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RESEARCH PAPER

Management-induced micro-habitats in crop fields alter the trait composition of arable plant communities

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ABSTRACT

Modern cropping systems typically involve extensive soil disturbance and high fertiliser use. Plants other than the crop are controlled to avoid potential crop yield losses. However, crop fields are not homogeneous ecosystems. Rather, they comprise several micro-habitats differing in disturbance intensity, inter-specific competition and resource availability. Understanding how weed and crop management affects the trait composition of arable plants could help finding management practices that favour less competitive species or species providing valuable ecosystem services. This study examined the traits within the arable plant community and their association with disturbance and competition levels. The relationship between micro-habitats and plant species traits was investigated using RLQ analysis, in which micro-habitats and traits were linked using species count data. The environmental variables forming micro-habitats were: biomass of main crop and intercropped service crop, frequency of mechanical disturbance and within-crop sampling location. Intermediate to high competition and intermediate disturbance reduced the presence of competitive arable plant species compared with low competition and highest and lowest disturbance, while favouring a diverse group of ruderal species. High service crop biomass in the main crop row, compared with low, reduced the presence of arable plant species that were associated both with ruderal and competitive traits (competitive-ruderals), while favouring the diverse group of ruderal species. The analysis showed distinctions in traits associated with different micro-habitats, but to better guide interpretations regarding species' harmfulness to crops, species characteristics based on combinations of traits have to be defined at a finer scale, especially for ruderal species.

Introduction

Suppressing arable plants in agroecosystems (i.e. weed control) is important to reduce competition for nutrients, water and light and hence avoids losses in crop yield and quality. Unlike natural ecosystems, agroecosystems often remain in a state of early secondary succession through recurring disturbance events such as soil tillage, crop rotation and herbicide application. Over time, this has selected for arable plant communities dominated by species adapted to regular disturbances (Smith, 2015). These species are characterised by rapid development (Fried et al., 2012; Trichard et al., 2013) and high demand for nutrients and light (Fried et al., 2009). Growing competitive crops, i.e. crops that establish fast and are good at absorbing incoming light, is an effective tool for weed control (Andrew et al., 2015).

Apart from exerting strong selection pressure, weed control measures have negative side-effects. For example, intensive soil tillage disturbs soil fauna (Torppa & Taylor, 2022) and increases the risk of soil erosion by wind and water (Montgomery, 2007). Herbicides alter plant species composition, thus affecting important ecosystem services such as nutrient cycling (DeLorenzo et al., 2001). Moreover, the strong selection imposed by intensive mechanical and chemical weed control measures has resulted in major losses of arable plant diversity (Albrecht et al., 2016). It has been suggested that less intensive soil disturbance combined with non-chemical weed control measures could exert weaker selection pressure on arable plant communities and have fewer negative side-effects (MacLaren et al., 2020). Arable plants can also provide different ecosystem services, such as food resources for pollinators and herbivores (Kubota et al., 2015; Storkey, 2006), so allowing beneficial species to co-exist with crops could contribute to mitigate some negative effects of agriculture.

Crops occupy a limited niche space within agroecosystems, leaving plenty of resources for other arable plants to utilise. Ideally, plant communities within agroecosystems should consist of intended and unintended species with largely non-overlapping niche spaces and

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complementary traits. Traits are defined as measurable characteristics (e.g. morphological, phenological or physiological) of individual organisms, measured at either the individual or other relevant level of organisation (cf. Dawson et al., 2021). Complementarity in species traits can be achieved by growing more than one crop simultaneously (intercropping) (Justes et al., 2021) or by allowing less competitive arable plant species to co-exist with crops (Liebman & Gallandt, 1997; Storkey & Neve, 2018). It has been shown that more diverse arable plant communities do not reduce crop yield to the same extent as communities with lower diversity (Adeux et al., 2019). However, little is known about how crop management affects the trait composition of arable plant communities (Díaz & Cabido, 2001; Westbrook et al., 2024) and hence the type of species that are selected for. Studies of the influence of spatial variation on the selection process are even rarer. Including analyses of community trait composition in studies of arable plants could provide a more accurate assessment of their competitiveness and their potential to provide ecosystem services. Ideally, an arable plant community should support organisms providing pest control and pollination, while not competing strongly with the crop (MacLaren et al., 2020).

