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Linking species traits to agroecosystem services: a functional analysis of weed communities

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Summary

There is a growing interest in the use of functional approaches for the study of weed assemblages, to disentangle underlying processes determining their composition and dynamics. Functional approaches are based on the assumption that weed community composition and dynamics can be best explained by a set of species traits expressing their response to agricultural disturbance. This knowledge should help develop more sustainable, ecologically based weed management systems. Trait-based data required for this kind of analysis are available from various sources, but most of them either cover mainly non-weedy species or, in the case of weed-focussed trait databases, they cover a limited number of species. In this work, we present a trait database for 240 weed species common throughout Europe, including not only response traits but also effect traits, that is linked to selected agroecosystem services and disservices. A case study is presented where our weed trait database is used in conjunction with appropriate statistical analysis to highlight the distribution of weed functional groups in soyabean crop communities from an experiment including different tillage and weed management systems. Finally, we discuss the strengths, weaknesses, opportunities and threats of this functional approach. By highlighting the links between weed species and agroecosystem (dis)services, this approach could be a useful resource for scientists, farm managers and policymakers.

Keywords: agroecology, biodiversity, database, disservice, RLQ analysis, tillage.

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Introduction

The assembly of weed communities in arable land depends on how the local species pool is filtered by environmental, biotic and management factors (Götzenberger *et al*., 2012; Borgy *et al*., 2016). In a continuously disturbed habitat like an arable field, weed species assemblage is highly dynamic, with a pace mainly dictated by the frequency and intensity of human disturbance (Fried *et al*., 2012; Gaba *et al*., 2014). From an ecological viewpoint, the probability of species occurrence depends on whether they have the right suite of attributes for 'response' traits which allow them to survive, reproduce and disperse in a given agroecosystem. This has been referred to as the trait-based approach to weed community assembly (Booth & Swanton, 2002; Garnier & Navas, 2012). In an arable ecosystem, the 'right' traits are probably

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those that either match with a temporally and spatially uniform disturbance regime, for example in the case of weeds developing resistance to herbicides (Neve *et al.*, 2014), or ensure adaptation to a wide range of disturbance regimes (Murphy & Lemerle, 2006).

In a cultivated field, it is not easy to single out the effect of individual management practices on weed community assembly. However, it is often recognised that practices like tillage and herbicides can act as strong filters (Bàrberi *et al.*, 1998). A few recent studies have addressed this issue by focusing on a trait-based approach (Ryan *et al.*, 2010; Colbach *et al.*, 2014). Prediction of which species would likely develop in a given management regime would be very important for on-farm weed control, especially in the context of Integrated or Ecological Weed Management (Bastiaans *et al.*, 2000).

The use of classical diversity indices (e.g. Shannon–Wiener) in weed science, despite being common (José-María *et al.*, 2013), does not help explain the role of diversity to reduce (or increase) the detrimental effects of weeds on crops. At the same level of abundance, a more diverse weed community could be more detrimental if mostly composed of highly competitive species for a given crop or cropping system. This issue can only be clarified by investigating whether the component species possess traits that could increase interference with the crop, that is exert a disservice.

Moreover, it is increasingly recognised that weeds can also support agroecosystem services related to production, for example by providing feed, shelter or reproduction sites to natural enemies of crop pests and/or pollinators, and by hosting mycorrhizae, thereby contributing to increased soil fertility (Kubota *et al.*, 2015). On top of this, some relatively recent works have pointed out the potential of arable weeds to provide other services, for example to support non-production-related biodiversity, like bird or arthropod populations (Storkey & Westbury, 2007; Rollin *et al.*, 2016). However, the potential of weeds to support production-related services has so far largely been neglected. Additional information and the application of fine-tuned approaches are needed to fully estimate the functional structure (*sensu* Garnier *et al.*, 2016) of weed communities. In this study, the potential of component species to support both production- and non-production-related agroecosystem services (Moonen & Bàrberi, 2008), as well as their potential to cause disservices, is examined.

This study presents a novel approach to the analysis of weed community functional diversity from an agroecological perspective. This approach relies on a database of weed functional (response and effect) traits that has been developed by taking into account the potential detrimental effects of weeds on crop yield, as well as their support to production- and non-production-related agroecosystem services. Weed abundance data are used to evaluate the functional traits possessed by each species present, and community composition is analysed by an appropriate statistical procedure. This study shows (i) the structure and content of this weed functional trait database, (ii) the statistical approach to the analysis of weed community functional diversity and (iii) an application of the methodology to a case study on the effect of tillage and herbicide use on soyabean weed communities. In the context of this work, we use the term ‘trait’ to identify a species feature that could be related to the expression of a given agroecosystem service or disservice, following the definition adopted by Garnier and Navas (2012).

