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

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Abstract

There is a pressing need for indicators and methods to quantify the provision of ecosystem services as a prerequisite to identify management options that optimize trade-offs between services. Arable weeds provide multiple services and are thus a good model to evaluate such trade-offs. This flora provides trophic resources (flowers or seeds) that support pollinators and pest natural enemies (pollination and pest control services) but can also be harmful for crop production (disservice). To date, few indicators are available to quantify the contribution of weeds to ecosystem services or their harmfulness, and no indicators account for intraspecific variability in weed traits that result from contrasting growing conditions, notably the location of weeds within fields (field edge vs field core) and crop type. Here, we developed nine proxies for potential weed harmfulness (competition, harvest difficulties and future weed infestations) and weed contributions to resources provision to pollinators (bees, bumblebees and hoverflies) and pest natural enemies (carabid beetles, birds and parasitoid wasps). These nine proxies accounted for individual weed plant response to growing conditions (combination of within-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 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 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 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 temporal (crop sequence) and spatial scales (landscape).

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

1. Introduction

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

While often considered as pests in agricultural landscapes, weeds interact with many organisms and are often associated with the provision of multiple ecosystem services (Blaix et al., 2018; Gaba et al., 2020). Weeds can be harmful to crop production if they outcompete crops for 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. 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 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 by mass flowering crops (Bretagnolle and Gaba, 2015). Functional approaches offer a robust framework to quantify and understand the mechanisms underlying the delivery of weed functions in agroecosystems (Navas, 2012). There have been substantial advances in the identification of weed traits that are key to specific functions (Cordeau et al., 2017; Gaba et al., 2017), and weed mean trait values (*i.e.* average value of a trait for a species, across a wide range of growing conditions) have become increasingly accessible in databases (*e.g.* TRY: (Kattge, 2012); LEDA: (Kleyer et al., 2008)). Functional approaches accounting for the pattern of weed competitive ability and the resulting impact on crop yield have been the focus of several studies (Adeux et al., 2019; Storkey, 2006). Similarly, quantification of weed traits have helped decipher the complex interactions between weeds and other trophic groups, for example floral traits and pollinators (Rosas-Guerrero et al., 2014) or seed traits and pest natural enemies (Storkey et al., 2013). In some rare instances, this knowledge has been mobilised to derive trait-based indicators of weed functions, for example valuations of weed species for different pollinator groups (Ricou et al., 2014), or index of ecological value (Fanfarillo and Kasperski, 2021; Hyvönen and Huusela-Veistola, 2008). One important limitation has been the assumption 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 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 area potentially less impacted by farming practices and crop competition (Dutoit et al., 1999). Several studies have demonstrated significant intraspecific differences in trait values in common weed species between the edge and the core of the field (Perronne et al., 2014). Second, the crop type and the agricultural practices that are implemented to grow each type of crop are substantial causes of variations in the growing environment of weed plants. For 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 canopy closure. This suggests a variation of the plant growth and thus in the timing and amount of flower and seed production. Crop management (tillage and sowing date, level of fertilisation, type and frequency of weeding operations) can also strongly modulate weed growth/phenology and hence their capacity to compete with the crop (Blackshaw et al., 2004) or to provide floral or seed resources throughout the season (Perron and Legere, 2000).

Here, we address the impact of intraspecific variability found in weed species on the estimation of several ecosystem services provided by weeds. We first present a framework and a set of nine proxies that were developed in order to account for the combined effect of within-field location (field edge *vs* field core) and crop type (six crop types) on plant contribution to ecosystem services and harmfulness. We applied these proxies to 155 weed species observed 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 hypothesised that traits and/or growing conditions of certain weed species may solve antagonisms between services and harmfulness. Specifically, we expected that species located in field edges have a higher contribution to ecosystem services due to the possibly lower crop competition and intensity of farming practices.

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.

2.1. Framework to develop proxies of weed contribution to ecosystem 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.

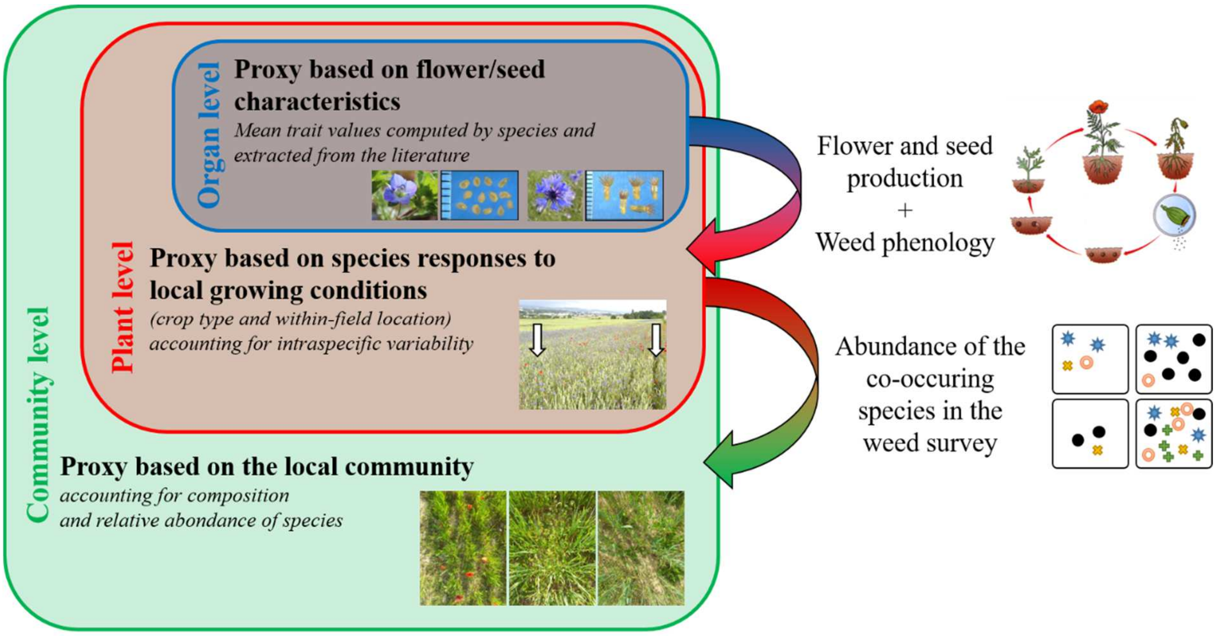


Figure 1: Methodological scheme presenting the three levels of organisation involved in the construction of proxies of ecosystem services and harmfulness provided by weeds.

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

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, Pol2, Pol3) and pest natural enemies (*i.e.* PCont1, PCont2, PCont3) and the future weed infestations (*i.e.* Harm3) are linked to characteristics of weed species organs which are 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 number of flowers or seeds produced by an individual weed plant. This step accounted for the effect of the within-field location and the crop type on the number of flowers and seeds per plant through the season (Yvoz et al., 2020a). Some potential weed contributions to ecosystem services and harmfulness are associated with characteristics of the plant not associated with a specific organ (*e.g.* maximum height at flowering being related to the competitive ability) but still varying with growing conditions. Thus, competition for resources (Harm1) and harvest difficulties (Harm2) were characterised at the plant level, based on traits and indicators describing the weed development in interaction with the growing conditions.