The aim of this study was to improve the understanding of how short-term differences in crop competition and disturbance influence the trait composition of the arable plant community. Our overarching hypothesis was that management-induced niche heterogeneity results in differences in taxonomy and trait composition of the arable plant community at the intra-field scale. We included data on traits, ecological indicator values, which were derived from several varying traits, and Grime's life strategies. We hereafter collectively refer to them as 'traits'. Data were collected at six field sites in which oats (*Avena sativa* L.) was intercropped with different leguminous service crops, combined with varying frequency of in-season mechanical weed control. Data on oat and service crop biomass, frequency of mechanical disturbance and within-crop sampling location were used to define different micro-habitats that were expected to impose differing selection pressures. RLQ analysis was performed to identify associations between environmental factors, competition and disturbance, and species traits of the observed arable plant communities (Dolédec et al., 1996; Dolédec & Chessel, 1994). This allows for a less biased interpretation of the species data, compared to using multivariate analyses that only connects species and environmental variables, as is commonly done today. The method has rarely been applied to agricultural contexts, and when used it has been applied to investigate long-term effects of distinctly different crop management practices or changes in crop management over time (e.g. Fried et al., 2012; Hofmeijer et al., 2021). To our knowledge, this is the first study to apply the RLQ method to investigate management-induced variations within fields over one crop season.

Materials and methods

Agroecosystem characteristics

Data collection was carried out at six sites in southern Sweden, in the years 2017 (site 1 and 3), 2018 (site 2 and 4) and 2019 (site 5 and 6) (Table 1). Mean annual temperature and precipitation were higher at the two most southerly sites (1, 2) than farther north (3–6). Soil texture classes at the sites ranged from loam to clay, and soil organic matter content from 2.0 % to 5.4 %. The experiments were all located in areas dominated by annual crop production. The six sites hence covered different climatic and soil conditions, but were located in similar landscapes. No herbicides were used during the data collection period, but two sites (5 and 6) were otherwise managed conventionally with herbicides. The other four farms were managed organically, with relatively high doses of manure and frequent mechanical weed control.

The experiments were designed to investigate the effect on the arable plant community posed by competition from oats and an intercropped service crop, and in-season soil disturbance by row-hoeing. The service crops were grown in mixtures and differed slightly between sites. Site 1–4 all had mixtures of *Trifolium resupinatum* L. + *T. squarrosum* (annuals) and *T. pratense, T. repens* + *Medicago lupulina* L. (perennials). Additionally, site 3 and 4 had a mixture of *T. incarnatum* + *Vicia villosa* Roth. (annuals). At site 5 and 6 a mixture of *T. squarrosum* + *T. pratense* were used. The service crops were either sown at the same time and in the same rows as oats (Fig. 1B), or in between oat rows during mechanical weed control one month after oat seeding (Fig. 1C). Seeding rates varied between 5.3 kg ha^{-1} and 24.5 kg ha^{-1} depending on species mixture (Appendix A). To vary the disturbance rate, the inter-row centres were weeded mechanically by row-hoeing once or twice during the growing season. Oats were sown in 7 cm wide bands (rows) at a seeding rate of 131 kg ha^{-1} and 180 kg ha^{-1} (Appendix A), with a distance between row centres of 25–33 cm, depending on site. Plot size at the different sites ranged between 3 m x 36 m and 9 m x 50 m, depending on available machinery. A more detailed description of the system design can be found in Lagerquist et al. (2022).