Materials and methods

Weed functional traits database

A database of 240 species, that is those recorded in 13 field trials distributed across 10 European countries included in the TILMAN-ORG Project (Reduced tillage and green manures for sustainable organic cropping systems, http://www.tilman-org.net), was created (see *Supporting Information*). Volunteer crops (e.g. common and durum wheat, lucerne, maize) were also included. The database was populated with data on 16 qualitative, semi-quantitative or quantitative traits chosen as those best expressing the potential of individual weed species to provide the agroecosystem services and disservices deemed relevant for the context (Table 1). These were (i) production-related services (soil fertility, facilitation, pollination) and (ii) disservices (interference with crop). Some of the traits (number 9, 10, 11 and 13 in Table 1) can be related either to services or disservices. It should be pointed out that pollination could also be considered as a non-production-related service where not relevant for target crops. The 16 traits are related to key life cycle stages of species (e.g. germination, flowering, seedbank); to growth, reproduction characteristics and life cycle duration (e.g. growth habit, type of propagules); and/or to the potential to provide selected agroecosystem services. As such, they include both ‘response’ and ‘effect’ traits (*sensu* Garnier & Navas, 2012). Some of these traits, such as support of pollinators and affinity to soil nutrient conditions, do not fit strictly into the standard definitions of traits (Violle *et al.*, 2007). However, there are traits that in a strict sense underlie these services [e.g. specific leaf area (SLA) and flower morphology have a strong bearing on nitrophily and attractiveness to pollinators respectively]. This array of traits which

Table 1 The 16 functional traits included in the database to express the potential of weed species to provide selected agroecosystem services or to give disservices, trait levels or values included in the database, type of trait, trait explanation and source of information

Trait (code)	Trait level/value	Trait type	Trait explanation	Source
1. Raunkiær life form (RLF)*	**1.1** Therophyte (Th) **1.2** Hemicryptophyte (Hr) **1.3** Geophyte (G) **1.4** Chamaephyte (Ch)	Qualitative; response and effect trait; potential disservice	Type and position of propagules in the most adverse season indicate species potential to adapt to disturbance regime (response trait) and hence to interfere with crop (effect trait)	A, B, C, D
2. Growth form (GTF)*	**2.1** Rosette **2.2** Ascending or creeping **2.3** Graminoid	Qualitative; response and effect trait; potential disservice	Indicates species potential to capture environmental resources (light, space) in a disturbance regime (response trait) and hence to interfere with crop (effect trait)	A, E
3. Lifespan × regeneration form (LSR)*	**3.1** Annual **3.2** Biennial **3.3** Stationary perennial **3.4** Creeping perennial (aboveground shoots, stolons) **3.5** Creeping perennial (underground plagiotropic shoots, rhizomes) **3.6** Creeping perennial (plagiotropic thickened roots) **3.7** Creeping perennial (co-presence of 2 or more structures)	Qualitative; response and effect trait; potential disservice	Propagule type and regeneration frequency indicate species potential to adapt to type, timing and intensity of disturbance regime (response trait) and hence to interfere with crop (effect trait)	A, E
4. Grime's life strategy (GLS)	**4.1** Competitive (C) **4.2** Stress tolerant (S) **4.3** Ruderal (R) **4.4** Competitive–stress tolerant (CS) **4.5** Competitive–ruderal (CR) **4.6** Stress tolerant-ruderal (SR) **4.7** Intermediate (CSR)	Qualitative; response and effect trait; potential disservice	Reaction to stress, disturbance and competition indicate species potential to adapt to environmental and management conditions (response trait) and hence to interfere with crop (effect trait)	E, F, I, M
5. Soil seed bank longevity (SBL)	**5.1** Transient (<1 year) **5.2** Short-term (1–5 year) **5.3** Long-term (>5 year)	Semi-quantitative; response and effect trait; potential disservice	Indicates species potential to endure in an agroecosystem (response trait) and hence to interfere with crop in a long-term perspective (effect trait)	F, I, K
6. Specific leaf area (SLA)	Mean value	Quantitative; response and effect trait; potential disservice	Indicates species potential to use radiation efficiently and hence to compete for light	K

Table 1. (Continued)