2.2. Application of the proxies to weed survey data

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 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 to the species level when possible, named according to Jauzein (1995) and their abundance visually estimated using the scale developed by Barralis (1976). Based on the records of farming operations (Yvoz et al., 2020b), weed surveys conducted less than one week after the last in-crop weeding practices (chemical or mechanical) were discarded. This resulted in three to six annual records per field across the six years, leading to a total of 826 weed records. (*i.e.* 413 in both field cores and field edges) associated with six crop types (winter oilseed rape, winter mustard, winter wheat, winter barley, spring barley and soybean). Altogether, this dataset contained a total of 155 weed species observed in 12 combinations of crop type by within-field location (Table 1), resulting in a dataset of 967 unique situations (*i.e.* an individual plant of a weed species observed in a within-field location of a particular crop type).

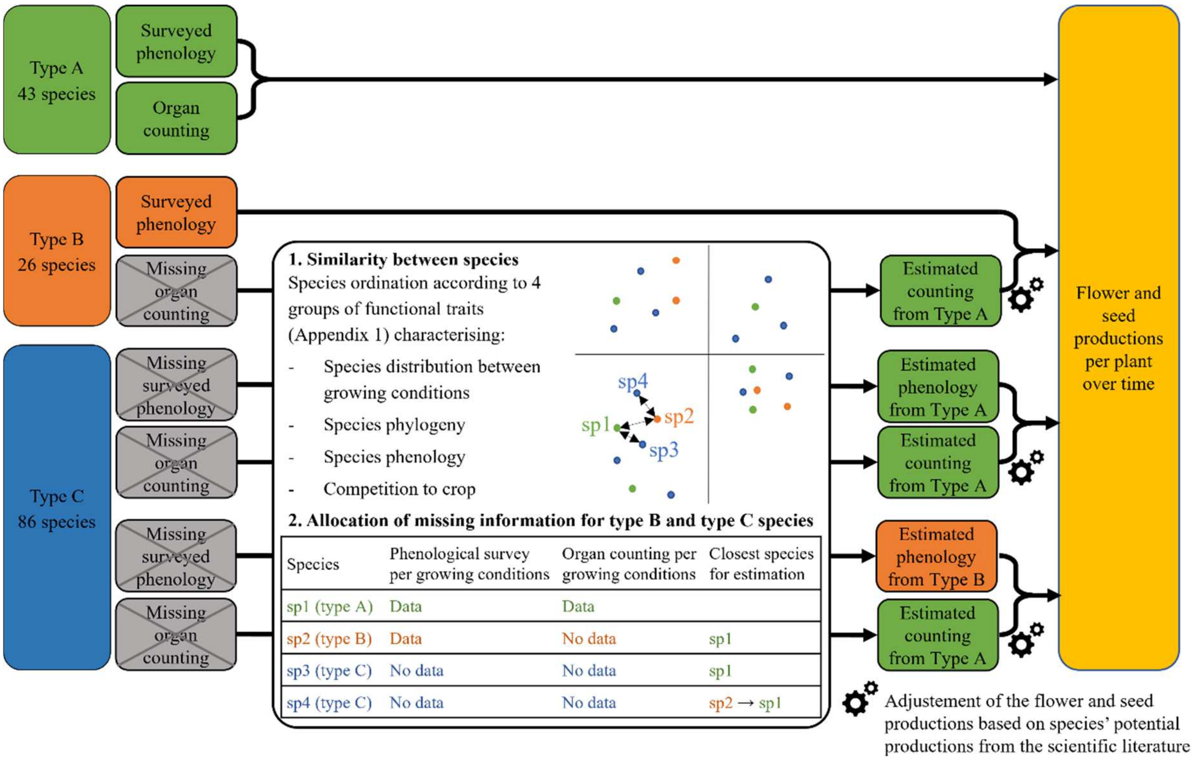
Table 1: Occurrence of the 155 studied weed species in each of the 12 combinations of within-field location by crop type (*i.e.* 967 unique situations of species by within-field location and crop type), based on weed surveys conducted over the 2008-2013 period on the Fénay platform (Dijon, France).

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***

2.2.2. Proxy calculation

To integrate weed plant responses to the local growing conditions (*i.e.* intraspecific variability) for the 155 weed species, we divided species into 3 categories (Type A, B and C, Figure 2) based on available phenological data (Yvoz et al., 2020a): phenology and flower/seed production were known for Type A species (N=43 species, Figure 2), only phenology was known for Type B species (N=26) and none of this information was collected for the Type C species (N=86). A procedure was thus developed to allocate missing information (grey boxes in Figure 2), based on the proximity between species in terms of their occurrence in and response to the set of growing conditions studied. Proximity was estimated through multidimensional distance between Type B or C species and Type A or B species, accounting 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 procedure, including traits description and selection, clustering methodology, identification of the closest species observed in the same growing conditions (within-field location by crop type), is presented in Appendix A.For Type A species, the production of flowers and seeds over time (*i.e.* every two-weeks) was calculated for each growing condition, based on the phenological surveys and organ counting (Figure 2). For Type B species, the production of flowers and seeds were estimated for each species (sp2 in Figure 2) across all growing conditions from the closest species observed in the same growing condition (*i.e.* sp1 in Figure 2, see details in Appendix A: Table A3). Production of flowers and seeds of sp2 (Type B) were then adjusted by the known 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 based on the phenological surveys of sp2.

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



Species	Phenological survey per growing conditions	Organ counting per growing conditions	Closest species for estimation
sp1 (type A)	Data	Data	
sp2 (type B)	Data	No data	sp1
sp3 (type C)	No data	No data	sp1
sp4 (type C)	No data	No data	sp2 → sp1

Figure 2: Methodology used to estimate phenological development and production of flowers and seeds of weed species when data were present (Type A) or missing (Type B and C species). When data were missing, the known data from the closest species (*i.e.* multivariate trait-based distance) observed in the same growing condition (within-field location-by-crop type) were attributed to the species (see Appendix A for the detailed procedure and 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, sp3, sp4) and counted (sp1) data. Adjustment = Potential production of the estimated species (sp2, 3 or 4)/Potential production of the counted species (sp1).

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 B) to sp4 (Type C), then adjusted (Eq. 1).

2.3. Data analyses

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

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

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

Groups of unique situations that exhibited similar values for multiple proxies, (called proxy bundles) were identified using the method proposed by Raudsepp-Hearne et al. (2010). The unique situations-by-proxies database was submitted to a PCA followed by a Hierarchical Clustering Analysis (HCA) based on the Ward's method, using the *HCPC* function from the [FactoMineR] package. Clear and non-redundant groups were identified through examination of the dendrogram and confirmed the grouping using the Elbow method computing the gain of explained variance when increasing the number of clusters. Groups were then characterised in 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 of all proxy values for each of the identified groups of plants using the *radarchart* function 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. Groups of unique situations were then characterised, first, by the proportion of situations associated with the different crop types and within-field locations and, second, by the six functional response traits (maximum height at flowering, SLA, leaf dry matter content (LDMC), Ellenberg.N and .L values, and seed mass) and five descriptors of weed phenology (germination onset and end, flowering onset and end, and leaf type) (traits description in Supp. Table. 1).

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 contributing largely to the pollination of crops in agricultural landscapes (Eilers et al., 2011). Weeds contribute to the conservation of pollinator populations by the provision of nectar and pollen before and after crop flowering, and by providing more diverse resources otherwise (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 et al., 2014) or flower symmetry (Wignall et al., 2006)), its accessibility (*e.g.* determined by the form and size of the corolla (Lehrer, 2005)) and the quantity and quality of the floral rewards (*e.g.* pollen (Hass et al., 2019) and/or nectar (Pamminger et al., 2019)).