Micro-habitat characteristics

Level of competition and level of disturbance were identified separately, representing different micro-habitat characteristics. Competition was characterised based on within-plot location, and on oat and service crop biomass, sampled at oat harvest, and was assumed to be highest in the oat row, and decrease with increasing distance from the oat row. Oat biomass was characterised as: low (<8 t ha^{-1}), intermediate (8–13 t ha^{-1}) or high (>13 t ha^{-1}), and service crop biomass as: low (<0.2 t ha^{-1}) or high (>0.2 t ha^{-1}). Oat and service crop biomass values were used as separate competition components to understand their relative contribution, and assuming some niche complementarity. This resulted in 18 unique micro-habitats based on competition. Disturbance was characterised by the number of row-hoeing events and within-plot sampling location, resulting in six unique micro-habitats. Disturbance was assumed to be highest in inter-row centres, since this location corresponded to the centre of the hoe tine.

Data collection

To determine arable plant community composition, samples were

Table 1

Characteristics of experimental sites 1–6. Clay, silt and sand are reported as % of total mineral fraction. SOM = soil organic matter content. Mean temperature and total precipitation are 30-year averages for the full year and (within brackets) the cropping season (April-July) (Swedish Meteorological and Hydrological Institute, https://www.smhi.se/data).

Site	Coordinates	No. sampling plots	Clay [%]	Silt [%]	Sand [%]	SOM [%]	pH H_2O	Mean temperature [°C]	Total precipitation [mm]
1	55.7 N, 13.2E	24	20	33	47	2.0	7.1	9.00 (13.6)	676 (202)
2	56.2 N, 12.9E	24	28	42	30	2.7	6.9	8.50 (12.9)	747 (241)
3	58.4 N, 15.3E	32	32	57	11	2.6	6.8	7.20 (12.4)	566 (220)
4	58.4 N, 15.3E	32	41	49	10	3.6	7.1	7.20 (12.4)	566 (220)
5	58.5 N, 15.4E	32	40	46	14	4.3	6.4	7.20 (12.4)	597 (225)
6	58.4 N, 15.6E	32	70	25	5.0	5.4	6.8	7.10 (12.2)	565 (222)

