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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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Version of Record: https://www.sciencedirect.com/science/article/pii/S1470160X21009869 Manuscript a94bcf01846cc4e5afe049c5a0ea0156

## **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

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

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

### 32 **1. Introduction**

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

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

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

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

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

## 95 **2. Materials and methods**

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

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

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



107

Figure 1: Methodological scheme presenting the three levels of organisation involved in the construction ofproxies 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 a seed for pollinators or pest natural enemies. The resource provision for pollinators (*i.e.* Pol1, 118 Pol2, Pol3) and pest natural enemies (i.e. PCont1, PCont2, PCont3) and the future weed 119 infestations (i.e. Harm3) are linked to characteristics of weed species organs which are 120 121 relatively stable over the growing conditions. We then extracted values from the literature or online databases when available. The values at the organ level were then multiplied by the 122 number of flowers or seeds produced by an individual weed plant. This step accounted for the 123 effect of the within-field location and the crop type on the number of flowers and seeds per 124 plant through the season (Yvoz et al., 2020a). Some potential weed contributions to ecosystem 125 services and harmfulness are associated with characteristics of the plant not associated with a 126 specific organ (e.g. maximum height at flowering being related to the competitive ability) but 127 still varying with growing conditions. Thus, competition for resources (Harm1) and harvest 128 129 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** 

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

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

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 Fénay platform (Dijon, France).

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

154

155 **2.2.2. Proxy calculation** 

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

178 
$$Adjustment = \frac{Potential \, organ \, production \, of \, sp_{2,3} \, or \, 4}{Potential \, organ \, production \, of \, sp_{1}}$$
 (Eq. 1)

179



### 181

180

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 differential ratio of the potential organ production derived from the literature between species with missing (sp2, 187 188 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

For Type C species, we attributed both the phenological profile and production of flowers and seeds from the closest species (see details in Appendix A: Table A3) when these data were known. If the closest species was a Type A species, we attributed the phenology and organ counting of sp1 (Type A) to sp3 (Type C) and then adjusted it (Eq. 1). If the closest species was 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**

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

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 Scaled proxy = 
$$rescale[Log10\left(\frac{proxy+1}{max(proxy)+1}\right), to = c(0,10)]$$
 (Eq. 2)

207

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

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

### 228 **3. Results**

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

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

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

Pollinators include a diversity of organisms such as bees, bumblebees and hoverflies 234 contributing largely to the pollination of crops in agricultural landscapes (Eilers et al., 2011). 235 Weeds contribute to the conservation of pollinator populations by the provision of nectar and 236 pollen before and after crop flowering, and by providing more diverse resources otherwise 237 238 (Carvalheiro et al., 2011). The benefits of a particular weed species depend on its attractiveness (e.g. associated with the flower colour (Backhaus, 1992), ultra-violet (UV) reflectance (Horth 239 et al., 2014) or flower symmetry (Wignall et al., 2006)), its accessibility (e.g. determined by the 240 form and size of the corolla (Lehrer, 2005)) and the quantity and quality of the floral rewards 241 (e.g. pollen (Hass et al., 2019) and/or nectar (Pamminger et al., 2019)). 242

Ricou et al. (2014) listed and integrated these aspects to develop an indicator of pollination 243 value of a large number of weed species for three groups of pollinators: bees (wild and honey 244 bees), bumblebees and hoverflies. Based on their work, we developed three proxies estimating 245 the contribution of individual weed plants to bees (Pol1), bumblebees (Pol2) and hoverflies 246 (Pol3). We used pollination values from Ricou et al. (2014) and exponentialized them as authors 247 showed a linear regression between pollination values and the natural logarithm of pollinator 248 visits. As they recommended, we multiplied these indicators by flower diameter, thus 249 accounting for the differences between species in flower size and resources quantity per flower 250 (Table 2). As pollinator values were missing for 34 of our 155 weed species, we computed the 251 mean value of the species belonging to the same genus for 12 species. For the 22 other species, 252 we imputed the values of the closest species among the 133 others, based on the 12 variables 253 describing flowers (*i.e.* nectar quantity and quality, pollen quantity, protein content of pollen, 254 flower symmetry, colour, size and shape, flower class, flower type and UV reflectance in the 255 centre and the petals, see details in Supp. Table 1), using the *imputeMFA* function from the 256 257 [missMDA] package.