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

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

Although farmland birds' diet is mainly composed of invertebrates (Barré et al., 2018), seeds 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-Williams, 2005). Gibbons et al. (2006) showed a positive correlation between seed preference and their energy concentration, somehow related to the seed lipid content (Greig-Smith and Wilson, 1985). Carabids can consume a third of their weight of seeds daily in spring and summer (Honek et al., 2003). Carabid preferences are also linked to the seed lipid content (Gaba 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 (PCont2), we thus considered the quantity of lipids per seed as a proxy of the energy resources (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 (Supp. Table 1). For 13 weed species where data were missing in the literature, we computed the average of the species belonging to the same genus.

Most parasitoid wasps rely on carbohydrate resources, provided by honeydew or by crop and weed floral and extra-floral nectar, to increase their longevity and fecundity (Leatemia et al., 1995). Beneficial effects of nectar could depend on the type of carbohydrate (Vattala et al., 2006), despite no consensus emerges on the best type. Baker and Baker (1983) showed preferences for nectar rich in saccharose, whereas recent studies showed no differences between saccharose, fructose and glucose effects on parasitoid longevity (Hausmann et al., 2005; Winkler et al., 2005). The contribution of weed species to parasitoidsis however restricted by 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 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) 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 important aspects. Rogers (1985) also highlighted the importance of the extra-floral nectar, 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 multiplying the flower diameter by three coefficients (between 0 and 1) representing the interest in terms of nectar quantity, flower shape and corolla depth (Table 2). This equation allows the computation of null values, as soon as at least one aspect is not favourable. The nectar quantity 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 six weed species producing extra-floral nectar (Table 2), namely *Cyanus segetum* Hill, *Centaurea jacea* L., *Centaurea scabiosa* L., *Fallopia convolvulus* (L.), *Sambucus ebulus* L. and *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 (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 until flowering. As adult parasitoids have a short life cycle and their prey are mainly associated with cereal crops, oilseed rape and mustard, we computed this proxy from March to June, the value being null otherwise.

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. 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 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 survey. Traits used in the equations are detailed in Supp. Table 1.

Proxies	**Equations**
Potential weed contribution to pollinators: - bees (**Pol1**) - bumblebees (**Pol2**) - hoverflies (**Pol3**)	$Polj = \sum_{i=1}^{155}(exp\ exp\ \left(PV_j(i)\right) \times FD(i) \times FN(i) \times A(i))$ - **PV$_j$**: Pollinator value from Ricou et al. (2014), j in {1, 2, 3} - **FD**: Flower diameter - **FN**: Average flower number per plant - **A**: Abundance of the species in the survey
Potential weed contribution to pest natural enemies - farmland birds (**PCont1**)	$PCont1 = \sum_{i=1}^{155}(SL(i) \times SM(i) \times SN(i) \times A(i))$ - **SL**: Seed lipid content - **SM**: Seed mass - **SN**: Average seed number per plant - **A**: Abundance of the species in the survey
Potential weed contribution to pest natural enemies - carabids (**PCont2**)	$PCont2 = \sum_{i=1}^{155}(SL(i) \times SM(i) \times SA(i) \times SN(i) \times A(i))$ - **SL**: Seed lipid content - **SM**: Seed mass - **SA**: Seed availability (1 if SM < 3mg; Linear decrease from 1 to 0 for SM=3 to 35mg; 0 if SM > 35mg) - **SN**: Average seed number per plant - **A**: Abundance of the species in the survey

<table>
<tr><th>Proxies</th><th>Equations</th></tr>
<tr><td>Potential weed contribution to pest natural enemies
- parasitoid wasps (PCont3)</td><td>

$$PCont3 = \sum_{i=1}^{155}(NQ(i) \times FF(i) \times CD(i) \times FN(i) \times A(i) + \sum_{k=1}^{9}(QEN(i) \times P(ki) \times REN(ki) \times A(i)))$$

- **NQ**: Nectar quantity (none = 0; little = 0.4; present = 0.8; plenty = 1)
- **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)
- **CD**: Corolla depth (<4.5 mm = 1; >4.5 mm but nectar available = 0.5; no nectar or unavailable = 0)
- **FN**: Average flower number per plant
- **A**: Abundance of the species in the survey
- **QEN**: Quantity of extra-floral nectar estimated as the maximum value of PCont3 per half month for the floral nectar part
- **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)
- **REN**: Rate of the maximum extra-floral nectar production depending of the phenological stage k

<table>
<tr><th>Phenological stage (Yvoz et al., 2020a)</th><th>REN 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>REN for <i>Cyanus segetum</i> Hill, <i>Centaurea jacea</i> L. and <i>Centaurea scabiosa</i> L.
Extra-floral nectar on flower parts</th></tr>
<tr><td>Seedling: A, B</td><td>0</td><td>0</td></tr>
<tr><td>Adult: C1</td><td>0.5</td><td>0</td></tr>
<tr><td>Adult: C2</td><td>0.7</td><td>0.5</td></tr>
<tr><td>Flowering: D1</td><td>0.8</td><td>0.8</td></tr>
<tr><td>Flowering: D2</td><td>1</td><td>1</td></tr>
<tr><td>Flowering: D3</td><td>1</td><td>1</td></tr>
<tr><td>Maturity: E1</td><td>0.7</td><td>0</td></tr>
<tr><td>Maturity: E2</td><td>0</td><td>0</td></tr>
</table>

</td></tr>
</table>

Proxies	**Equations**
Potential weed competition against crop (**Harm1**)	$Harm1 = \sum_{i=1}^{155} (GP(i) \times FP(i) \times RH(i) \times EN(i) \times SLA(i) \times GS(i) \times A(i))$ - **GP**: Germination period synchrony (details in Supp. Table 2) - **FP**: Flowering period synchrony (details in Supp. Table 3) - **RH**: Relative height = height(weed)/height(crop) - **EN**: Relative Ellenberg.N = Ellenberg.N(weed)/Ellenberg.N(crop) - **SLA**: Relative SLA = SLA(weed)/SLA(crop) - **GS**: Growing success = 1-proportion of plant dead without reaching the stage C1, *i.e.* adult plant (Yvoz et al., 2020a) - **A**: Abundance of the species in the survey
Potential weed contribution to harvest difficulties (**Harm2**)	$Harm2 = \sum_{i=1}^{155} (\left(\left(H(i) \times S(i)\right) - 15\right) \times PG(i) \times A(i))$ - **H**: Maximum height (cm) - **PG**: Proportion of plants still green at harvest - **S**: Synchrony between weed flowering period and crop harvest - **A**: Abundance of the species in the survey
Potential weed contribution to future infestations (**Harm3**)	$Harm3 = \sum_{i=1}^{155} (SP(i) \times SN(i) \times A(i))$ - **SP**: Seed longevity - **SN**: Average seed number per plant - **A**: Abundance of the species in the survey

3.1.3. Competition with crop (Harm1)

Weeds compete with crops for resources, such as nitrogen, light and water (Blackshaw et al., 2004; Swanton et al., 2015). Weeds outcompete crops when they share the same space at the same time and highlight a higher efficiency to uptake a limiting resource. Moreau et al. (2013) showed that the Ellenberg's indicator value N (Ellenberg et al., 1992), a simple ordinal classification of plants according to the position of their realized ecological niche along an 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 increases the intensity of competition (Fried et al., 2015), the outcome being dictated by the 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 competitiveness. Fried et al. (2019) also showed that a high SLA is generally associated with a high ability of weed to compete with crop by intercepting more of the incident radiations for a given leaf biomass unit.

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 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 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 when the weed growth is synchronic with the crop. Since certain weed plants die without reaching the vegetative stage (Yvoz et al., 2020a), we subtracted a proportion of plants (GS in Table 2), hypothesizing they do not cause significant yield loss in their early growth (Adeux et al., 2019).