Trait (code)	Trait level/value	Trait type	Trait explanation	Source
7. Plant height (PLH)	Mean of maximum reported values	Quantitative; response and effect trait; potential disservice	Indicates species reaction to environmental and management conditions (response trait) as well as competitive ability (effect trait)	G, H, K
8. Seed weight (SWT)	Mean value	Quantitative; response and effect trait; potential disservice	Seed mass is affected by environmental and management conditions (response trait) and indicates seedling potential to emerge from soil and to compete with crop in early growth stages (effect trait)	F, J
9. Seasonality of germination (SSG)	**9.1** Autumn **9.2** Spring **9.3** Summer **9.4** Winter **9.5** Non-seasonal	Qualitative; effect trait; potential services (any) or disservice	Indicates breadth of species adaptation and hence potential to provide agroecosystem services or interfere with crop	F
10. Beginning of flowering period (BFF)	Month	Qualitative; response and effect trait; potential services (pollination) or disservices	Indicates species potential to adapt to environmental and management conditions and to persist (response trait) as well as to attract pollinators† or to compete with crop (effect traits)	G
11. Duration of flowering period (DFF)	Months	Quantitative; response and effect trait; potential services (pollination) or disservices	Indicate species potential to adapt to environmental and management conditions and to persist (response trait) as well as to provide floral resources to pollinators† and to escape disturbance (effect traits)	G
12. Affinity to soil nutrient conditions (SNC)	**12.1** Oligotrophic soils with low amounts of nitrate, phosphorus and organic matter (value = 1, 2) **12.2** Nutrient-poor soils (value = 3, 4) **12.3** Soils with humus, well stocked with nutrients (value = 5, 6) **12.4** Soils with high concentration of nutrients (value = 7, 8) **12.5** Soils with excessive concentration of nitrogen and phosphorus (value = 9) **12.6** Wide range (value = 10)	Semi-quantitative; response and effect trait; potential disservices	Indicate species potential to adapt to nutrient-rich or nutrient-poor soil (response trait) and hence to compete with crop under a given set of conditions (effect trait)	B

Table 1. (Continued)

Trait (code)	Trait level/value	Trait type	Trait explanation	Source
13. Root system (PRT)	**13.1** Fibrous root **13.2** Taproot	Qualitative; effect trait; potential services (soil fertility, facilitation) or disservices	Indicates species potential to compete with crop for water and nutrients or to share soil resources†	G
14. Support of Arbuscular Mycorrhizal Fungi (SAM)	**14.1** Non-host **14.2** Mostly non-host **14.3** Presumably non-host **14.4** Host **14.5** Mostly host **14.6** Presumably host	Qualitative; effect trait; potential service (soil fertility, facilitation)	Mycotrophic species can capture part of soil resources through symbiosis; hence, they usually do not compete with crop and contribute to enhanced soil fertility†	L
15. N_2-fixing ability (NFA)	**15.1** Yes **15.2** No	Qualitative; effect trait; potential service (soil fertility)	Biological N fixation allows species to capture part of resources without competing with crop and contribute to enhanced soil fertility†	G
16. Support of pollinators (PSP)	**16.1** Yes **16.2** No	Qualitative; effect trait; potential service (pollination)	Indicates species potential to attract pollinators hence contributing to crop production (insect-pollinated crops) and enhanced agroecosystem biodiversity	E

Upon the goal of our functional database, response traits indicate how species respond to environmental and management drivers. Effect traits indicate the potential delivery of agroecosystem services, either related or unrelated to crop production, or disservices.

*Traits number 1, 2 and 3 provide complementary information.

†Production-related service; for traits 10 and 11 in case of insect-pollinated crop. Depending on the scope of the study, all traits or part of them can be included in the analysis. Codes for sources of information: A: Pignatti (1982); B: Pignatti *et al.* (2005); C: Bolòs *et al.* (2005); D: Raunkiær (1934); E: Klotz *et al.* (2002); F: Fitter and Peat (1994); G: Font (2016); H: Missouri Botanical Garden (2016); I: Grime *et al.* (2007); J: Kew Royal Botanical Gardens (2016); K: Kleyer *et al.* (2008); L: Prof. M. Giovannetti (University of Pisa, Italy), pers. comm.; M: Hodgson (2016).

does not fit the classical definition makes sense, if we aim at developing approaches for translating fundamental functional ecology into the arena of weed management. Trait values were retrieved from published literature (refereed articles and books), online sources (e.g. databases) and expert knowledge (mycotrophy; Prof. M. Giovannetti, University of Pisa, Italy). Regarding the traits 'beginning of flowering' and 'duration of the flowering period', for those species that can live across a wide range of European environments, it was decided to assign one value for Mediterranean climates and one for northern climates. Traits 12 and 16 (affinity to soil nutrients and support of pollinators), although not strictly adhering to the standard trait definition, were included because they can serve as proxies for functional traits related to stress tolerance (Gunton, 2011) and floral morphology, for which functional data are not available or are difficult to retrieve. For some species, it was not possible to retrieve full information for all the traits; in the case of mycotrophy, gaps were filled using the trait value of taxonomically and/or functionally closest species.