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

Many studies highlighted that weed species may impact the longevity and fecundity of pest 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).

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

278

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

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

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

**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> )	$Polj = \sum_{i=1}^{155} (exp \ exp \ (PV_j(i)) \times FD(i) \times FN(i) \times A(i))$ $- \mathbf{PV_j}: \text{ Pollinator value from Ricou et al. (2014), j in \{1, 2, 3\}}$ $- \mathbf{FD}: \text{ Flower diameter}$ $- \mathbf{FN}: \text{ Average flower number per plant}$ $- \mathbf{A}: \text{ Abundance of the species in the survey}$
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> <li>SL: Seed lipid content</li> <li>SM: Seed mass</li> <li>SN: Average seed number per plant</li> <li>A: 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> <li>SL: Seed lipid content</li> <li>SM: Seed mass</li> <li>SA: 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>SN: Average seed number per plant</li> <li>A: Abundance of the species in the survey</li> </ul>

315

Proxies	Equations								
Potential weed contribution to pest natural enemies - parasitoid wasps ( <b>PCont3</b> )	$PCont3 = \sum_{i=1}^{155}$	$(NQ(i) \times FF(i) \times CD(i) \times FN(i) \times A(i))$	$i) + \sum_{k=1}^{9} (QEN(i) \times P(ki) \times REN(ki) \times A(i)))$						
	<ul> <li>NQ: Nectar qu</li> <li>FF: Flower for head shaped =</li> <li>CD: Corolla de</li> <li>FN: Average f</li> <li>A: Abundance</li> <li>QEN: Quantity nectar part</li> <li>P: Proportion of 2020a)</li> <li>REN: Rate of f</li> </ul>	<ul> <li>NQ: Nectar quantity (none = 0; little = 0.4; present = 0.8; plenty = 1)</li> <li>FF: 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>CD: Corolla depth (&lt;4.5 mm = 1; &gt;4.5 mm but nectar available = 0.5; no nectar or unavailable = 0)</li> <li>FN: Average flower number per plant</li> <li>A: Abundance of the species in the survey</li> <li>QEN: Quantity of extra-floral nectar estimated as the maximum value of PCont3 per half month for the floral nectar part</li> <li>P: 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>REN: Rate of the maximum extra-floral nectar production depending of the phenological stage k</li> </ul>							
	Phenological stage (Yvoz et al., 2020a)	<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: DI	0.8	0.8						
	Flowering: D2 Flowering: D3	1 1	1						
	Maturity: F1	0.7	1						
	Maturity: E2	0	ů 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> <li>GP: Germination period synchrony (details in Supp. Table 2)</li> <li>FP: Flowering period synchrony (details in Supp. Table 3)</li> <li>RH: Relative height = height(weed)/height(crop)</li> <li>EN: Relative Ellenberg.N = Ellenberg.N(weed)/Ellenberg.N(crop)</li> </ul>
	<ul> <li>SLA: Relative SLA = SLA(weed)/SLA(crop)</li> <li>GS: Growing success = 1-proportion of plant dead without reaching the stage C1, <i>i.e.</i> adult plant (Yvoz et al., 2020a)</li> <li>A: Abundance of the species in the survey</li> </ul>
Potential weed contribution to harvest difficulties ( <b>Harm2</b> )	$Harm2 = \sum_{i=1}^{155} \left( \left( \left( H(i) \times S(i) \right) - 15 \right) \times PG(i) \times A(i) \right)$
	<ul> <li>H: Maximum height (cm)</li> <li>PG: Proportion of plants still green at harvest</li> <li>S: Synchrony between weed flowering period and crop harvest</li> <li>A: 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> <li>SP: Seed longevity</li> <li>SN: Average seed number per plant</li> <li>A: Abundance of the species in the survey</li> </ul>