3.1.4. Harvest difficulties (Harm2)

Even if weed species emerging late in season are generally low competitors, they may remain green at harvest and cause harvest difficulties for farmers (Swanton et al., 2015). They can also 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).

The proxy for the potential weed contribution to harvest difficulties (Harm2) was estimated by the estimated height of green biomass located above the cutting bar at harvest. Since weed species reach their maximum green biomass at flowering, we multiplied the maximum height of weed species found in the literature by a coefficient of synchrony between the weed flowering period and the crop harvest period, for each weed:crop couples, to account for weed growth (Supp. Table 3). For instance, the height of green tissues was equal to the maximum weed height for a weed plant flowering at crop harvest (*i.e.* high synchrony) when it was decreased by the synchrony coefficient if the weed plant flowers later than crop harvest (*i.e.* being smaller than its maximum height). We then subtracted 15 cm, the average cutting height, from the weed height, *i.e.* only the green tissues located above contributing to harvest difficulties. Finally, we multiplied these values by the proportion of individual weed plants still green at harvest (*i.e.* phenological stages between C1 (adult plants) and E1 (end of flowering) assessed in Yvoz et al. (2020a)) (Table 2).

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).

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.

3.2.1. Correlations between proxies

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 correlated with Harm3 and Harm1, separating weed plants by their ability to produce flowers and seeds. Proxies representing the contribution of weeds to pollination and pest control were highly positively correlated at the plant level, as their computation was related to the same organs (flowers for Pol1, Pol2, Pol3, PCont3, and seeds for PCont1, PCont2, Table 2). The 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 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.

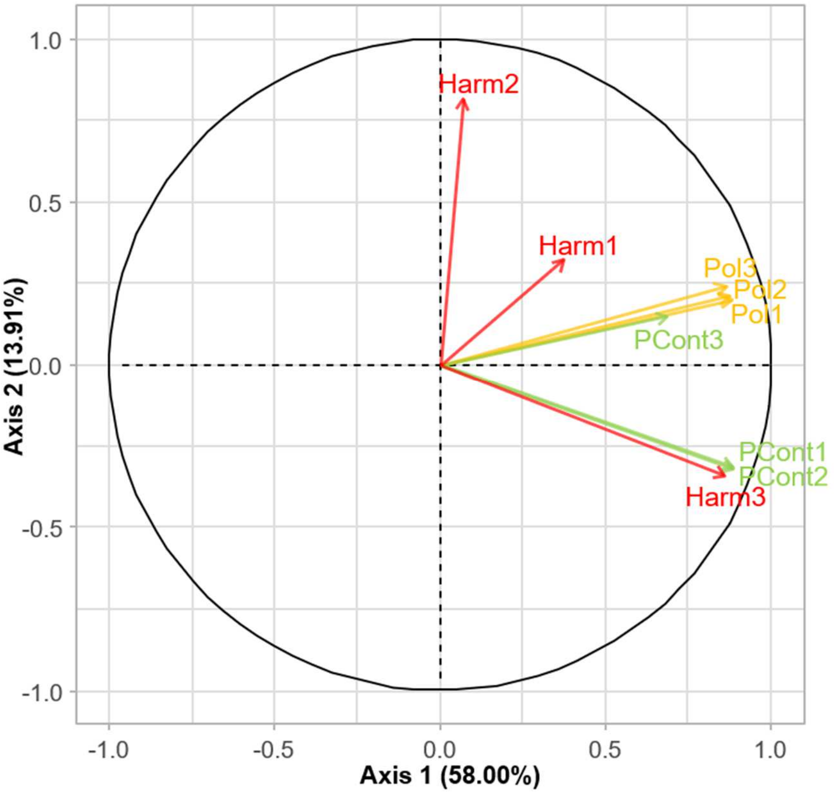


Figure 3: Correlations between the nine proxies (detailed in Table 2) and the two first dimensions of the principal component analysis. Potential weed contribution to pollinators (bees: Pol1, bumblebees: Pol2, hoverflies: Pol3), Potential weed contribution to pest natural enemies (farmland birds: PCont1, 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).

3.2.2. Identification of proxy bundles

Five PB were identified by the clustering analysis. PB1 (196 unique situations) had low contribution values to both ecosystem service and harmfulness proxies (Figure 4). PB2 (162 unique situations) had low values of harmfulness (except for Harm2) and PCont1/PCont2 services, but an intermediate contribution to pollinators (Pol1, Pol2, Pol3) and parasitoids (PCont3). PB3 (256 unique situations) showed an intermediate contribution to pollinators and pest natural enemies (except for PCont3), a low weed:crop competition, but a high contribution 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 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.

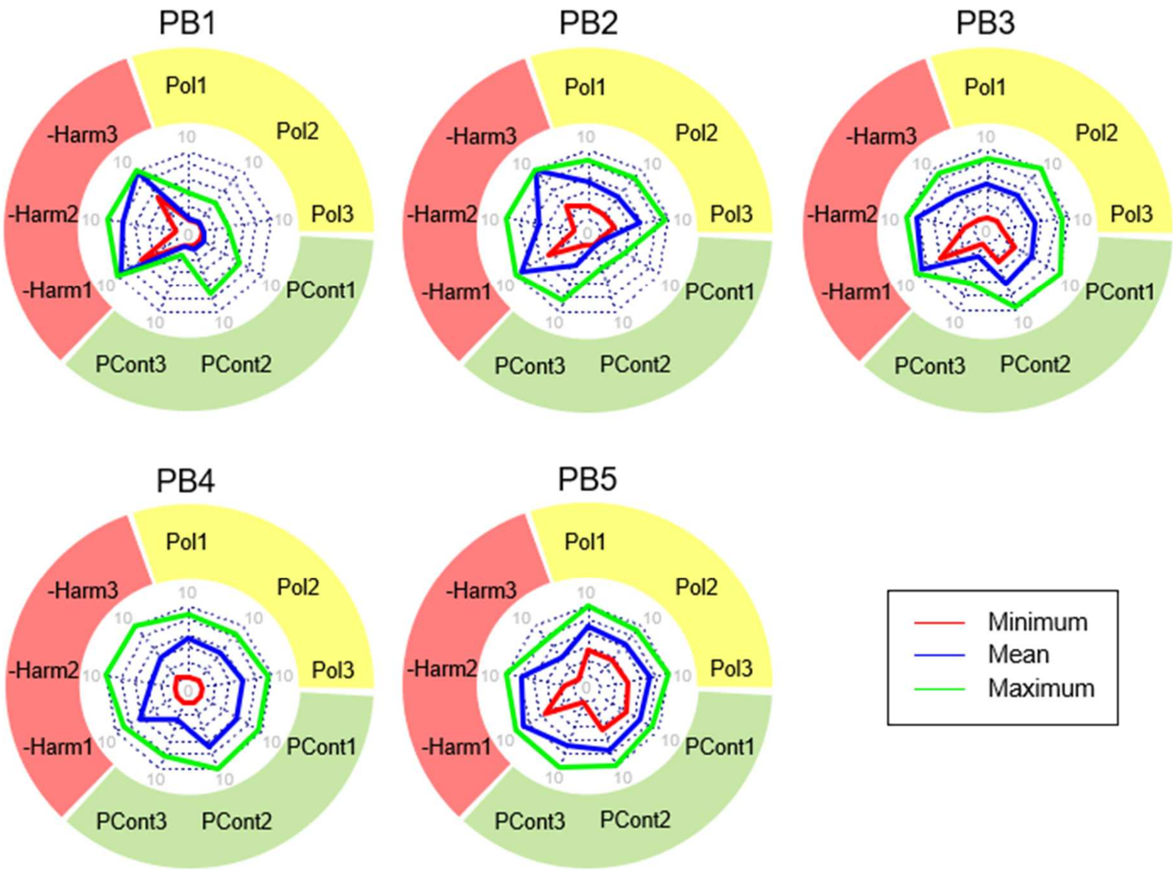


Figure 4: Radar plots of the minimum (red line), mean (blue line) and maximum (green line) values of the nine proxies (detailed in Table 2) calculated for the five identified proxy bundles (PB). Values were log10-transformed and scaled from 0 to 10. Harm1, Harm2 and Harm3 were reversed before plotting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

