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The effect of agronomic filters on arable plant communities: What weeds are we selecting for?

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ABSTRACT

Functional diversity in arable plant communities affects their detriment, as different arable plants occupy different niche spaces which dictate their competitiveness to the crop. This functional diversity can be examined using Grime's CSR triangle; most common arable plants are thought to occupy a region of this triangle indicating low levels of stress tolerance, and preference for disturbance and abundant nutrition. Prior research has, however, only examined this with regard to specific management practices or cropping systems, rather than the ecological conditions they generate, the 'agronomic filters' applied. Using a dataset of all arable plant species in Sweden, we used multivariate statistics to determine the functional characteristics of problematic weeds, and how they differed from other plant species present in these communities. This was examined with regard to Grime's life strategy, perceived detriment, conservation status, and preference for agronomic filters relating to nutrition, disturbance, moisture, and light. Our results show that intense agronomic management constrains the niche and limits the function of the non-crop community, with stress-tolerators (S) being absent and, as theorised, competitive and pure ruderals (CR and R respectively) overrepresented. CR strategists favoured nutrition, light and disturbance, and were often considered problematic according to agronomic experts. R strategists generally showed less preference for nutrition, and were more often considered rare and non-weedy, probably due to their lesser competitiveness. These findings can be applied by modifying the agronomic filters favoured by problematic weeds. Specifically, more effective nutrient management would break the 'agronomic trap' of fertilisation benefitting dominant, competitive weeds. Increased grazing or mowing is also suggested to limit plant height in favour of less competitive species, and increased cropping diversity will also alter selection for agronomic filters depending on crop niche. Using these agronomic filters, we provide a theoretical guide to achieving ecological weed management in practice.

1. Introduction

Arable plants can cause significant crop yield losses when allowed to thrive without appropriate agronomic management (Milberg and Hallgren, 2004). Under such circumstances, where potential negative impacts of a species on agroecosystem function outweigh its benefits, we refer to these arable plants as weeds. Designation as a weed is therefore highly dependent on abundance and spatial overlap with the crop, its species-specific functional traits in relation to those of the crop (niche overlap), the pedoclimatic context, and agronomic practice.

Synthetic herbicides have become ubiquitous as an apparently easy solution to weed problems, but they indiscriminately remove arable plants from fields, including those with a negligible or positive impact on crop production. This has historically lead science to overlook distinctions between arable plants in their impact on crops, and neglect the ecological context of how and why certain plants become problematic weeds (MacLaren et al., 2020). However, with the proliferation of herbicide resistance and deepening regulation of synthetic agrochemicals now casting serious doubt on the future availability and reliability of herbicides, this neglect of weed ecology is limiting our capacity to pose

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effective alternatives (Bagavathiannan et al., 2019). As such, interest in understanding the ecological dynamics underpinning weed detriment has been growing in recent times (Neve et al., 2009).

There is increasing evidence of the importance of weed community composition in determining impact on the crop (Adeux et al., 2019), and multiple studies suggest that landscape simplification, and intensive use of chemical weed control and synthetic fertilisers select for more simplistic, problematic weed communities (Moss et al., 2004; Storkey et al., 2021; Berquer et al., 2023). These factors are also associated with arable plant diversity decline, as less adapted and less competitive species are forced into extinction (Fried et al., 2009; Pinke and Gunton, 2014). These so-called 'rare weeds', amongst the less problematic species distinguished as '*aliae plantae*' by Merfield (2022), can benefit agroecosystem function (Storkey and Westbury, 2007; Twerski et al., 2021). Diversity of arable plants at low abundances occupy and support a wide range of ecological niches and beneficial species like pollinators (e.g. Storkey et al., 2013; Gaba et al., 2020; Balfour and Ratnieks, 2022), and can therefore negate yield losses from plant interference (Cierjacks et al., 2016; Storkey and Neve, 2018; MacLaren et al., 2020).

The most persistent weeds are theoretically the species most specialised to the arable environment, the 'best weeds' (alternatively the 'worst weeds' for farmers), adapted to thrive in these systems and tolerate attempts at management (Storkey and Neve, 2018). Given the specificity of a conventional agroecosystem to its crop, little niche space exists for other plant species. The adaptation of a dominant weed therefore represents increased niche overlap, competition, detriment, and yield loss (Hofmeijer et al., 2021). From an ecological perspective, dominant weeds are thus 'functional outliers' (Violle et al., 2017), adhering to a narrow set of functional traits required for survival in an agroecosystem (Bàrberi et al., 2018; Bourgeois et al., 2019; Metcalfe et al., 2019; Mahaut et al., 2020). Interspecific variation between traits in arable plant communities remains, however, which could be used to inform targeted management in favour of less detrimental species (e.g. Fried et al., 2012).

A useful framework to explore trait variation is Grime's CSR triangle, which classifies species as competitive (C), stress-tolerant (S), or ruderal (R), to varying degrees (Grime, 1977). Each strategy is the combined effect of multiple traits that combine to give certain qualities, like rapid resource acquisition and growth (C), defence and resource conservation (S), or abundant and mobile propagules (R), among others.

It is expected that an arable weed is primarily ruderal, enabling rapid population growth and exploitation of disturbed environments like intensively-managed agricultural fields (Gunton et al., 2011). Some species are also competitive (C) (Kuester et al., 2014), having adapted to exist alongside the crop by outcompeting it. Many are also highly responsive to nutrient inputs, a key competitive trait (Jäck et al., 2021). MacLaren et al. (2020) therefore hypothesised that most dominant arable weeds straddle the R-C portion of Grime's triangle (Fig. 1), in keeping with results reported by Bàrberi et al. (2018). Complementing this perspective, Bourgeois et al. (2019) used nine traits to conclude that an arable weed was typically 'an early and long-flowering therophyte (a species quick-growing in favourable conditions but capable of surviving harsh conditions as a seed), with a high affinity for nutrient-rich and sunny environments', supporting a CR classification.