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

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

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

343

### 3.1.4. Harvest difficulties (Harm2)

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

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

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

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

Weeds can shed seeds at maturity and regenerate the soil seedbank, with some species capable of remaining viable for several years in the soil (Mahé et al., 2020), increasing the probability of high abundance and weed:crop competition in the following years (Jabbour et al., 2014).

Our proxy for the potential weed contribution to future weed infestations (Harm3, Table 2) was based on the seed production and persistence in the soil (as categories, *i.e.* 1, 3, 5 and 10 years or more) extracted from the literature and databases (Table 2, Supp. Table 1).

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

Proxy values calculated at the organ and plant levels are detailed in Appendix B. The distributions of the proxy values of the 967 unique situations showed a non-symmetric distribution with few high values (Supp. Figure 1), highlighting that most of the situations 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 the six proxies of services (i.e. Pol1, Pol2, Pol3, PCont1, PCont2, PCont3) and negatively 375 correlated with Harm3 and Harm1, separating weed plants by their ability to produce flowers 376 and seeds. Proxies representing the contribution of weeds to pollination and pest control were 377 highly positively correlated at the plant level, as their computation was related to the same 378 organs (flowers for Pol1, Pol2, Pol3, PCont3, and seeds for PCont1, PCont2, Table 2). The 379 380 second PCA axis (13.9% of the variability, Figure 3) was correlated with Harm2, which was not correlated with the six proxies of services. There was a general antagonism between high 381

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



384

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

390

### **3.2.2. Identification of proxy bundles**

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



402

Figure 4: Radar plots of the minimum (red line), mean (blue line) and maximum (green line) values of the nine
proxies (detailed in Table 2) calculated for the five identified proxy bundles (PB). Values were log10-transformed
and scaled from 0 to 10. Harm1, Harm2 and Harm3 were reversed before plotting the radar plot so that 0 indicates
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

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

Ellenberg.N values (6.2) and seed mass (2.2 mg), high LDMC (186 mg/g) and SLA 418 (27.1 mm<sup>2</sup>/mg) and early germination and flowering onsets and end of the germination period 419 (in October, end of April and April, respectively), as Poa annua L. and Viola arvensis Murray. 420 Unique situations in PB3 occurred mostly in field edges of winter oilseed rape. PB4 was 421 associated with tall (113 cm) grasses (a third of the species) with high Ellenberg.N values (7.1), 422 seed mass (4.3 mg), SLA (27.5 mm<sup>2</sup>/mg) and LDMC (190 mg/g) and with late flowering onset 423 (in Mid-May), as Echinochloa crus-galli (L.) and Chenopodium album L. Unique situations in 424 PB4 mostly occurred in the field cores and field edges of soybean. Finally, PB5 was associated 425 426 with species having a high Ellenberg.L (7.2) and low Ellenberg.N (6.2) values, low LDMC (165 mg/g) and height (60 cm), early germination and flowering onsets and late end of 427 428 germination (in September, beginning of April and in June, respectively), as Veronica persica Poir. and Geranium dissectum L. Unique situations in PB5 mainly occurred in the field cores 429 430 and field edges of winter oilseed rape and in the field edges of winter mustard.

Within the 12 growing conditions (within-field location-by-crop type), a weed species was
found to be associated with one to all identified PB (Table 3, Supp. Table 4): 39 weed species
were associated with a unique PB in all the growing conditions, and 48, 44, 19 and 5 species
were associated with 2, 3, 4 or 5 PB, respectively.







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

442

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

and under-represented in the proxy bundle, respectively.