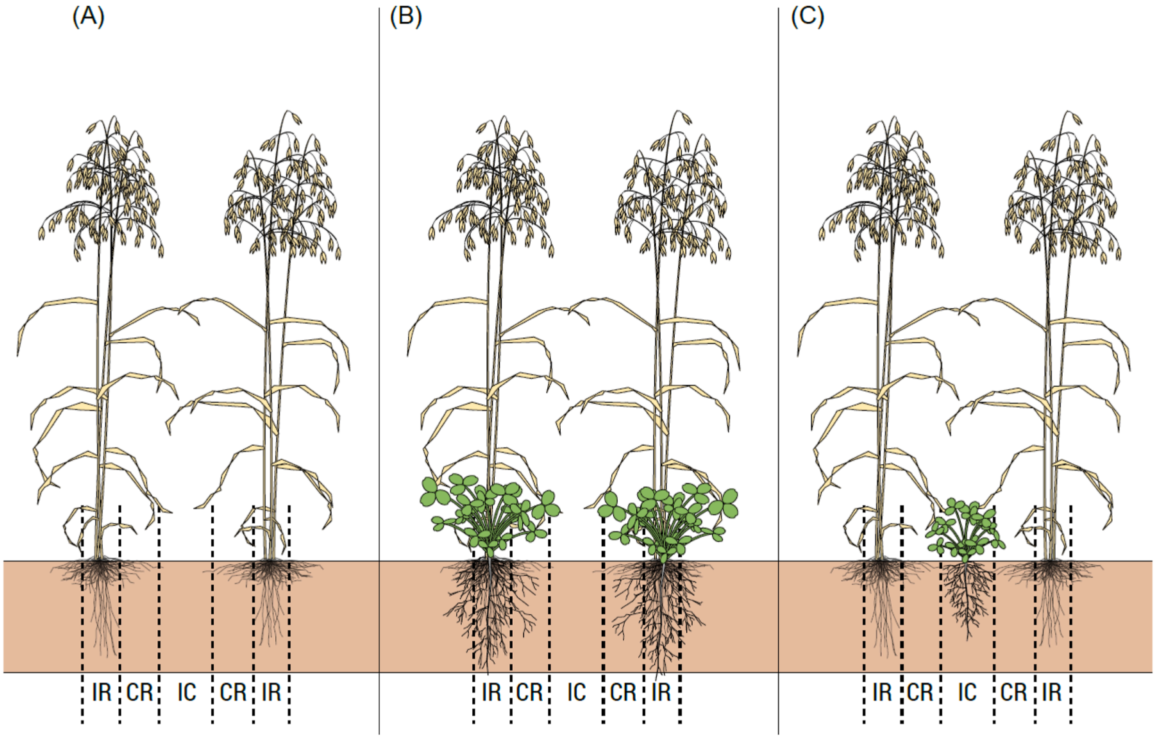

Fig. 1. Plant count locations within the sampling area in each plot. IC = inter-row centre, CR = close to oat row, IR = in oat row. Three cropping systems are shown: (A) no service crop, (B) service crop within oat rows (sown early) and (C) service crop between oat rows (sown late). Widths of IC and CR varied since row distances varied. Illustrated by Fredrik Stendahl.

taken from four areas per plot (only three at site 3), each encompassing two 50-cm lengths of oat rows and two inter-row sections. The sampling areas were fixed at the start of the experiment, avoiding wheel tracks and with sufficient distance to plot borders. Each area was subdivided into within-plot locations according to Fig. 1. Arable plants were counted at species level within two weeks before oat harvest. Number of individuals per species at each of the within-plot locations was extrapolated to number per m^2.

Oat biomass and service crop biomass were collected in conjunction with the counting of arable plants. The plants were cut at ground level and oven-dried at 60 °C for 48 h before weighing.

Data analysis

An initial correspondence analysis (ter Braak, 1986) showed that the species composition differed between sites. Therefore partial RLQ analysis was used, including experimental sites as a co-variable, which eliminates site-specific effects in the analysis (Wesuls et al., 2012). Although the species composition differed between sites, there was an overlap of species across sites. If a species occurred in less than two sites it was excluded from the analysis. The competition and disturbance levels were used as environmental data, and the number of individuals of each arable plant species as species data. Trait data were derived from two databases (Bàrberi et al., 2018; Tyler et al., 2021). To ease interpretation and readability of the results, the traits were plotted according to what they are relevant for, i.e. (i) life cycle, (ii) environmental adaptation and (iii) service provision (Table 2). Traits within the group of service provision were traits that support other organisms. Missing trait data were replaced with data for similar species. Missing data on seed dormancy for *Chenopodium album* L., *Euphorbia helioscopia* L., *Galeopsis bifida* Boenn., *Matricaria discoidea* DC. and *Myosotis arvensis* L. were replaced by values for similar species in the respective genus, except for *M. discoidea*, for which no comparable species was found. To reduce the impact of this unknown on the analysis, the most common value among all other species was used. Furthermore, for *Fallopia convolvulus* L., Grime's life strategy and values of specific leaf area (SLA) and plant height for *Convolvulus arvensis* L. were used, due to its similar morphology. *Silene noctiflora* L. was assigned a ruderal life strategy, based on the most common strategy in the rest of the dataset, SLA was set to 20 cm^2 g^{-1} by comparing with values of plants with similar morphology and plant height was set to 0.4 m, as that was the estimated height of the highest *S. noctiflora* plants observed in the field. For *Fumaria officinalis* L., the value for nectar production was set to 4 (nectar production modest, 5–20 g), modified from a "Yes" on support for pollinators in Bàrberi et al. (2018). *Chenopodium pratericola* Rydb. and *Taraxacum officinale* G.H. Weber ex Wiggers were excluded from the analysis, since they were not included in the traits dataset. *Lamium* and *Veronica* species were only identified to genus level, so averages of trait scores from species within these genera that are commonly found in Swedish agroecosystems were used. For *Lamium,* the species considered were *L. album* L., *L. amplexicaule* L. and *L. confertum* Fr., while for *Veronica* they were *V. agrestis* L., *V. hederifolia* L., *V. persica* Poir., *V. opaca* Fr. and *V. polita* Fr.