While there is evidence that agricultural management can alter the functional space occupied by the weed community present, this has, to date, only been explicitly connected to specific farming practices (Bàrberi et al., 2018), or cropping systems (Fried et al., 2022). Here we take a step further to see if CSR classifications can generalise the link between ecological conditions generated by farming practices and cropping systems. We furthermore examine the different plant species present, in terms of how detrimental they are perceived to be and/or whether they are in need of conservation. We do this firstly by exploring links between life history strategy and ecological indicators across the entire pool of arable species in Sweden, predominantly informed by the preceding work of Tyler et al. (2021). Ecological indicators measure affinity for certain ecological conditions, such as nutrient or light availability, or disturbance. Farm management practices and cropping systems create specific ecological conditions, 'agronomic filters' to select for weed species with affinity for them. The link between ecological indicators and life history strategy can therefore indicate which weeds will occur under different farm management practices, based on the ecological conditions that those management practices create. Secondly, we investigate links between life strategies and expert perceptions of different weed species, an area which has received little attention so far. It has previously been posed that more problematic

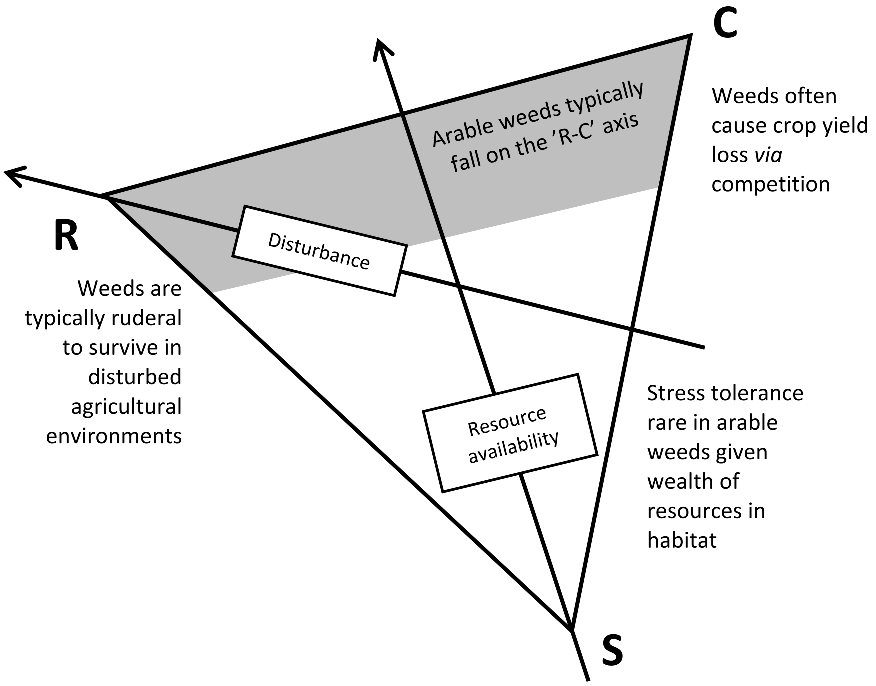

Fig. 1. The typical positioning of agricultural weeds within the CSR matrix, adapted from MacLaren et al. (2020).

weeds will tend toward C rather than R (MacLaren et al., 2020), but it has not yet been assessed whether experts and practitioners in weed management share this view. The ecological theory that certain weeds will be more problematic due to characteristics such as rapid resource acquisition and growth may not equate to the characteristics that actually cause problems in farmers' fields, given the complex interactions between weeds, cropping systems and farm management.

Considering these issues, the objective of this study was to identify differences in preference for agronomic filters, life history strategy, and socio-economic perception, across arable flora in Sweden. This is intended to inform management strategies which specifically select against problematic, dominant weeds, and which favour more benign or beneficial species. We therefore tested the hypotheses that arable flora occurring across all cropping systems in Sweden would (1) generally tend towards R species (as has been shown in many other contexts for weeds previously), but (2) the subset of weeds considered problematic by weed management experts would more typically be CR or C strategists. It is expected that these species will show a high affinity for nutrient-rich conditions, given that these life strategies are based on rapid resource acquisition, and therefore we also hypothesise that (3) C and CR weed species will be less likely than R, SR and S species to have become rare or threatened, given that high nutrient levels are more typical of modern, intensive farming systems than historical ones. In short, we test whether common, problematic species and rare, non-weedy species across Sweden can be distinguished by their life strategy, and whether imposing different agronomic filters *via* farm management could select for weeds with more desirable life strategies.

2. Materials & methods

We initially assessed plant life strategies using CSR classifications available on the TRY plant trait database (Kattge et al., 2020). However, it was unclear whether classifications assigned in other countries would apply at high latitudes (e.g. Novakovskiy et al., 2021), so we also used a recently published database of ecological indicator values of vascular plants in Sweden (Tyler et al., 2021). These values describe a plant species' response to certain conditions, effectively making them agronomic filters in an arable setting, from which their overall life history strategies can be inferred (Bengtsson, 1998; McGill et al., 2006). We assessed whether species would be considered problematic weeds or not through expert opinion, and used species' conservation status and affinity for arable land as indicators of prevalence in Swedish farmland (also Tyler et al., 2021). Taken together, the relationship between life strategy, agronomic filters, and 'weediness', can inform management strategies to reduce agricultural weed detriment by supporting a more benign floral community.

2.1. Data selection and curation

The data used in this study can be grouped into (1) ecological indicator values, (2) life strategy (Grime's CSR), and (3) other socio-ecological categories (weediness, conservation status, and arable affinity), that describe how arable plants relate to human values and agricultural landscapes.

Data for Swedish plant species and their ecological indicator values were acquired from Tyler et al. (2021). We extracted seven sets of ecological indicator values (Table 1), chosen based on their importance for thriving in agroecosystems, and competing with other species. These values exist on different scales for the dataset derived, as described in Table 2. Species with no recorded occurrence on arable land were excluded, leaving 146 species for further analysis. European and Mediterranean Plant Protection Organization (EPPO) codes were used for all species to facilitate legible labelling in figures.