Case study

To show the potential use of our weed trait database, we give one example of functional analysis of data on weed communities from an agronomic experiment setup at the Centro Interdipartimentale di Ricerche Agro-Ambientali E. Avanzi (CIRAA) of the University of Pisa (lat. 43°40′N, long. 10°23′E) in 1993. The experiment aimed to test the effect of different tillage and weed management systems on weed community dynamics in a 2-year rotation between durum wheat (*Triticum durum* Desf.) and soyabean (*Glycine max* (L.) Merr). It included four combinations of two tillage systems (mouldboard ploughing at ca. 35–40 cm depth *vs* no tillage with pre-sowing glyphosate application) and two weed management systems (standard post-emergence herbicide application *vs* no herbicides; hoeing was applied in soyabean in the ploughed system only), giving a total of eight crop × management combinations.

Each crop × management combination was divided in three sampling areas, where nine 25 × 30 cm frames were placed (total = 27 frames). All weeds inside the frame were identified, harvested and oven-dried at 105°C until constant weight for estimation of biomass by species. Here, we use weed biomass data sampled pre-harvest of soyabean in 1993.

Data analysis

Several multivariate techniques can be combined to relate species traits to environmental characteristics (Kleyer *et al.*, 2012), their choice depending on the aim of the analysis. We have used the RLQ analysis, a technique for addressing the 'fourth-corner' problem (Dray & Legendre, 2008), that is to analyse links among three tables: the R table, which contains the environmental (or management) variables per site (in our case: ploughing *vs* no tillage, herbicide *vs* no herbicide); the L table, which contains species abundances in each site (biomass data by species in our case); and the Q table, containing the selected species trait data. This analysis follows a comparative approach, that is it is not based on measures of functional diversity *per se* (Schleuter *et al.*, 2010), as the aim of the case study was to explore the distribution of traits across different agronomic treatments, that is the functional structure of the weed community *sensu* Garnier *et al.* (2016). Where the researcher is interested in direct measures of functional diversity, for example adopting the analytical framework proposed by Díaz *et al.* (2007), several indices, such as functional richness, evenness and divergence, can be used.

Traits to be included in the RLQ analysis should be chosen according to the aim of the study: in this case study, 10 of 16 traits were included in the functional weed community analysis, namely Raunkiær life form (trait #1 in Table 1), Grime's life strategy (#4), soil seedbank longevity (#5), SLA (#6), plant height (#7), seed weight (#8), affinity to soil nutrient conditions [Ellenberg's nitrophily indicator values, #12; treated as a continuous variable (Hill & Carey, 1997)], root system (#13), support of arbuscular mycorrhizal fungi (AMF) (#14; levels were re-coded into either 'host' or 'non-host') and support of pollinators (#16). These traits were chosen to represent both the potential disservices caused by weeds (traits known to be strongly related to weed competitive ability with crops or to previous field management) and the potential agroecosystem services provided by weeds (e.g. the ability of supporting AMF or insect pollinators). Traits are expected to reflect the response of weed species to both resource availability (e.g. Ellenberg's values indicate plant species preference for soil according to N content) and disturbance levels (e.g. Grime's CSR system classifies species upon the mechanisms by which they can respond to disturbances) (Gaba *et al.*, 2014).

The three data tables were first analysed via ordination methods [correspondence analysis for the L table, Hill-Smith ordination (Hill & Smith, 1976) for the Q and R tables], and results were then used to perform the RLQ analysis. This co-inertia analysis searches for the combination of traits and environmental variables that maximises their covariance, mediated by species abundance. The association between traits and environmental variables was then tested via the fourth-corner statistic (Dray & Legendre, 2008).

Functional groups were identified by means of hierarchical cluster analysis, applying Ward's method on the Euclidean distances of species scores in the RLQ ordination space; the use of functional groups instead of the original species allows an easier interpretation of the underlying environmental dynamics. Subsequently, the distribution of trait values within each functional group was explored to single out the underlying filtering mechanisms that selected these specific groups and to relate them to the environmental variables. All the analyses were performed with the R software (R Development Core, 2011); the ade4 package (Dray & Dufour, 2007) was used to perform the RLQ analysis.

Results

In our case study, 23 weed species were found. Their Latin names and EPPO codes (http://eppt.eppo.org, accessed 22 April 2016) are reported in Table 2. The co-inertia associated with the first and second axes of the RLQ ordination was 89.1% and 10.9% of the total variation respectively. The biplot in Fig. 1A shows both the environmental (management) and the trait variables. The first ordination axis discriminated clearly between tillage systems and was positively correlated with tall competitive–ruderal (CR) species, while it was negatively correlated with competitive (C) or competitive–stress tolerant (CS and CSR) species, species with fibrous root system and those with high SLA values. The second ordination axis discriminated between weed control systems; it was positively correlated with ruderal (R) species, species supporting pollinators, and negatively correlated with geophytes, species with short-lived seedbank and high values of nitrophily, and species supporting AMF.