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

PB1 was significantly associated with tall forb species (Figure 5, 1 m on average), with high Ellenberg.N values (6.6), low SLA (23.0 mm²/mg), and late germination and flowering onsets (on average in December and mid-May, respectively), as *Aethusa cynapium* L. and *Atriplex patula* L. Besides, unique situations in PB1 mainly occurred in field cores of cereal crops (Table 3). PB2 was associated with tall species (93 cm) with low SLA (23.5 mm²/mg), high 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 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

Ellenberg.N values (6.2) and seed mass (2.2 mg), high LDMC (186 mg/g) and SLA (27.1 mm²/mg) and early germination and flowering onsets and end of the germination period (in October, end of April and April, respectively), as *Poa annua* L. and *Viola arvensis* Murray. Unique situations in PB3 occurred mostly in field edges of winter oilseed rape. PB4 was associated with tall (113 cm) grasses (a third of the species) with high Ellenberg.N values (7.1), seed mass (4.3 mg), SLA (27.5 mm²/mg) and LDMC (190 mg/g) and with late flowering onset (in Mid-May), as *Echinochloa crus-galli* (L.) and *Chenopodium album* L. Unique situations in PB4 mostly occurred in the field cores and field edges of soybean. Finally, PB5 was associated 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 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 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.

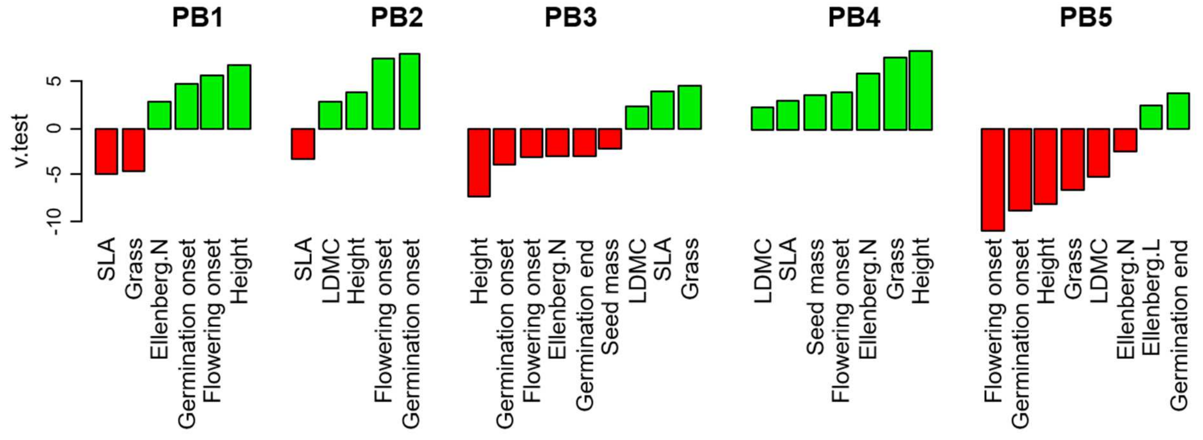
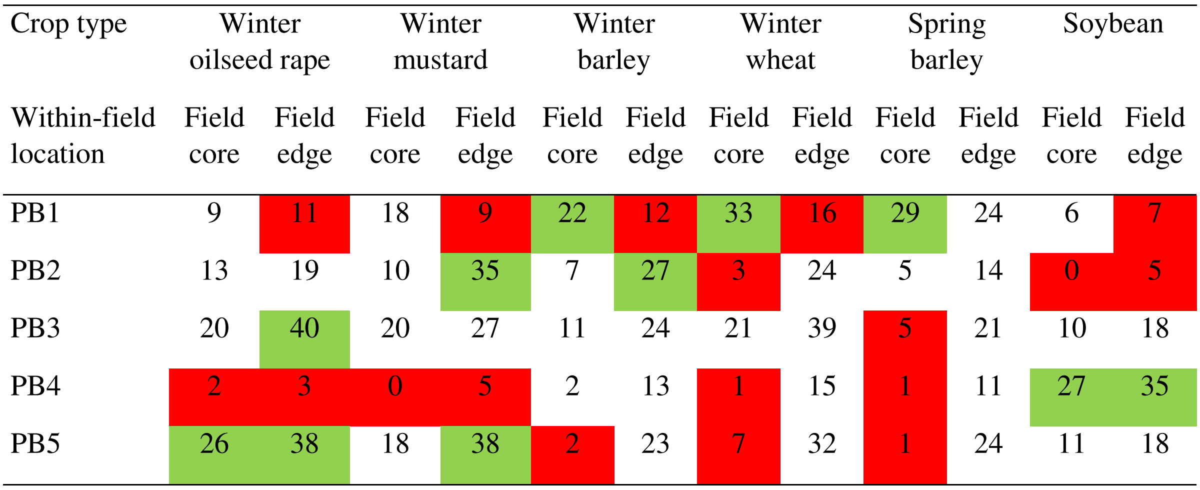


Figure 5: Response traits associated with each of the five proxy bundles (PB). Associations between traits and PB were estimated by a one-way analysis of variance implemented with the *catdes* function from the [FactoMineR] package. Only significant (p-value < 0.05) traits were presented, green and red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

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

4. Discussion

The rationale of the study was to propose a generic framework to quantify the potential contribution of weed species to multiple ecosystem services and harmfulness and develop a set of trait-based proxies that could translate weed surveys into values of their contribution to these 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 addition to the development of nine proxies of services and harmfulness, we provided a 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 general antagonism between the delivery of ecosystem services and the degree of harmfulness 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.

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 are scientifically robust, what they call the “design validation”.

Our proxies were based on a comprehensive review of the literature to identify the most relevant 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 weed growing conditions, an aspect missing so far despite its important implications for the outcome of ecological interactions (Bolnick et al., 2011). Here, field-based measures of intraspecific variability were only available for part of the weed species recorded in the study area. For the others, we assessed their similarity with species for which we had field measures by using a number of species characteristics, namely 15 traits and 12 variables describing their occurrence in different growing conditions. This procedure integrated most of the traits translating species response to crop competition and farming practices. We however acknowledge that its outcome was dependent on (i) the choice of species characteristics it was based on (ii) the species pool for which we had field-based measures and (iii) the accuracy of 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 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 services were included or if new trait data became available. Research efforts should also be devoted to field-based studies quantifying intraspecific variability of weed flower and seed production in a wider range of environmental and agronomic conditions. Finally, we implemented a design validation to assess weed contribution to parasitoids (PCont3) because the available literature was scarce; we thus validated our proxy construction with experts and reached a consensus, a crucial step towards validation (Bockstaller and Girardin, 2003).