In addition to ecological indicator values, we also used the classifications of Tyler et al. (2021) for conservation status and occurrence on arable land. Conservation status (identifying threatened species), was originally drawn from the Swedish red-list (SLU Artdatabanken, 2020), using International Union for Conservation of Nature (IUCN) status categories. As multiple IUCN categories contained a small number of selected species, we simplified this categorisation into 'red-listed' or 'not red-listed'. The score for occurrence on arable land in Tyler et al. (2021) consists of a value between 0 and 10 indicating the proportion of the species total Swedish population found on arable land (on a 10 % scale). In our study we simplified this to 'low' (values 1–3), 'medium' (values 4–6), and 'high' (values 7–10), again reducing the number of categories containing a low number of species to facilitate the examination of trends. Importantly, this does not provide judgement on how abundant a species is in Sweden, rather what proportion of its population occurs on arable land. As examples, the highly abundant arable weeds *Stellaria media* (STEME) and *Chenopodium album* (CHEAL) are scored as 2 and 3

Table 1
Ecological indicator values presented in Tyler et al. (2021) and used in this study. Full methods for assigning a value to each species are described in the source publication; the 'minimum' and 'maximum' columns indicate the range of values found within the arable plant subset. The values provided are scores assigned by the authors to indicate degree of preference.

Ecological indicator	Description (from Tyler et al. 2021)— degrees of scale provided in parentheses	Minimum	Maximum
Light	Optimal light/shade conditions (7)	**4** (half-shade)	**7** (always full sun)
Moisture	Realised moisture/water niche (12)	**2** (dry)	**9** (wet-temporarily inundated)
pH	Mean realised soil (water) pH niche (8)	**3** (moderately acidic; pH 4.5–5.5)	**8** (alkaline; pH > 7.5)
Nitrogen	Mean realised soil (water) nitrogen availability niche (9)	**2** (moderately–very N-poor)	**8** (confined to the naturally most N-rich soils)
Phosphorus	Mean realised soil phosphorus availability niche (5)	**1** (avoiding soils with high P availability)	**5** (confined to soils with high P availability)
Grazing/ mowing	Species response to grazing and mowing (8)	**1** (does not endure any grazing/mowing)	**6** (strongly favoured by regular grazing/ mowing, but endures some years without management)
Soil disturbance	Relationship between soil disturbance and species occurrence and survival (9)	**2** (colonizes already established vegetation, successfully competes for some time, but in the long run outcompeted if there is no soil disturbance)	**9** (not competitive in closed vegetation, requires yearly soil disturbance)

Table 2
Descriptions of Trait and Socio-ecological indicator values used for this study: References are provided from which further details can be found.

Trait/ Socio-ecological indicator values	Description	Reference
Arable affinity	Divided into 'low' (10–30 % of Swedish population found on arable land), 'medium' (40–60 %), and 'high' (70–100 %)	Derived from Tyler et al. (2021)
Conservation status	Divided into 'red-listed' (IUCN classifications 'Near-Threatened', 'Vulnerable', 'Endangered', or 'Critically Endangered'), and 'Not red-listed' (IUCN classification 'Least Concern').	Derived from Tyler et al. (2021), and SLU Artdatabanken (2020).
Grime's life strategy	'C'- 'Competitive', 'S'- 'Stress-tolerant', and 'R'- 'Ruderal', including combinations of these three classifications.	From the TRY database (Kattge et al., 2020).
Perceived weediness	'Weedy' (majority of respondents described as categories 4 or 5), or 'Non-weedy' (majority of respondents described as categories 1–3).	Original data (see Section 2.2)

respectively (both 'low affinity'), because they occur in large numbers in other environments, notably on waste ground (classified as 'Ruderal' land by Tyler et al. 2021). We term this variable "arable affinity" throughout the remainder of the paper.

These data were supplemented using information from the TRY plant trait database (Kattge et al., 2020), specifically codes for Grime's life strategy (Grime, 1977). Lastly, we also categorised arable plants as "weedy" or "non-weedy" using an online expert questionnaire described in Section 2.2. These metrics are summarised in Table 2.

2.2. *Determining weediness by questionnaire*

An online questionnaire was developed to collect opinions concerning weediness of the species contained within the dataset described in Section 2.1; this allowed the incorporation of a socio-economic perspective on weediness rather than any attempts to determine this trait based on the physiology of the plant (or any relation to the ecological indicator values previously described). The questionnaire consisted of questions to collect basic, potentially-explanatory demographic data followed by a randomised list of the 146 arable plant species, including links to their information pages at SLU Artdatabanken (https://artfakta.se/artinformation). Five possible responses were provided for each species, the precise meanings of which were open to the interpretation of the respondents:

1. Not known
2. Never seen in an arable field
3. Not considered a weed
4. Weedy in large population densities
5. Weedy even at low population densities

Questionnaires were shared with advisors, researchers, botanists, and public authority employees in Sweden, to determine their consensus on each species. A total of 23 responses were received, which were entirely anonymised by the questionnaire system.

For further analyses, questionnaire scores 4–5 were used to indicate a problematic weed, while categories 1–3 did not, with each species allocated according to the majority of responses.

2.3. *Exploring trait space in swedish arable plants*

Principal component analyses (PCAs) were conducted on the arable flora of Sweden and ecological indicator values described in Table 1 (from Tyler et al., 2021), using package *stats* in R version 4.3.0. (R Core Team, 2023). Missing values meant that 15 species were excluded from these analyses, leaving a total of 131 species.

We then explored trends within the arable flora by overlaying 'dependent' variables as grouping factors on the PCA. Specifically, we explored (1) the arable affinity of each species (low/ intermediate/ high, as described in Section 2.1.), (2) Grime's life strategy (obtained from the TRY database (Kattge et al., 2020)), (3) conservation status (red-listed or not, again described in Section 2.1.), and (4) weediness according to our own questionnaire (Section 2.2.). Permutational ANOVA (PERMANOVA) tests were used to identify significant differences between the mean locations of each level of each factor in the distance matrix underpinning the PCA, using function *adonis2* in package *vegan* (Oksanen et al., 2022. vegan: Community Ecology Package.). Differences between factor levels were visualised by overlaying means and 95 % confidence ellipses (based on a multivariate *t*-distribution) onto PCA biplots. The many possible Grime's life strategies (a total of seven; the three individual classifications and their various combinations) meant that placement of confidence ellipses did not assist in understanding trends, so these were omitted in PCA plots with grouping by Grime's life strategy.