Hierarchical cluster analysis was performed to determine which species were most commonly found together. The clusters were analysed in the ordination space, to connect them to environments, and also separately in relation to species traits. The analysis was performed with Ward's D2 method, based on Euclidean distances, and was set to provide three clusters, as this was the highest number of clusters showing a clear distinction on the first three axes in the RLQ analysis.

In the RLQ analysis, each dataset was converted into an ordination object. The species data were converted into a correspondence analysis ordination. The species scores from this ordination object were used as row weights for the other two ordination objects, using the Hill-Smith ordination method, which can handle both quantitative and categorical data. The three datasets were merged into one, and the individual sites were added as a factor in the partial RLQ analysis. Correlations between pairs of environmental and trait variables were tested for

Table 2
Species functional traits (FT) and ecological indicators (EI) used in the trait dataset, divided into three groups: life cycle, environmental adaptation and service provision. Where no reference is cited, data were derived from Tyler et al. (2021). More detailed descriptions of the traits can be found in the references cited.

Trait	Description	Score range
Life cycle		
Longevity (FT)	Life form	1–4, where 1 is strictly annual and 4 is long-lived perennial
Seed dormancy (FT)	Time requirement between seed dissemination and germination	1–4, where 1 is non-dormant and 4 is intermediate or deep physiological or morphophysiological dormancy
Seed bank (FT)	Longevity of seeds in the soil	1–4, where 1 is transient (max 2 years) and 4 is semipermanent (<25 years)
Grime's life strategy (EI) (Bàrberi et al., 2018)	Life strategies based on tolerance to stress, disturbance and competition	Competitive (C), stress tolerant (S), ruderal (R) and combinations of these: CS, CR, SR, CSR
Environmental adaptation		
Light (EI)	Light requirement	1–7, where 1 is deep shade and 7 is always full sun
Moisture (EI)	Moisture requirement	1–12, where 1 is very dry and 12 is deep permanent water
Nitrogen (EI)	Nitrogen requirement	1–9, where 1 is very N-poor and 9 is mostly found on artificially N-enriched soils
Phosphorus (EI)	Phosphorus requirement	1–5, where 1 is avoiding soils with high P availability and 5 is plants confined to soils with high P availability
Soil reaction (EI)	pH requirement	1–8, where 1 is strongly acid (<4.5) and 8 is alkaline (>8)
Soil disturbance (EI)	Requirement for disturbance	1–9, where 1 is plants that colonise already established vegetation, 9 is plants that require yearly soil disturbance
Height (FT) (Bàrberi et al., 2018)	Indication of competitive ability	Mean of maximum reported values
Specific leaf area (FT) (Bàrberi et al., 2018)	Indication of radiation use efficiency and light competition	Mean value reported for species
Service provision		
Biodiversity relevance (FT)	Indication of species importance as a food source, substrate, shelter or mutualistic partner for other organisms	1–8, where 1 indicates <6 associated species and 8 indicates >400 associated species
Nectar production (FT)	Indication of species importance for pollinators	1–7, where 1 is no nectar production and 7 is very large nectar production
Phenology (FT)	Indicates onset of flowering	1–15, where 1 is late February, and 15 is late September
Mycorrhiza (FT)	Ability to form mycorrhizal associations	No Myc = no mycorrhizal associations, ArbuscularMyc = arbuscular mycorrhizal association known

significance using fourth-corner analysis (Dray & Dufour, 2007).

