehensive review of the literature to identify the most relevant  
470 species traits involved in each of the ecosystem functions we assessed. In addition, the  
471 framework we developed accounted for the intraspecific variability of traits according to the  
472 weed growing conditions, an aspect missing so far despite its important implications for the  
473 outcome of ecological interactions (Bolnick et al., 2011). Here, field-based measures of  
474 intraspecific variability were only available for part of the weed species recorded in the study  
475 area. For the others, we assessed their similarity with species for which we had field measures  
476 by using a number of species characteristics, namely 15 traits and 12 variables describing their  
477 occurrence in different growing conditions. This procedure integrated most of the traits  
478 translating species response to crop competition and farming practices. We however  
479 acknowledge that its outcome was dependent on (i) the choice of species characteristics it was  
480 based on (ii) the species pool for which we had field-based measures and (iii) the accuracy of  
481 the field-based estimation of traits in the various growing conditions. Despite these potential  
482 caveats, the methodology developed here to estimate proximity between weed species has a  
483 generic value for future studies on weed multifunctionality, as intraspecific variability in weeds  
484 remains to date poorly documented. Additional traits could be included in future studies if more  
485 services were included or if new trait data became available. Research efforts should also be  
486 devoted to field-based studies quantifying intraspecific variability of weed flower and seed  
487 production in a wider range of environmental and agronomic conditions. Finally, we  
488 implemented a design validation to assess weed contribution to parasitoids (PCont3) because  
489 the available literature was scarce; we thus validated our proxy construction with experts and  
490 reached a consensus, a crucial step towards validation (Bockstaller and Girardin, 2003).

491 A true “output validation” (as defined by Bockstaller and Girardin (2003)) of most of our  
492 proxies appears challenging and probably not well adapted to weeds as it is usually conducted  
493 by using a weed survey at a particular time of the season, whereas the temporal dynamic of the  
494 provision of services is crucial. For instance, assessing properly yield loss at the annual scale  
495 (*i.e.* Harm 1) requires comparing the yield in weedy zones to that in weed-free controls without  
496 chemical or mechanical weeding (Adeux et al., 2019). Thus, it requires frequent labour and  
497 attention over the course of the crop season to ensure controls to be actually weed-free, weed  
498 and crop biomass sampling at crop flowering and grain harvest at maturity (Colbach et al.,  
499 2020). However, future studies should validate our estimated values to in-field measurement of  
500 the services and harmfulness, such as the carabids activity, parasitoids and pollinators

501 visitations, in a way to validate their significance and robustness in different production  
502 situations and weed contexts.

## 503 **4.2. Assessing proxy bundles delivered by weed communities**

504 The framework and quantification of multiple weed services we developed here is a necessary  
505 step to analyse potential trade-offs between positive and negative aspects of weeds. Our analysis  
506 reveals a general antagonism between services and harmfulness for the 967 unique situations,  
507 although there were some exceptions (see 4.3). The underlying causes of this antagonism lie in  
508 the fact that some proxies are estimated using the same organs (flower or seed). For instance,  
509 our results clearly showed that Harm3, the proxy describing the weed contribution to future  
510 weed infestations, was highly correlated with some services. Indeed, when weed species shed  
511 seeds on the ground, it increases Harm3 and also increases seed resources for birds (PCont1)  
512 and beetles (PCont2). Nevertheless, high values of PCont1 and PCont2 also suggest potential  
513 for a reduction of the proportion of seeds entering the soil seedbank (Holland et al., 2008; Honek  
514 et al., 2003). Similarly, flower and seed production is related to weed biomass (Senseman and  
515 Oliver, 1993), and competition (Harm1) is mainly driven by relative weed:crop biomass  
516 (Milberg and Hallgren, 2004). We therefore logically observed that proxies of services are  
517 positively correlated with those of harmfulness. It should however be mentioned that benefits  
518 obtained by the increase of pollination (Pol1, Pol2, Pol3) of some crops such as oilseed rape  
519 (Bretagnolle and Gaba, 2015) could compensate, at least partially, for weed:crop competition  
520 (DiTommaso et al., 2016). Accounting for such positive and negative feedbacks between  
521 services could partially change the general antagonism we detected here. However, interactions  
522 between services are to date hardly documented but their study probably represents an  
523 important scientific challenge for future research assessing ecosystem multifunctionality.