2.4. *Exploring associations between socio-ecological categories*

Chi-square tests of independence were used to test for associations among pairwise categories of Grime's life strategy, weediness, arable affinity and conservation status. In other words, we tested whether plant species falling in one category of each variable were more likely to fall into a particular category of another variable, for example, whether a higher proportion of non-weedy species were red-listed than would be expected by chance. A separate chi-square test was used for each pair of variables. Due to the sometimes low number of species in certain combinations of categories, *p*-values were computed using Monte Carlo simulation within R package *stats* (R Core Team, 2023).

3. Results

3.1. *PCA and species presence*

The PCA of ecological indicator values separated along two dimensions, which together explained 54 % of the variability (Fig. 2A). PC1 was negatively associated with response to grazing/mowing, and positively with optimal nitrogen, phosphorus and soil disturbance. PC2 was associated negatively with nitrogen, phosphorus and moisture, and positively with light (Table 3). The majority of species in the study had a higher dispersion of values of PC1 compared to PC2, and low to intermediate values of PC2 (Fig. 2B), indicating plants with a preference for environments rich in nitrogen and phosphorus, and affinity for soil disturbance.

3.2. *Trends in data grouping within PCA*

Examination of the principal components underpinning the response of Swedish arable plants to ecological indicators identified a number of determinants (Fig. 2A) cohering to Grime's life strategy theory (Grime, 1977). There were significant differences in the ecological indicator values of species assigned to different Grime's life strategy categories in the TRY database. Separation of species by CSR strategy (Fig. 3) indicates that CR species in particular tended towards the right of the plot, associated with high values for ecological indicators for nutrients, disturbance, light, and pH. Species associated with the CR strategy had a tendency towards the lower right quadrant in strong association with

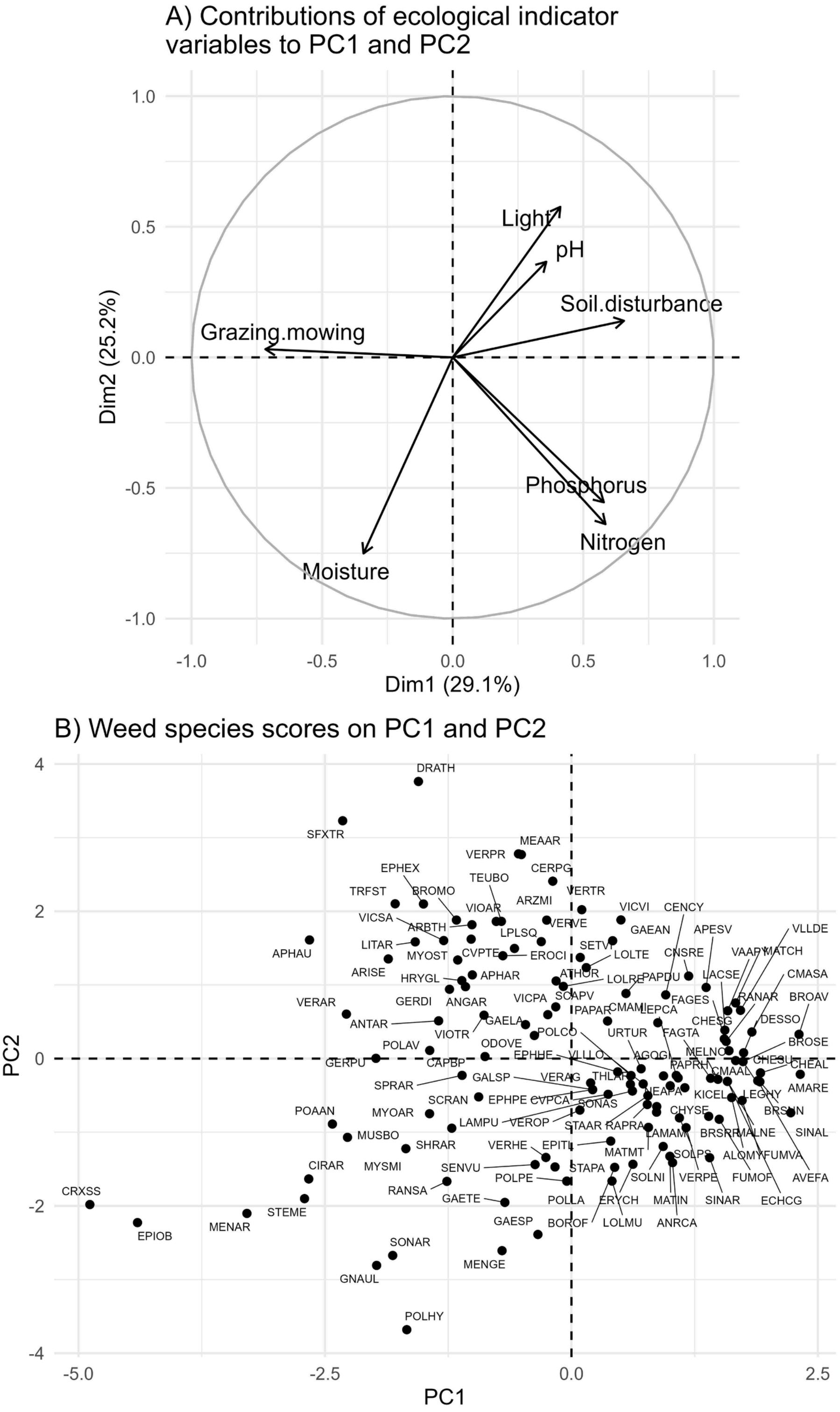

Fig. 2. A) Principal component axes of agronomic filters on arable plant species community composition; B) Distribution of 131 arable plant species (labelled by EPPO code) from Tyler et al. (2021) across these axes.

nutrient indicator values, while R strategists were spread more widely, but generally associated with high indicator values for disturbance, as hypothesised.

There were small but significant differences between socio-ecological outcomes in multivariate space (Table 4). Arable affinity increases with nutrition-related agronomic filters (phosphorus and nitrogen), as well as soil disturbance at high levels (Fig. 4A). The majority of red-listed species skewed away from high nutrient environments in comparison to non-red-listed species (Fig. 4B). Weediness according to questionnaire respondents followed the opposite trend (Fig. 4C), with weedy species apparently favouring high nutrient levels in comparison to those which were not identified as problematic weeds.