Crop type	Winter oilseed rape		Winter mustard		Winter barley		Winter wheat		Spring barley		Soybean	
Within-field location	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**

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

### 459

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

The equations that estimate weed contribution to different services and harmfulness have not all been validated with external data as it is often recommended (Girardin et al., 1999), either originating from field observations (Gaba et al., 2020) or outputs of model simulations (Mézière et al., 2015). The proxies we developed for pollination, for a large number of species, were similar to those developed by Ricou et al. (2014), these latter being validated with flower visits by pollinators. However, alternative approaches have been identified to evaluate indicators. Bockstaller and Girardin (2003) highlighted that the most important aspect to validation is to design indicators according to a scientific approach, and then evaluate if the indicators arescientifically 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 framework we developed accounted for the intraspecific variability of traits according to the 471 weed growing conditions, an aspect missing so far despite its important implications for the 472 outcome of ecological interactions (Bolnick et al., 2011). Here, field-based measures of 473 intraspecific variability were only available for part of the weed species recorded in the study 474 475 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 translating species response to crop competition and farming practices. We however 478 479 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 caveats, the methodology developed here to estimate proximity between weed species has a 482 483 generic value for future studies on weed multifunctionality, as intraspecific variability in weeds remains to date poorly documented. Additional traits could be included in future studies if more 484 services were included or if new trait data became available. Research efforts should also be 485 devoted to field-based studies quantifying intraspecific variability of weed flower and seed 486 production in a wider range of environmental and agronomic conditions. Finally, we 487 implemented a design validation to assess weed contribution to parasitoids (PCont3) because 488 the available literature was scarce; we thus validated our proxy construction with experts and 489 reached a consensus, a crucial step towards validation (Bockstaller and Girardin, 2003). 490

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

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

Another factor that could modulate the general antagonism we detected is the fact that proxy 524 525 values of individual plants did not account for the community in which they occurred. We provided proxy values at the individual plant level, *i.e.* an individual of a weed species in a 526 527 particular growing condition. Weed plants however rarely occur in isolation and the presence of neighbouring plants (either weeds or crops) likely affects the contribution of individual weed 528 529 plants to services and harmfulness. Exploring how weed diversity and/or abundance within a community affects the provision of services could improve the computation of proxies. For 530 531 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,

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

### 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. To gain in genericity, we provided a trait-based analysis of the species providing similar values 547 of multiple proxies, called proxy bundles. The clustering analysis allowed us to identify species 548 groups with distinct PB and particularly PB5 and PB3 which did not follow the general 549 antagonism between services and harmfulness mentioned above. PB5 was characterised by 550 small species with low LDMC and Ellenberg.N values, and with early germination and 551 552 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 due to their low height and tend to produce many flowers and seeds during the crop cycle, thus 554 highly contributing to ecosystem services. PB3 was the second-best proxy bundle and also 555 556 gathered small species, with low Ellenberg.N values, with a high LDMC. Compared to the species expressing PB5, those expressing PB3 have a longer life cycle and are less adapted to 557 558 disturbances of farming practices. At the other end of the spectrum, PB4 was the least interesting proxy bundle, composed of tall species with high SLA, LDMC and Ellenberg.N 559 560 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 the functional profiles of weed with response traits to farming practices provides insights on which crops and associated farming practices could favour the presence and abundance of certain species responsible for the delivery of the best PB (Cadotte et al., 2015).

### 570 **5. Conclusion**

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

586

### 587 Acknowledgements

We would like to thank Christian Bockstaller (INRAE) who provided the pollination values 588 database from Ricou et al. (2014) and for his advice on the missing values estimation, and data 589 validation. We are grateful to Antoine Gardarin (INRAE) for his expertise and his validation of 590 the proxy related to parasitoid wasps. We are grateful to Ann K. Bybee-Finley (Cornell 591 University, NY, USA) for her constructive revisions. Séverin Yvoz and Alexandre Ploteau were 592 593 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 metaprogram "ecosystem services". Authors acknowledge financial support from INRAE. 595

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