According to the fourth-corner statistics (Table 3), tillage system was the most relevant management factor and it was significantly associated with Grime's CSR strategy, plant height, seed weight and root system, whereas the effect of weed management system was not significant for any of the traits. Four functional groups were identified as a result of the cluster analysis (see *Supplementary material*). The distribution of values for each of the 10 traits within each group is reported in Fig. 2. These results indicated that functional group C mainly included competitive species with low SLA and high nitrophily. Group A was characterised by species with fibrous root system, high SLA and low nitrophily, showing a rather uniform distribution across Grime's CSR strategies. Group D was composed of large-seeded CR species with high nitrophily, while group B was composed of creeping or short plants with high SLA and a uniform distribution across Grime's CSR strategies, seedbank types and root systems. When comparing the identified functional groups with the biplot showing the environmental (management) and trait data (Fig. 1A and 1B), some trends can be clearly outlined: groups A, C and D were typical of tilled plots; group A is correlated with lack of herbicide treatment, while group D includes species that have been selected by herbicide treatments.

Table 2 Scientific names and relative EPPO codes of the 23 weed species recorded in the community of the case study

Species name	EPPO code
Amaranthus retroflexus L.	AMARE
Ammi majus L.	AMIMA
Avena fatua L.	AVEFA
Beta vulgaris L.	BEAVV
Calystegia sepium (L.) R. Br.	CAGSE
Chenopodium album L.	CHEAL
Convolvulus arvensis L.	CONAR
Cynodon dactylon (L.) Pers.	CYNDA
Digitaria sanguinalis (L.) Scop.	DIGSA
Echinochloa crus-galli (L.) P. Beauv.	ECHCG
Equisetum arvense L.	EQUAR
Kickxia spuria (L.) Dumort.	KICSP
Lolium multiflorum Lam.	LOLMU
Picris echioides L.	PICEC
Plantago lanceolata L.	PLALA
Polygonum aviculare L.	POLAV
Polygonum lapathifolium L.	POLLA
Setaria viridis (L.) P. Beauv.	SETVI
Solanum nigrum L.	SOLNI
Sorghum halepense (L.) Pers.	SORHA
Triticum aestivum L.	TRZAX
Verbena officinalis L.	VEBOF
Xanthium strumarium L.	XANST

Discussion

Case study

According to the functional analysis of the case study, tillage system came out as the most ecologically relevant management factor filtering weed species composition in the community. Functional group B, the one more strongly correlated with no-till, evenly included species belonging to all Grime's CSR strategies, meaning that in the absence of relevant soil disturbance, there are opportunities for species possessing different growth strategies. Under no-till conditions, a uniform distribution pattern was shown across all levels of seedbank longevity. In contrast, ploughing was positively correlated with plant height, as already found by Armengot *et al.* (2016) [but see Fried *et al.* (2012)]; this