3.3. *Associations among socio-ecological outcome variables*

The data in Figs. 4B and 4C suggest that species that are considered

Table 3
Correlations of each input variable with the first two principal components of the PCA. Values in parenthesis are the proportion of observed variability explained by each PC. Correlations > 0.3 or < -0.3 are highlighted in bold.

Variable	PC1 (29.1 %)	PC2 (25.2 %)
Light	0.29	**0.43**
Moisture	−0.24	**−0.56**
pH	0.25	0.28
Nitrogen	**0.41**	**−0.48**
Phosphorus	**0.41**	**−0.42**
Grazing/mowing	**−0.50**	0.02
Soil disturbance	**0.46**	0.11

weedy, and that are not of conservation concern, occupy a similar space in the PCA to one another. This implies associations among these variables, for which we found some evidence using chi-square tests (Table 5). Weediness of arable plant species correlated with some Grime's life strategies ($P = 0.047$), with 'weedy' species more likely to have a CR strategy, and less likely to have an SR strategy (Fig. 5A), while 'weedy' species were also less likely to be red-listed ($P < 0.001$) (Fig. 5E). However, there was no significant association between Grime's life strategy and conservation status ($P = 0.988$) (Fig. 5B). Weeds with a high arable affinity were more likely to be red-listed ($P = 0.025$) (Fig. 5F), and SR species may have been overrepresented in 'non-weedy species' (Fig. 5A), with a low arable affinity (Fig. 5C), but this was not conclusive (Table 5). Overall, these results indicate that strong generalisations between these groups cannot be made – in particular, arable affinity is not equated to being a successful (not red-listed), nor problematic ('weedy') arable species, while a CR strategy increases the chances, but does not alone determine, that a plant species will be considered a problematic weed.

4. Discussion

Our evaluation of temperate arable flora in terms of ecological indicators and Grime's life strategies supports our premise that conditions typical of intensive arable systems favour both a large number of R strategists (Hypothesis 1), and more problematic weeds that follow a CR strategy (Hypothesis 2). As expected, a CR strategy was associated with strong arable filters particularly for nutrition, soil disturbance and light. Species with a CR strategy, or sharing similar ecological indicator values, were also more likely to be considered by experts as problematic weeds. There is also a cross-section of predominantly R strategist arable plant species which are rare in spite of high arable affinity (Hypothesis 3). Our analyses suggest that this may relate to them trending away from high indicator values for nutrients in comparison to less specialised species (Fig. 4A). This is logical as many 'rare weeds' are most successful in relatively nutrient-poor systems (*e.g.* extensive, traditionally-managed agriculture) (Storkey et al., 2012; Pinke and Gunton, 2014). Indeed, many of the associations we describe are implicitly established in existing literature (Table 6).

4.1. The weeds we have, and why they are detrimental

According to our results, there is a complete absence of S strategists and a near absence of C or CS strategists occurring on temperate arable land in the dataset obtained from Tyler et al. (2021), to the point that we are essentially left with a 'CR-SR-R' matrix rather than CSR. This builds on previous work suggesting that community assembly in an arable

Table 4
Results of the PERMANOVAs testing whether ecological indicators and socio-economic outcomes shown in Figs. 3 and 4 have significantly different means within multivariate space (F tests), and how much variance in the distance matrix is explained by each variable (R^2).

Variable tested	d.f.	Sum of squares	R^2	F statistic	P value
Weediness	1	34.2	0.038	5.038	**0.001**
Residual	129	875.8	0.962		
Conservation status	1	24.8	0.027	3.619	**0.002**
Residual	129	885.2	0.973		
Arable affinity	2	52.7	0.058	3.934	**0.001**
Residual	128	857.3	0.942		
Grime's life strategy	5	143.6	0.158	4.684	**0.001**
Residual	125	766.4	0.842		

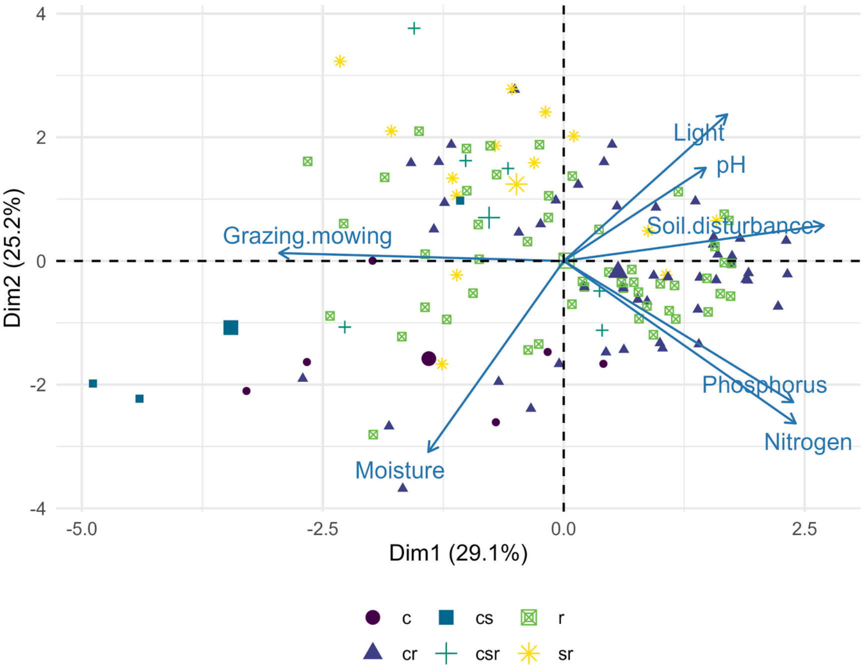

Fig. 3. Principal components analysis of agronomic filters on Swedish arable plants grouped by Grime's life strategy (c= 'Competitive'; s = 'Stress-tolerant'; r = 'Ruderal'; all other classifications are combinations of these categorisations), according to the TRY database (Kattge et al., 2020).