A true “output validation” (as defined by Bockstaller and Girardin (2003)) of most of our proxies appears challenging and probably not well adapted to weeds as it is usually conducted by using a weed survey at a particular time of the season, whereas the temporal dynamic of the 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 chemical or mechanical weeding (Adeux et al., 2019). Thus, it requires frequent labour and attention over the course of the crop season to ensure controls to be actually weed-free, weed 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 the services and harmfulness, such as the carabids activity, parasitoids and pollinators visitations, in a way to validate their significance and robustness in different production situations and weed contexts.

4.2. Assessing proxy bundles delivered by weed communities

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 reveals a general antagonism between services and harmfulness for the 967 unique situations, although there were some exceptions (see 4.3). The underlying causes of this antagonism lie in 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 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) and beetles (PCont2). Nevertheless, high values of PCont1 and PCont2 also suggest potential 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 Oliver, 1993), and competition (Harm1) is mainly driven by relative weed:crop biomass (Milberg and Hallgren, 2004). We therefore logically observed that proxies of services are positively correlated with those of harmfulness. It should however be mentioned that benefits obtained by the increase of pollination (Pol1, Pol2, Pol3) of some crops such as oilseed rape (Bretagnolle and Gaba, 2015) could compensate, at least partially, for weed:crop competition (DiTommaso et al., 2016). Accounting for such positive and negative feedbacks between services could partially change the general antagonism we detected here. However, interactions between services are to date hardly documented but their study probably represents an important scientific challenge for future research assessing ecosystem multifunctionality.

Another factor that could modulate the general antagonism we detected is the fact that proxy 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 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 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 instance, weed:crop interference has mainly been studied considering only one weed species at a time (Colbach et al., 2020). Hence, little is known about the competitive effect of weeds in 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 associated with low weed biomass and reduced interference with the crop. Beside the effect of weed diversity/evenness, they also showed that the composition of weed communities was a 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 with the way we have constructed our harmfulness proxies based on similarities between crop and weed trait values (Table 2). Finally, the increase of our weed harmfulness proxies does not necessarily lead to significant yield loss if weed:crop interference remains low (Adeux et al., 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 their perception of weeds vary according to their own experience (Wilson et al., 2009).

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

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 of multiple proxies, called proxy bundles. The clustering analysis allowed us to identify species groups with distinct PB and particularly PB5 and PB3 which did not follow the general antagonism between services and harmfulness mentioned above. PB5 was characterised by small species with low LDMC and Ellenberg.N values, and with early germination and flowering onset. As LDMC is positively correlated with biomass conservation (Pierce et al., 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 highly contributing to ecosystem services. PB3 was the second-best proxy bundle and also 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 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 values. Indeed, SLA represents their ability to intercept light (Ackerly et al., 2002) and the height is generally used as a proxy for competition for light (Gaba et al., 2017).

Our results also showed that some plants provided neither services nor harmfulness. They were mostly located in the field core of cereal crops, known to be highly competitive crops, due to their small row spacing and their high tillering ability (Jha et al., 2017). Besides, due to herbicide program targeting forbs (Markéta et al., 2018), species occurring in cereal crops are 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).

5. Conclusion

We presented here a novel framework to estimate the contribution of individual weed plants to a set of services and harmfulness under contrasting growing conditions. The division of the proxy calculations into three nested levels of organisation (*i.e.* organ, plant and community) allowed us to integrate intraspecific variability of the weed contribution to ecosystem services and harmfulness. The application of these proxies at the plant level, on 967 unique situations, highlighted a general trend where a high weed plant contribution to ecosystem services was generally synonymous of a high harmfulness to the crop. We however identified a group of plants gathering small species with a short life cycle and mainly associated to mustard and oilseed rape, presenting the optimum proxy combination, *i.e.* high services and low levels of harmfulness. These plants produce flowers and seeds while being not too competitive to the crop. The proxy database provided and detailed methodology of data imputation based on 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 values to field observations and then assess the multifunctionality of weed communities occurring in arable landscapes.

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References

Ackerly, D., Knight, C., Weiss, S., Barton, K., Starmer, K., 2002. Leaf size, specific leaf area and microhabitat distribution of chaparral woody plants: contrasting patterns in species level and community level analyses. Oecologia 130, 449-457.

Adeux, G., Vieren, E., Carlesi, S., Barberi, P., Munier-Jolain, N., Cordeau, S., 2019. Mitigating crop yield losses through weed diversity. Nature Sustainability 2, 1018-1026.

Backhaus, W., 1992. Color vision in honeybees. Neurosci. Biobehav. Rev. 16, 1-12.

Baker, H.G., Baker, I., 1983. A brief historical review of the chemistry of floral nectar. The biology of nectaries, 126-152.

Barralis, G., 1976. Méthode d'étude des groupements adventices des cultures annuelles. In: 5ème Colloque International sur l'Ecologie et la Biologie des Mauvaises herbes. INRA, Dijon. 59-68.

Barré, K., Le Viol, I., Julliard, R., Kerbiriou, C., 2018. Weed control method drives conservation tillage efficiency on farmland breeding birds. Agriculture, Ecosystems & Environment 256, 74-81.

Blackshaw, R.E., Molnar, L.J., Janzen, H.H., 2004. Nitrogen fertilizer timing and application method affect weed growth and competition with spring wheat. Weed Sci 52, 614-622.

Blaix, C., Moonen, A.C., Dostatny, D.F., Izquierdo, J., Le Corff, J., Morrison, J., Von Redwitz, C., Schumacher, M., Westerman, P.R., 2018. Quantification of regulating ecosystem services provided by weeds in annual cropping systems using a systematic map approach. Weed Res 58, 151-164.

Bockstaller, C., Girardin, P., 2003. How to validate environmental indicators. Agricultural Systems 76, 639-653.

Bolnick, D.I., Amarasekare, P., Araújo, M.S., Bürger, R., Levine, J.M., Novak, M., Rudolf, V.H.W., Schreiber, S.J., Urban, M.C., Vasseur, D.A., 2011. Why intraspecific trait variation matters in community ecology. Trends in Ecology & Evolution 26, 183-192.

Borgy, B., Perronne, R., Kohler, C., Grison, A.L., Amiaud, B., Gaba, S., 2016. Changes in functional diversity and intraspecific trait variability of weeds in response to crop sequences and climate. Weed Res 56, 102-113.

Bretagnolle, V., Gaba, S., 2015. Weeds for bees? A review. Agron. Sustainable Dev. 35, 891-909.

Cadotte, M.W., Arnillas, C.A., Livingstone, S.W., Yasui, S.-L.E., 2015. Predicting communities from functional traits. Trends in Ecology & Evolution 30, 510-511.

Carvalheiro, L.G., Veldtman, R., Shenkute, A.G., Tesfay, G.B., Pirk, C.W.W., Donaldson, J.S., Nicolson, S.W., 2011. Natural and within-farmland biodiversity enhances crop productivity: Weeds maximize nature benefits to crops. Ecol. Lett. 14, 251-259.

Colbach, N., Petit, S., Chauvel, B., Deytieux, V., Lechenet, M., Munier-Jolain, N., Cordeau, S., 2020. The Pitfalls of Relating Weeds, Herbicide Use, and Crop Yield: Don't Fall Into the Trap! A Critical Review. 2, 29.

Cordeau, S., Ryan, M.R., Bohan, D.A., Reboud, X., Chauvel, B., 2017. Which traits allow weed species to persist in grass margin strips? Weed Sci 65, 381-394.

DiTommaso, A., Averill, K.M., Hoffmann, M.P., Fuchsberg, J.R., Losey, J.E., 2016. Integrating insect, resistance, and floral resource management in weed control decision-making. Weed Sci 64, 743-756.