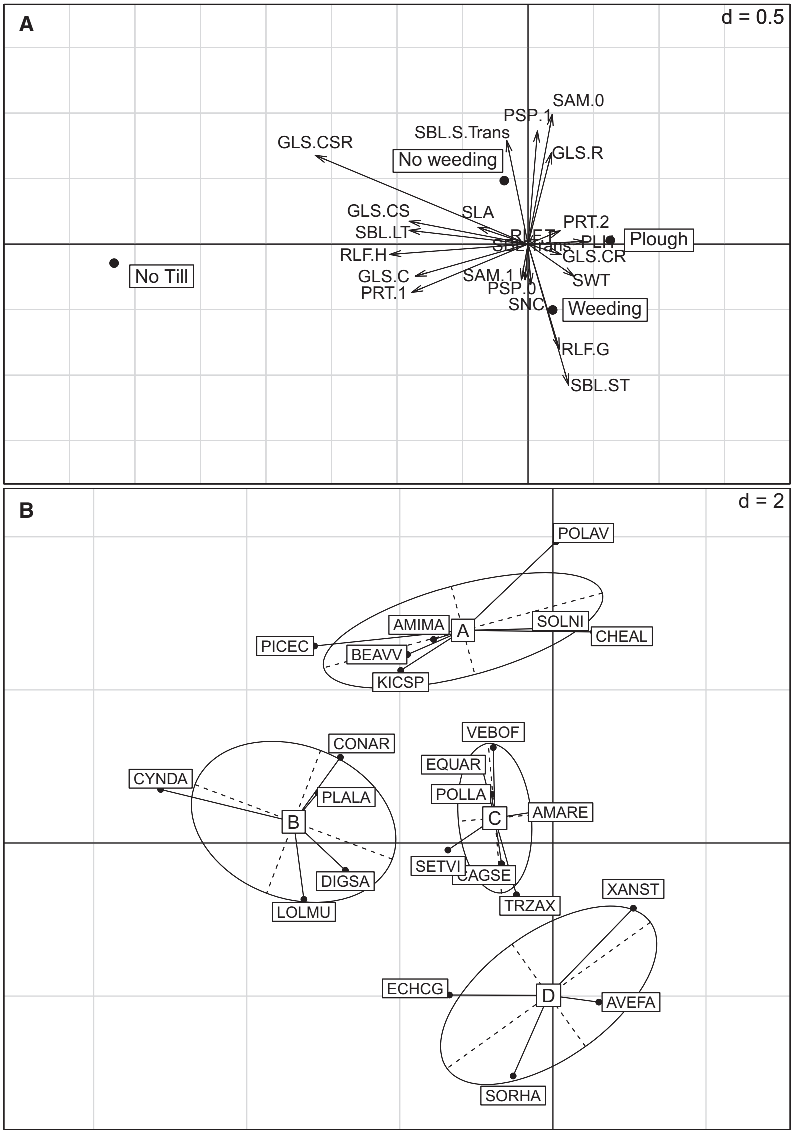

Fig. 1 Above (A): biplot representing trait (arrows) and environmental (boxes) data. For categorical traits, all levels are reported, using the form 'Trait code.trait value', for example LF.G stands for *Life Form Geophyte*; for explanation of codes, refer to Table 1. Below (B): ordination plot of the weed species grouped according to the functional groups detected by means of hierarchical cluster analysis. EPPO codes are used to identify species (see Table 2). The grid indicates the scale of the plot, whose size is given by the *d* value.

Table 3 Adjusted *P*-values (using Holm correction method) of the fourth-corner statistics for traits and management data: association between two categorical variables was tested via the Pearson chi-square statistics (χ^2); association between a categorical variable and a continuous one was tested through a pseudo-F (ns: non-significant, $**P < 0.01$, $*P < 0.05$)

	RLF	GLS	SWT	PLH	SLA	SAM	SNC	PRT	PSP	SBL
Tillage	ns	χ^2:0.04*	*F*:0.02*	*F*:0.01**	ns	ns	ns	χ^2:0.01**	ns	ns
Weed management	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

RLF, Raunkiær's life form; GLS, Grime's life strategy; SWT, seed weight; PLH, plant height; SLA, specific leaf area; SAM, support of arbuscular mycorrhizal fungi; SNC, affinity to soil nutrient conditions; PRT, root system; PSP, support of pollinators; SBL, soil seedbank longevity.

is likely to be an indirect effect of tillage on weeds. Tillage is known to mobilise soil resources for the crop promoting its development; this in turn may act as a filtering effect on the weed community, that is only taller species which are better able to compete with well-developed crops would be selected. This hypothesis is in line with findings from other authors who have highlighted the role of plant height as a proxy for competition for light (Violle *et al.*, 2009) and for other traits generally correlated with higher competitive ability (Gaba *et al.*, 2014). An alternative hypothesis could be that the tillage management filter has acted directly on seed weight and only indirectly on plant height (the two traits were significantly correlated in our study).