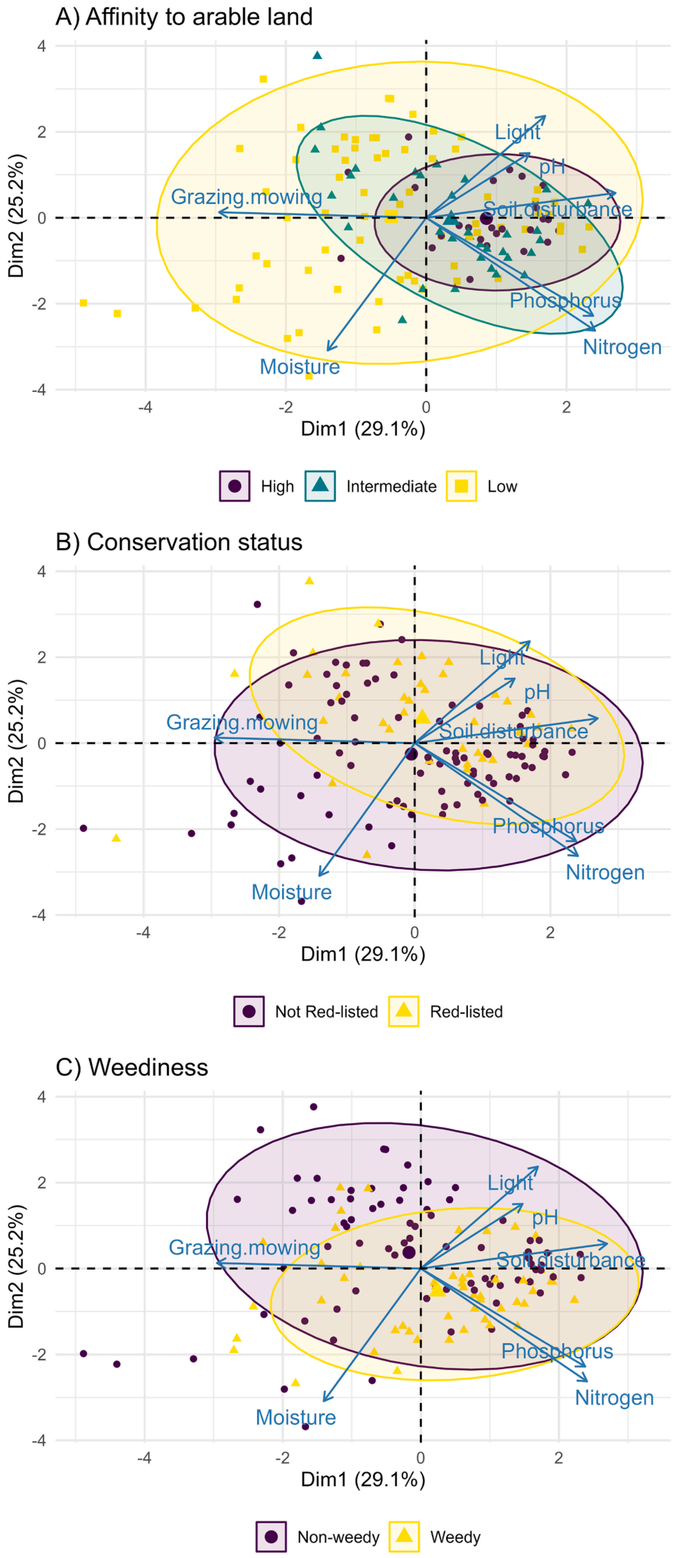

Fig. 4. Principal components analysis of agronomic filters on arable plants grouped by, A) specialisation to arable land, with confidence ellipses; B) presence or absence from the 2020 Swedish red list of species (SLU Artdatabanken, 2020); and C) weediness according to a questionnaire answered by 23 weed experts in Sweden. Ellipses indicate 95 % confidence intervals of the data for each level, based on a multivariate t-distribution.

Table 5
Results of the chi-square tests assessing whether species were distributed evenly among categories within pairs of variables, or whether, for example, a greater than expected proportion of 'non-weedy' species were red-listed. The P-values in this table can be used to identify where proportions shown in Fig. 5 are significantly different from one another.

Variable pair	chi-square statistic	Simulated P-value
Grime's life strategy, weediness	10.871	**0.047**
Grime's life strategy, conservation status	0.636	0.988
Grime's life strategy, arable affinity	14.004	0.165
Arable affinity, weediness	4.353	0.12
Conservation status, weediness	19.605	**< 0.001**
Conservation status, arable affinity	7.613	**0.025**

system is limited in function by a constrained niche space in an intensely managed environment (Storkey, 2006; Metcalfe et al., 2019). By contrast, communities in the unmanaged systems that Grime's life strategy triangle was originally developed from are more functionally even (Bàrberi et al., 2018).

The majority of Swedish arable plant species are either CR or R strategists, likely due to the frequent disturbance imposed by agricultural management (Gunton et al., 2011; MacLaren et al., 2020). Intense soil disturbance is a major filter of ruderality (Hodgson et al., 1999), although grazing or mowing will also select for R species to some extent, and against CR species for which height is typically a key competitive trait (*e.g.* due to repeated cutting of aboveground tissues or trampling) (Díaz et al., 2007; MacLaren et al., 2020).

Arable plant species also correlate with high nitrogen input, known to be a major determinant of plant community composition (Cleland and Harpole, 2010); increasing nitrogen inputs correlate with reduced arable plant diversity (Moss et al., 2004; Berquer et al., 2023), the result of selection for nitrophilic C or CR strategists which outcompete other species around them. The CR species present in Swedish arable land therefore encompass many of the problematic weeds identified by experts. These species are also largely the 'usual suspects' of modern, conventional, temperate agriculture; the likes of *Chenopodium album* (CHEAL), *Stellaria media* (STEME), *Tripleurospermum inodorum* (MATIN), and *Sinapis arvensis* (SINAR). Even when these species are not present in such conditions, it is probable that their niche space will be occupied by a functionally-similar species (see Storkey, 2006; Fried et al., 2012). To alter the functions in the community, we must therefore consider management practices with potential to alter niche space to the benefit of less common, less detrimental species.