524 Another factor that could modulate the general antagonism we detected is the fact that proxy  
525 values of individual plants did not account for the community in which they occurred. We  
526 provided proxy values at the individual plant level, *i.e.* an individual of a weed species in a  
527 particular growing condition. Weed plants however rarely occur in isolation and the presence  
528 of neighbouring plants (either weeds or crops) likely affects the contribution of individual weed  
529 plants to services and harmfulness. Exploring how weed diversity and/or abundance within a  
530 community affects the provision of services could improve the computation of proxies. For  
531 instance, weed:crop interference has mainly been studied considering only one weed species at  
532 a time (Colbach et al., 2020). Hence, little is known about the competitive effect of weeds in  
533 complex communities or how weed diversity might affect crop productivity (Storkey and Neve,

534 2018). Adeux et al. (2019) recently demonstrated that high levels of weed diversity were always  
535 associated with low weed biomass and reduced interference with the crop. Beside the effect of  
536 weed diversity/evenness, they also showed that the composition of weed communities was a  
537 main factor explaining variations in the degree of interference with the crop, reporting higher  
538 yield losses when competitive trait values were high at the community level. This is congruent  
539 with the way we have constructed our harmfulness proxies based on similarities between crop  
540 and weed trait values (Table 2). Finally, the increase of our weed harmfulness proxies does not  
541 necessarily lead to significant yield loss if weed:crop interference remains low (Adeux et al.,  
542 2019). We suggest either to compare the species ranking of harmfulness provided by our  
543 method (Appendix B) to field measurements, or to confront our ranking to farmers' view since  
544 their perception of weeds vary according to their own experience (Wilson et al., 2009).

### 545 **4.3. Species traits-by-growing conditions providing best proxy bundles**

546 It is well known that weed species pools differ according to regions and production situations.  
547 To gain in genericity, we provided a trait-based analysis of the species providing similar values  
548 of multiple proxies, called proxy bundles. The clustering analysis allowed us to identify species  
549 groups with distinct PB and particularly PB5 and PB3 which did not follow the general  
550 antagonism between services and harmfulness mentioned above. PB5 was characterised by  
551 small species with low LDMC and Ellenberg.N values, and with early germination and  
552 flowering onset. As LDMC is positively correlated with biomass conservation (Pierce et al.,  
553 2013), these weed species exhibit short life cycle and rapid growth, do not outcompete crops  
554 due to their low height and tend to produce many flowers and seeds during the crop cycle, thus  
555 highly contributing to ecosystem services. PB3 was the second-best proxy bundle and also  
556 gathered small species, with low Ellenberg.N values, with a high LDMC. Compared to the  
557 species expressing PB5, those expressing PB3 have a longer life cycle and are less adapted to  
558 disturbances of farming practices. At the other end of the spectrum, PB4 was the least  
559 interesting proxy bundle, composed of tall species with high SLA, LDMC and Ellenberg.N  
560 values. Indeed, SLA represents their ability to intercept light (Ackerly et al., 2002) and the  
561 height is generally used as a proxy for competition for light (Gaba et al., 2017).

562 Our results also showed that some plants provided neither services nor harmfulness. They were  
563 mostly located in the field core of cereal crops, known to be highly competitive crops, due to  
564 their small row spacing and their high tillering ability (Jha et al., 2017). Besides, due to  
565 herbicide program targeting forbs (Markéta et al., 2018), species occurring in cereal crops are  
566 mainly grasses, species with low contribution to the pollination service. The characterisation of



567 the functional profiles of weed with response traits to farming practices provides insights on  
568 which crops and associated farming practices could favour the presence and abundance of  
569 certain species responsible for the delivery of the best PB (Cadotte et al., 2015).

## 570 **5. Conclusion**

571 We presented here a novel framework to estimate the contribution of individual weed plants to  
572 a set of services and harmfulness under contrasting growing conditions. The division of the  
573 proxy calculations into three nested levels of organisation (*i.e.* organ, plant and community)  
574 allowed us to integrate intraspecific variability of the weed contribution to ecosystem services  
575 and harmfulness. The application of these proxies at the plant level, on 967 unique situations,  
576 highlighted a general trend where a high weed plant contribution to ecosystem services was  
577 generally synonymous of a high harmfulness to the crop. We however identified a group of  
578 plants gathering small species with a short life cycle and mainly associated to mustard and  
579 oilseed rape, presenting the optimum proxy combination, *i.e.* high services and low levels of  
580 harmfulness. These plants produce flowers and seeds while being not too competitive to the  
581 crop. The proxy database provided and detailed methodology of data imputation based on  
582 species proximity will help future research to either directly mobilise these data or compute  
583 their own proxy values on a wider set of species and growing conditions, so as to confront  
584 values to field observations and then assess the multifunctionality of weed communities  
585 occurring in arable landscapes.

586

## 587 **Acknowledgements**

588 We would like to thank Christian Bockstaller (INRAE) who provided the pollination values  
589 database from Ricou et al. (2014) and for his advice on the missing values estimation, and data  
590 validation. We are grateful to Antoine Gardarin (INRAE) for his expertise and his validation of  
591 the proxy related to parasitoid wasps. We are grateful to Ann K. Bybee-Finley (Cornell  
592 University, NY, USA) for her constructive revisions. Séverin Yvoz and Alexandre Ploteau were  
593 funded by the European Union's Horizon 2020 research and innovation program under grant  
594 agreement No 727321 (IWM PRAISE). Séverin Yvoz was also funded by the INRAE  
595 metaprogram “ecosystem services”. Authors acknowledge financial support from INRAE.

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