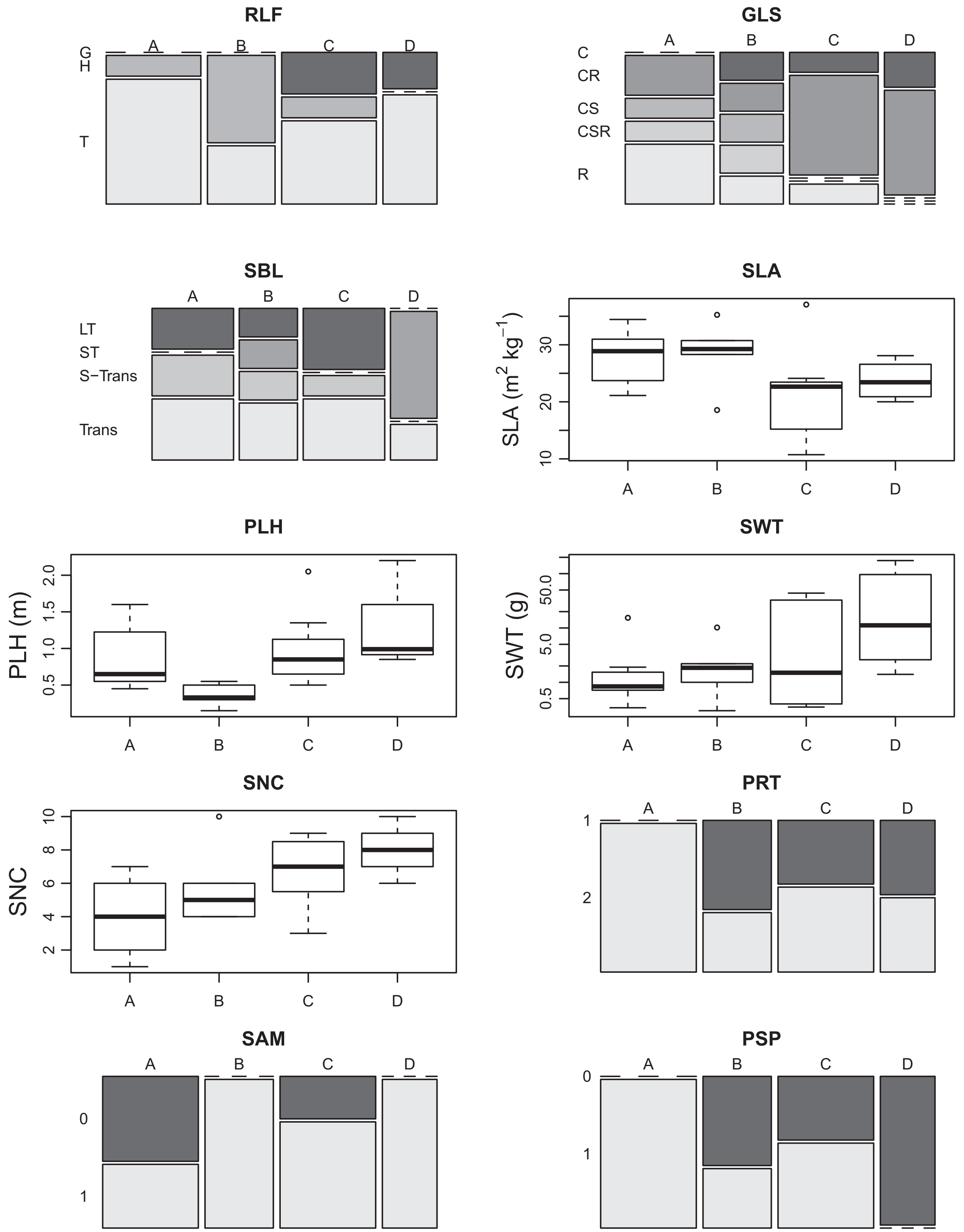

Fig. 2 Distribution of the trait values within the four functional groups selected. Boxplots are used for continuous traits while mosaic plots are used for categorical traits; in the case of SWT, the *y*-axis is on a logarithmic scale. In each mosaic plot, the same colour is used for tiles referring to the same level of a trait.

Ploughing was also positively correlated with tap-rooted species (especially the highly abundant *Xanthium strumarium*) and CR species. The four characteristic species in group D [*Avena fatua* L., *Echinochloa crus-galli* (L.) P. Beauv., *Sorghum halepense* (L.) Pers. and *Xanthium strumarium* L.] are well-known agricultural weeds, especially of spring–summer crops. In terms of provision of agroecosystem services, it is interesting to note that none of the species in this group can support insect pollinators, while the opposite is true for group A, the one related to lack of herbicide use, where all species are able to support pollinators.

Weed functional traits database: a SWOT analysis

Besides the above-described case study, our weed functional trait database was fine-tuned and tested on data collected in 13 different trials within the TILMAN-ORG project, including five long-term (>7 years), four mid-term (3–7 years) and four short-term trials (<3 years). These trials had reduced tillage and/or green manure as main factors and were run in 10 European countries: Austria, Estonia, France, Germany, Italy, Luxemburg, Spain, Switzerland, the Netherlands and the United Kingdom (Sans *et al.*, 2014). It is possible to draw some preliminary conclusions on the pros and cons of this approach, hereafter presented in the form of a SWOT analysis (strengths, weaknesses, opportunities and threats).

The main strength of our approach is the scope of our weed functional traits database. Although the importance of evaluating at the same time the services and disservices associated with weed communities is gaining pace (Mézière *et al.*, 2015), it is not common to see weed trait databases that explicitly address traits related to both issues. Inevitably, this results in a somewhat ‘hybrid’ database, where ‘response’ and ‘effect’ traits (Garnier & Navas, 2012) are intermingled. However, we think that this is more in line with an agroecological approach to the analysis of arable weed communities and of their relationship with agroecosystem (dis)services. A further strength of our database is its Europe-wide coverage in terms of species, which should make it useful or easily adaptable to a variety of arable cropping systems across the continent, as in the case of the supporting trials. Previously developed weed traitbases (Storkey *et al.*, 2015) are more comprehensive in terms of data completeness, but address a lower number of species. On the other hand, other extensive plant trait databases (e.g. BiolFlor) cover a large set of plant species, most of which are not weeds; hence, the use of such data in agronomic studies require extra effort in terms of data filtering, cleaning and re-grouping.