4.2. The 'weeds' we want, and why they are rare

The majority of red-listed species in this dataset are R strategists and not CR strategists (Fig. 3), illuminating that ruderality alone is not a strong indicator of dominance or detriment. These are species with a high arable affinity which are particularly associated with soil disturbance indicator values compared to generalists (Fig. 4A), emphasising the importance of disturbance in arable species selection (Bàrberi et al., 2018). The most specialised species are also those which can best tolerate the disturbance of regular management (Metcalfe et al., 2019). On the other hand, pure R strategists are often poor competitors, ill-equipped to effectively utilise the added resources that come with agricultural intensification, and unable to tolerate the competition of more dominant species either. They have therefore become rarer in modern conventional systems (Epperlein et al., 2014; Twerski et al., 2021). The positive correlation between rarity and arable affinity is highly concerning from a biodiversity standpoint, indicative that these species are unlikely to return in the event of their local extinction, given that few other viable habitats exist from which they could originate. This coheres with the findings of Metcalfe et al. (2019), that the species

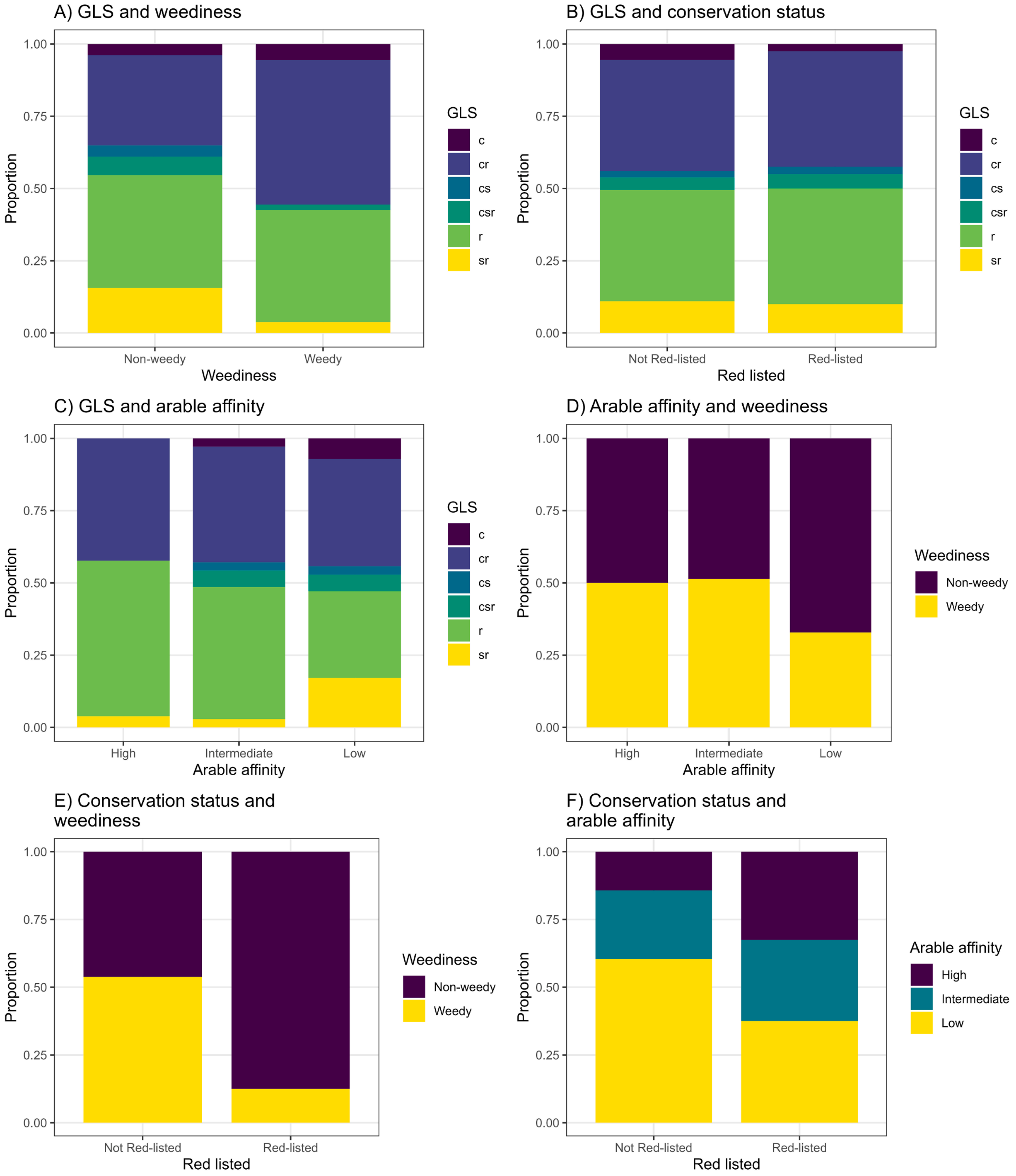

Fig. 5. Stacked barplots showing the proportion of weed species that fall within pairwise combinations of the GLS, weediness, arable affinity and conservation status variables. Chi-square tests indicate significant differences in the groupings in panels A, E, and F ($P < 0.05$).

specialised for survival in an arable field are typically poor competitors in comparison to those which can colonise from other environments, which are therefore the more detrimental, but with lower arable affinity.

High levels of nutrient addition can thus create an ‘agronomic trap’ where, beyond the crop, increased nutrition chiefly benefits these problematic, persistent, nitrophilic CR strategists which outcompete more benign species and drive declining floral diversity (Moss et al., 2004; Storkey et al., 2021; Berquer et al., 2023). Incidentally, there are consistencies between the red-listed R strategist species identified in this study and those listed previously as potentially beneficial and uncompetitive (Storkey and Westbury, 2007). This may be due to their resource investment in developing positive interactions with the ecosystem

Table 6
A summary of agronomic filters examined in this study and the Grime life strategy they relate to at increasing levels (unless specified).

Ecological indicator	Grime's life strategy selection	Supporting references
Grazing/ mowing	SR (Away from C)	Milchunas et al. (1988); Moog et al. (2005)
Light	Away from S	Valladares and Niinemets (2008)
Moisture	Away from S at low levels, towards S at high levels	Striker (2012); Volaire (2018)
Nitrogen	C	Zheng et al. (2019)
pH	Away from S	Kidd and Proctor (2001)
Phosphorus	C	Balemi and Negisho (2012)
Soil disturbance	R	Hodgson et al. (1999)

rather than in competing with other species (Storkey, 2006).