Duru, M., Therond, O., Martin, G., Martin-Clouaire, R., Magne, M.A., Justes, E., Journet, E.P., Aubertot, J.N., Savary, S., Bergez, J.E., Sarthou, J.P., 2015. How to implement biodiversity-based agriculture to enhance ecosystem services: a review. Agron. Sustainable Dev. 35, 1259-1281.

Dutoit, T., Gerbaud, É., Ourcival, J.-M., 1999. Field boundary effects on soil seed banks and weed vegetation distribution in an arable field without weed control (Vaucluse, France). Agronomie 19, 579-590.

Eilers, E.J., Kremen, C., Smith Greenleaf, S., Garber, A.K., Klein, A.-M., 2011. Contribution of pollinator-mediated crops to nutrients in the human food supply. Plos One 6, e21363.

Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W., Paulissen, D., 1992. Indicator values of central European plants. Scripta Geobotanica 18, 1-258.

Fanfarillo, E., Kasperski, A., 2021. An index of ecological value for European arable plant communities. Biodiversity and Conservation 30, 2145-2164.

Fried, G., Chauvel, B., Munoz, F., Reboud, X., 2019. Which traits make weeds more successful in maize crops? Insights from a three-decade monitoring in France. Plants 9, 40.

Fried, G., Chauvel, B., Reboud, X., 2015. Weed flora shifts and specialisation in winter oilseed rape in France. Weed Res 55, 514-524.

Gaba, S., Cheviron, N., Perrot, T., Piutti, S., Gautier, J.L., Bretagnolle, V., 2020. Weeds enhance multifunctionality in arable lands in South-West of France. Frontiers in Sustainable Food Systems 4, 71.

Gaba, S., Deroulers, P., Bretagnolle, F., Bretagnolle, V., 2019. Lipid content drives weed seed consumption by ground beetles (Coleopterea, Carabidae) within the smallest seeds. Weed Res 59, 170-179.

Gaba, S., Perronne, R., Fried, G., Gardarin, A., Bretagnolle, F., Biju-Duval, L., Colbach, N., Cordeau, S., Fernández-Aparicio, M., Gauvrit, C., Gibot-Leclerc, S., Guillemin, J.P., Moreau, D., Munier-Jolain, N., Strbik, F., Reboud, X., 2017. Response and effect traits of arable weeds in agro-ecosystems: a review of current knowledge. Weed Res 57, 123-147.

Gibbons, D.W., Bohan, D.A., Rothery, P., Stuart, R.C., Haughton, A.J., Scott, R.J., Wilson, J.D., Perry, J.N., Clark, S.J., Dawson, R.J.G., Firbank, L.G., 2006. Weed seed resources for birds in fields with contrasting conventional and genetically modified herbicide-tolerant crops. Proceedings of the Royal Society B: Biological Sciences 273, 1921-1928.

Girardin, P., Bockstaller, C., Van der Werf, H., 1999. Indicators: Tools to evaluate the environmental impacts of farming systems. Journal of Sustainable Agriculture 13, 5-21.

Greig-Smith, P.W., Wilson, M.F., 1985. Influences of seed size, nutrient composition and phenolic content on the preferences of bullfinches feeding in ash trees. Oikos, 47-54.

Hass, A.L., Brachmann, L., Batáry, P., Clough, Y., Behling, H., Tscharntke, T., 2019. Maize-dominated landscapes reduce bumblebee colony growth through pollen diversity loss. J. Appl. Ecol. 56, 294-304.

Hausmann, C., Wäckers, F.L., Dorn, S., 2005. Sugar convertibility in the parasitoid Cotesia glomerata (Hymenoptera: Braconidae). Archives of Insect Biochemistry and Physiology: Published in Collaboration with the Entomological Society of America 60, 223-229.

Holland, J.M., Hutchison, M.A.S., Smith, B., Aebischer, N.J., 2006. A review of invertebrates and seed-bearing plants as food for farmland birds in Europe. Ann Appl Biol 148, 49-71.

Holland, J.M., Smith, B.M., Southway, S.E., Birkett, T.C., Aebischer, N.J., 2008. The effect of crop, cultivation and seed addition for birds on surface weed seed densities in arable crops during winter. Weed Res 48, 503-511.

Holmes, R.J., Froud-Williams, R.J., 2005. Post-dispersal weed seed predation by avian and non-avian predators. Agriculture, Ecosystems & Environment 105, 23-27.

Honek, A., Martinkova, Z., Jarosik, V., 2003. Ground beetles (Carabidae) as seed predators. Eur. J. Entomol. 100, 531-544.

Horth, L., Campbell, L., Bray, R., 2014. Wild bees preferentially visit Rudbeckia flower heads with exaggerated ultraviolet absorbing floral guides. Biology Open 3, 221-230.

Hyvönen, T., Huusela-Veistola, E., 2008. Arable weeds as indicators of agricultural intensity–a case study from Finland. Biological Conservation 141, 2857-2864.

Jabbour, R., Zwickle, S., Gallandt, E.R., McPhee, K.E., Wilson, R.S., Doohan, D., 2014. Mental models of organic weed management: Comparison of New England US farmer and expert models. Renew Agric Food Syst 29, 319-333.

Jauzein, P., 1995. Flore des champs cultivés. SOPRA-INRA Ed. 898 pages.

Jayanthi, R., Nalini, T., Selvamuthukumaran, T., 2019. Diversity of extra-floral nectaries (EFN) bearing plants and its ant assemblage. Plant Archives 19, 1684-1691.

Jervis, M., 1998. Functional and evolutionary aspects of mouthpart structure in parasitoid wasps. Biological Journal of the Linnean Society 63, 461-493.

Jha, P., Kumar, V., Godara, R.K., Chauhan, B.S., 2017. Weed management using crop competition in the United States: A review. Crop Protection 95, 31-37.

Kattge, J., 2012. TRY - Categorical Traits Dataset. Max Planck Institute for Biogeochemistry, Jena.

Kazakou, E., Violle, C., Roumet, C., Navas, M.L., Vile, D., Kattge, J., Garnier, E., 2014. Are trait-based species rankings consistent across data sets and spatial scales? Journal of Vegetation Science 25, 235-247.

Keeler, K.H., 1979. Species with extrafloral nectaries in a temperate flora (Nebraska). Prairie Naturalist 11, 33-38.

Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P., Thompson, K., Sonnenschein, M., Poschlod, P., Van Groenendael, J.M., Klimeš, L., Klimešová, J., 2008. The LEDA Traitbase: a database of life-history traits of the Northwest European flora. Journal of Ecology 96, 1266-1274.

Kremen, C., Ostfeld, R.S., 2005. A call to ecologists: measuring, analyzing, and managing ecosystem services. Front. Ecol. Environ. 3, 540-548.

Leatemia, J.A., Laing, J.E., Corrigan, J.E., 1995. Effects of adult nutrition on longevity, fecundity, and offspring sex ratio of Trichogramma minutum Riley (Hymenoptera: Trichogrammatidae). The Canadian Entomologist 127, 245-254.

Lehrer, M., 2005. Generalization of convex shapes by bees: what are shapes made of? J. Exp. Biol. 208, 3233-3247.

Mahé, I., Cordeau, S., Bohan, D.A., Derrouch, D., Dessaint, F., Millot, D., Chauvel, B., 2020. Soil seedbank: old methods for new challenges in agroecology? Ann Appl Biol, 1-16.

Markéta, M., Jan, M., Josef, S., 2018. Effects of selective herbicide treatment on weed community in cereal crop rotation. Plant, Soil and Environment 64, 413-420.