The main weakness of the present version of our database is its incompleteness, as for some species/trait combinations no information could be retrieved. The main gaps were for seasonality of germination (98 gaps, ca. 41% of total species), support of AMF and pollinators (22%), soil seedbank longevity (21%) and SLA (10%). Missing data for Grime’s CSR strategy, plant height, seed weight, beginning of flowering, duration of flowering period and affinity to soil nutrient conditions vary between 2% and 7%. Lifespan × regeneration form has only one missing value, while full information is available for the remaining five traits. Weeds are known to host pests, pathogens, viruses and nematodes (disservice; Meinecke *et al.*, 2014) but also natural enemies (service; Norris & Kogan, 2000); this is a relevant issue, but the available information is so scant and interactions among taxa are so complex and crop and context specific that including these data in a one-table database was not feasible.

The main opportunity for our functional weed trait database is that it addresses an emerging area of weed and agroecological research with interesting possibilities for on-farm practical application. It may, for example, be useful for evaluating the pros (e.g. weed species providing food to pollinators and natural enemies; Bommarco *et al.*, 2013) and cons of keeping a certain amount of weeds in arable fields depending on the traits of component species and hence possibly help national and regional policies (e.g. agri-environmental schemes) addressing multifunctional agriculture. Our weed functional trait database is versatile, in the sense that it can easily accommodate (i) new information, once available and (ii) new traits, should other agroecosystem services or disservices become relevant for future farming and policymaking. Agricultural practices can influence the ability of plant communities to provide ecosystem services only when there is an overlap between plant ‘response traits’ (those associated with environmental factors) and the ‘effect traits’ (those linked to the service). In this respect, our trait database can be useful to test associations among traits, environmental filters and agroecosystem services (Lavorel & Garnier, 2002).

Data provided by our database can be analysed with a variety of statistical tools: we have proposed the RLQ approach, but an alternative approach based on the use of community-level weighted mean of trait values was used in a recent paper on data from a subset of the trials that were used to populate our database (Armengot *et al.*, 2016). By making this database available to the scientific community, we aim at promoting a functional perspective in weed science. In our opinion, one of the main aims for researchers in the near future should be the development of analytical approaches able to disentangle the responses of weed communities to weed management practices and foresee their influence on other trophic levels in agroecosystems. The main limitation of this perspective is not exclusive to our approach but more general in scope. There is still a gap in our understanding and a general lack of research on the links between management, traits and ecosystem services. To date, this gap impedes the exploitation of the combination of various plant functional traits for the design of sustainable management strategies in multifunctional agroecosystems (Faucon *et al.*, 2017).

One potential threat of our approach is the hazard of misinterpreting the outcome of the functional weed community analysis, that is to under- or overestimate its consequences for the provision of agroecosystem services or the risk of disservices. This fact may stem from different causes. On the one hand, there is inherent variability in some traits, such as leaf N and C content, SLA, leaf dry matter content or reproductive plant height, due to intraspecific genetic variation or phenotypic plasticity (Jung *et al.*, 2010; Kazakou *et al.*, 2014). On the other hand, any trait-based analysis highlights the *potential* of a weed community to provide selected agroecosystem (dis)services, that is it cannot predict whether this potential could turn into *actual* provision/risk. Questions like 'how many plants per metre square of a given species are needed to observe a tangible effect in terms of AMF support' cannot be answered to date. Another potential threat could be the subjectivity associated with 'dual' traits, that is those that can be linked to either services or disservices. On the one hand, this subjectivity may lead to under- or overestimation of species importance for the provision/risk of these (dis)services depending on the analyst's perspective. On the other hand, dual traits increase the flexibility of the database, making it able to accommodate different priorities.

In conclusion, we hope that tools like the one proposed in this study could pave the road to a better understanding of the functional value of weed communities and of the role that weeds can play in the provision of agroecosystem services. Nevertheless, to fully exploit the potential of weed functional trait databases, further basic knowledge on functional trait values for several weed species is needed. Trait-based agronomic and agroecological research is likely to expand in the near future; thus, we can reasonably expect that new knowledge on the functional role of weeds and weed communities could soon be generated.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1 Dendrogram representing the result of hierarchical cluster analysis of the weed species in the RLQ ordination space. Rectangles indicate the four functional groups (A, B, C, D) selected from the dendrogram.

Appendix S1 Our weed trait database is an Excel file with 240 weed species and 16 traits.