4.3. *Towards targeted ecological weed management?*

Having identified how temperate arable plant communities respond to key agronomic filters, the outstanding question is how to apply this knowledge to benefit crop production. Previous studies have indicated that a low-diversity community dominated by CR strategists is most detrimental to crop production, while a high-diversity community composed mainly of R and SR strategists is likely to be more benign or even beneficial (Storkey and Neve, 2018; Adeux et al., 2019; MacLaren et al., 2020).

Our results suggest that nutrient management to reduce availability to weeds (*e.g.* by delaying and reducing fertilisation to optimise crop uptake), could be an important lever in shifting community structure in this way. In practice, however, it remains to be seen how far it is possible to minimise nutrient availability to weeds without also limiting the crop. Still, current agricultural nitrogen usage levels are widely regarded as unsustainable and environmentally damaging, and maybe even counterproductive for crop protection (Swarbreck et al., 2019; Martinez et al., 2021; Richardson et al., 2023). More efficient uptake and utilisation of nitrogen in crop breeding (e.g. Asplund et al., 2016), through crops with elevated nitrogen use efficiency, may therefore indirectly supplement efforts to create a less competitive weed community. This may also be achieved through more targeted application of fertiliser for the crop to utilise, such as in precision or deep fertiliser placement (Diacono et al., 2013; Rychel et al., 2023). This would create a more stressful environment specifically for non-crop species, in disfavour of CR weeds and in favour of R and SR species.

Alteration of the 'grazing/mowing' filter could also be a powerful strategy against problematic weeds, as it selects for R and SR species and away from CR strategists. Of course, plant height is constrained by grazing or mowing, with consequences for interspecific competition (Le Bagousse-Pinguet et al., 2012). One could consider the diverse floral communities of grazed grasslands as substantiation of this theory (Moog et al., 2005), and indeed there is substantial evidence that grazing can benefit plant diversity, particularly at low nutrient levels (e.g. Hickman et al., 2004). A possible avenue for achieving this in arable systems is to integrate low stocking densities of grazing livestock on forage crops or leys in rotation with arable crops (MacLaren et al., 2019).

More broadly, it is important to remember that different crops require different niches, which occupy different positions within the PCA plots that we present. As management is built around the crop, the associated arable plant community is also, to some extent, pushed towards its niche space (e.g. Légère et al., 2005). There is therefore credence, in line with the tenets of ecological weed management, in diversifying rotations and using cover crops which may show differences in preference for these filters (MacLaren et al., 2020). Our results therefore constitute a theoretical basis for ecological weed management in disfavour of the highly detrimental species which are so antagonistic to productivity.

A community-level shift away from CR and toward conditions promoting R and SR species would favour the re-establishment of rarer, more beneficial arable plants. It is possible to reintroduce individual species without significant changes in management (Epperlein et al., 2014), which may in fact be required if those with desired functional traits are absent from the seedbank. Crucially, though, these species would be antagonised by competition if entering an established community of CR strategists (Armengot et al., 2017), emphasising the need for different management strategies in favour of this more benign plant community. Precision management strategies using emergent technology could benefit in tailoring a specific arable plant community, separating the weeds we have and the 'weeds' we want. Recent work has attempted to apply such ecological perspectives to the development of weeding robots in a complementary manner (Zingsheim and Döring, 2024).

4.4. *On the applicability of arable plant indicator data*

The extent to which the trends we report here can be applied to arable plant communities in other regions (especially those dissimilar to Sweden) remains an open question, which could only be answered with the use of a sufficiently extensive species and trait database. Unfortunately, such quality and quantity of data is only currently available for Central and Northern Europe, where arable floral communities are relatively similar (Tyler et al., 2021; Kattge et al., 2020). On a related note, it has been observed that the selection pressures of agricultural management can force trait divergence from typical individuals (Bommarco et al., 2010), usually (and understandably) in the direction of ruderality (Leiss and Müller-Schärer, 2001), but also often influenced by the crop present (Romillac et al., 2023). One might therefore expect that the trait space occupied both within and across species may differ between distinct agricultural systems with different crops, as these provide altered niche spaces (consider Fried et al., 2022). Incidentally, this suggests the value of crop diversification for weed management (MacLaren et al., 2020).

Plant adaptability is concerning for research into ecological indicators and functional traits, as it raises the question of how representative the sampled individuals are for their species. Tyler et al. (2021) considered phenotypic variation on a latitudinal scale as a motivation in creating a database specific to Sweden (e.g. Wasof et al., 2013; Novakovskiy et al., 2021), but this may be further hindered by differences in habitat which could force further divergence in plant functional identity.

5. Conclusion

This study confirms that temperate arable plants predominantly follow ruderal strategies, with many being pure ruderals. However, problematic weeds more often follow a CR strategy of high nutrient acquisition, rapid growth and competition with other plant species, including the crop, in agroecosystems. These findings therefore vindicate the necessity of efforts to understand the composition and constituent interactions of an arable plant community, with a focus on the functions of these species.

The strong selection pressures of agronomic intensification, be they related to herbicides, nutrients, or mechanical management, will inevitably force a community shift to a few well-adapted outlier species that become problematic weeds. Therefore, weed management should focus on building a sustainable and self-regulating agroecosystem to benefit the crop, specifically in shifting selection pressure away from dominant weeds and in favour of more benign or beneficial species.

Although this work provides some insight into trends modulating arable plant communities, it is caveated by its geographic remit, and by a focus only on interspecific and not intraspecific variability. Deeper examination of the nature and incidence of trait variability in arable plant species, and in a wider range of arable plant communities, would facilitate the deployment of more specific ecological weed management approaches based on the composition of the community present.

CRediT authorship contribution statement

Menegat Alexander: Writing – review & editing, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Hickman Darwin T:** Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis, Data curation. **MacLaren Chloe:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Authors' contributions

AM conceived the ideas and designed methodology; All authors curated, analysed and visualised the data; DTH led the writing of the manuscript. All authors contributed critically to drafts and gave final approval for publication.

Data availability

Most data used have previously been published and has been referenced as such in the manuscript; additional data have been published on Zenodo as specified on the title page.

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