Marshall, E.J.P., Brown, V.K., Boatman, N.D., Lutman, P.J.W., Squire, G.R., Ward, L.K., 2003. The role of weeds in supporting biological diversity within crop fields. Weed Res 43, 77-89.

Mézière, D., Petit, S., Granger, S., Biju-Duval, L., Colbach, N., 2015. Developing a set of simulation-based indicators to assess harmfulness and contribution to biodiversity of weed communities in cropping systems. Ecol. Indicators 48, 157-170.

Milberg, P., Hallgren, E., 2004. Yield loss due to weeds in cereals and its large-scale variability in Sweden. Field Crops Research 86, 199-209.

Moreau, D., Milard, G., Munier-Jolain, N., 2013. A plant nitrophily index based on plant leaf area response to soil nitrogen availability. Agron. Sustainable Dev. 33, 809-815.

Navas, M.L., 2012. Trait-based approaches to unravelling the assembly of weed communities and their impact on agro-ecosystem functioning: Functional structure of weeds. Weed Res 52, 479-488.

Orr, D.B., Pleasants, J.M., 1996. The potential of native prairie plant species to enhance the effectiveness of the Ostrinia nubilalis parasitoid Macrocentrus grandii. J. Kans. Entomol. Soc., 133-143.

Pamminger, T., Becker, R., Himmelreich, S., Schneider, C.W., Bergtold, M., 2019. The nectar report: quantitative review of nectar sugar concentrations offered by bee visited flowers in agricultural and non-agricultural landscapes. PeerJ 7, e6329.

Perron, F., Legere, A., 2000. Effects of crop management practices on Echinochloa crus-galli and Chenopodium album seed production in a maize/soyabean rotation. Weed Res 40, 535-547.

Perronne, R., Gaba, S., Cadet, E., Le Corre, V., 2014. The interspecific and intraspecific variation of functional traits in weeds: diversified ecological strategies within arable fields. Acta Botanica Gallica 161, 243-252.

Petit, S., Boursault, A., Bohan, D.A., 2014. Weed seed choice by carabid beetles (Coleoptera: Carabidae): Linking field measurements with laboratory diet assessments. Eur. J. Entomol. 111, 615-620.

Pierce, S., Brusa, G., Vagge, I., Cerabolini, B.E.L., 2013. Allocating CSR plant functional types: the use of leaf economics and size traits to classify woody and herbaceous vascular plants. Functional Ecology 27, 1002-1010.

Pocock, M.J.O., Evans, D.M., Memmott, J., 2012. The robustness and restoration of a network of ecological networks. Science 335, 973-977.

R Core Team, 2021. R: A language and environment for statistical computing, 4.04 ed. R Foundation for Statistical Computing, Vienna, Austria.

Raudsepp-Hearne, C., Peterson, G.D., Bennett, E.M., 2010. Ecosystem service bundles for analyzing tradeoffs in diverse landscapes. Proceedings of the National Academy of Sciences 107, 5242-5247.

Requier, F., Odoux, J.F., Tamic, T., Moreau, N., Henry, M., Decourtye, A., Bretagnolle, V., 2015. Honey bee diet in intensive farmland habitats reveals an unexpectedly high flower richness and a major role of weeds. Ecol Appl 25, 881-890.

Reyers, B., Biggs, R., Cumming, G.S., Elmqvist, T., Hejnowicz, A.P., Polasky, S., 2013. Getting the measure of ecosystem services: a social–ecological approach. Front. Ecol. Environ. 11, 268-273.

Ricou, C., Schneller, C., Amiaud, B., Plantureux, S., Bockstaller, C., 2014. A vegetation-based indicator to assess the pollination value of field margin flora. Ecol. Indicators 45, 320-331.

Rogers, C.E., 1985. Extrafloral nectar: entomological implications. Bulletin of the Entomological Society of America 31, 15-20.

Rosas-Guerrero, V., Aguilar, R., Martén-Rodríguez, S., Ashworth, L., Lopezaraiza-Mikel, M., Bastida, J.M., Quesada, M., 2014. A quantitative review of pollination syndromes: do floral traits predict effective pollinators? Ecol. Lett. 17, 388-400.

Salisbury, E.J., 1909. The extra-floral nectaries of the genus Polygonum. Ann. Bot. os-23, 229-242.

Senseman, S.A., Oliver, L.R., 1993. Flowering patterns, seed production, and somatic polymorphism of three weed species. Weed Sci 41, 418-425.

Storkey, J., 2006. A functional group approach to the management of UK arable weeds to support biological diversity. Weed Res 46, 513-522.

Storkey, J., Brooks, D., Haughton, A., Hawes, C., Smith, B.M., Holland, J.M., 2013. Using functional traits to quantify the value of plant communities to invertebrate ecosystem service providers in arable landscapes. Journal of Ecology 101, 38-46.

Storkey, J., Neve, P., 2018. What good is weed diversity? Weed Res 58, 239-243.

Swanton, C.J., Nkoa, R., Blackshaw, R.E., 2015. Experimental methods for crop–weed competition studies. Weed Sci 63, 2-11.

van Oudenhoven, A.P.E., Petz, K., Alkemade, R., Hein, L., de Groot, R.S., 2012. Framework for systematic indicator selection to assess effects of land management on ecosystem services. Ecol. Indicators 21, 110-122.

Vattala, H.D., Wratten, S.D., Phillips, C.B., Wäckers, F.L., 2006. The influence of flower morphology and nectar quality on the longevity of a parasitoid biological control agent. Biological Control 39, 179-185.

Vitousek, P.M., 1997. Human domination of earth's ecosystems. Science 277, 494-499.

Wäckers, F.L., 2004. Assessing the suitability of flowering herbs as parasitoid food sources: flower attractiveness and nectar accessibility. Biological Control 29, 307-314.

Wäckers, F.L., Van Rijn, P.C.J., Bruin, J., 2005. Plant-provided food for carnivorous insects: a protective mutualism and its applications. Cambridge University Press.

Walsh, M., Newman, P., Powles, S., 2013. Targeting weed seeds in-crop: A new weed control paradigm for global agriculture. Weed Technol 27, 431-436.

Weber, M.G., Porturas, L.D., Keeler, K.H., 2015. World list of plants with extrafloral nectaries, World list of plants with extrafloral nectaries.

Wignall, A.E., Heiling, A.M., Cheng, K., Herberstein, M.E., 2006. Flower symmetry preferences in honeybees and their crab spider predators. Ethology 112, 510-518.

Wilson, R.S., Hooker, N., Tucker, M., LeJeune, J., Doohan, D., 2009. Targeting the farmer decision making process: A pathway to increased adoption of integrated weed management. Crop Protection 28, 756-764.

Winkler, K., Wäckers, F.L., Buitriago, L., van Lenteren, J.C., 2005. Herbivores and their parasitoids show differences in abundance on eight different nectar producing plants. Wageningen University The Netherlands, pp. 125-130.

Yvoz, S., Cordeau, S., Zuccolo, C., Petit, S., 2020a. Crop type and within-field location as sources of intraspecific variations in the phenology and the production of floral and fruit resources by weeds. Agriculture, Ecosystems & Environment 302, 10.

Yvoz, S., Petit, S., Biju-Duval, L., Cordeau, S., 2020b. A framework to type crop management strategies within a production situation to improve the comprehension of weed communities. European Journal of Agronomy 115, 10.

Zhu, P., Zheng, X., Xie, G., Chen, G., Lu, Z., Gurr, G., 2020. Relevance of the ecological traits of parasitoid wasps and nectariferous plants for conservation biological control: a hybrid meta-analysis. Pest Manag Sci, ps.5719.