All analyses were performed using R version 4.1.2 (R Core Team, 2021) and the *ade4* package (Dray & Dufour, 2007).

Limitations of the study

This study investigated short-term effects of crop competition and in-season disturbance (row-hoeing) on trait composition of the arable plant community. However, the seedbank, determining which species could emerge and at what abundance, is largely affected by previous years' management, (Cordeau et al., 2022) but this is not taken into consideration here.

The two major study variables, competition and disturbance, were derived from the same experimental plots, so there was a background signal of disturbance in the competition variable and of competition in the disturbance variable. However, all levels of competition were represented within each disturbance level and in most cases all disturbance levels were represented within each competition level.

Competition was only defined by aboveground biomass, although competition happens also below ground (Sauter et al., 2021). This was mainly due to the difficulty in obtaining good data on belowground competition, and aboveground biomass was considered the most reliable proxy for competition.

Results

The first axis in the RLQ-ordination explained 54 % of total variation (Fig. 2). Along this axis, micro-habitats with low oat biomass (small symbols; Fig. 2A) deviated from those with intermediate and high oat biomass (larger symbols; Fig. 2A), while micro-habitats with high disturbance (triangles, Fig. 2B) deviated from those with lower disturbance (squares and circles; Fig. 2B). Micro-habitats with low oat biomass and high disturbance scored higher on longevity, lower on soil disturbance requirement, were more associated with competitive species (Grime's C) and/or scored higher on most service-providing traits than other micro-habitats (Fig. 2D-2F).

The second axis explained 26 % of total variation (Fig. 2). Along this axis, the clearest effect of competition was seen within the oat row (squares), where micro-habitats without a service crop (light grey squares) deviated from the other micro-habitats. For disturbance, there was a gradual shift along the second axis, with low disturbance (in the oat row) on the positive side and increasing disturbance on the negative side. The area within the oat row was mainly associated with competitive-ruderal species (Grime's CR), with high SLA, low light requirement and/or high moisture requirements, especially in the absence of a service crop. With increasing disturbance, mainly driven by location (symbols in Fig. 2B) and to some degree also by competition from the service crop (mainly within and close to the oat row; squares and circles, respectively, in Fig. 2A), the micro-habitats were more associated with a large group of ruderal species (Grime's R). Within this group, arable plants with high light requirements were more associated with micro-habitats with low service crop biomass than micro-habitats with high service crop biomass.

The species detected were grouped into three different clusters (I-III) based on the relationships between species abundance and environments (Fig. 2C). Cluster I, the largest cluster, was associated with a broad set of environments with intermediate to high competition and intermediate disturbance (Fig. 2A-2C). Cluster II was associated with location within the oat row (squares in Fig. 2D), especially when service crop biomass was low (dark grey squares in Fig. 2A), while cluster III was associated with low oat biomass (small symbols in Fig. 2A) and high disturbance (large triangle in Fig. 2B).

To better understand the traits promoted in each species cluster, i.e. by certain micro-habitat characteristics, the proportions of trait scores in each cluster were visualised (Fig. 3, Fig. A1). Cluster I contained species that benefit from annual or biannual disturbance, while cluster III consisted of species which are good at colonising established vegetation (Fig. 3A). The species in cluster II had intermediate need of soil disturbance (Fig. 3A). Cluster II species were mainly found within the oat row and showed traits suitable for more shaded environments, i.e. low light requirements and high SLA (Fig. 3B-3C), while species mainly found between rows (clusters I and III) had higher light requirement and lower SLA. Species belonging to cluster II and III, associated with Grime's CR and C strategies, were generally taller than the ruderal species in cluster I (Fig. 3D). Species in cluster III had the potential to provide most services assessed in this study, with a high number of associated species, relatively high nectar production and more arbuscular mycorrhiza associations, followed by cluster II (Fig. 3E-3G). Species in cluster I ranged from low to high scores on the service-providing traits and the large

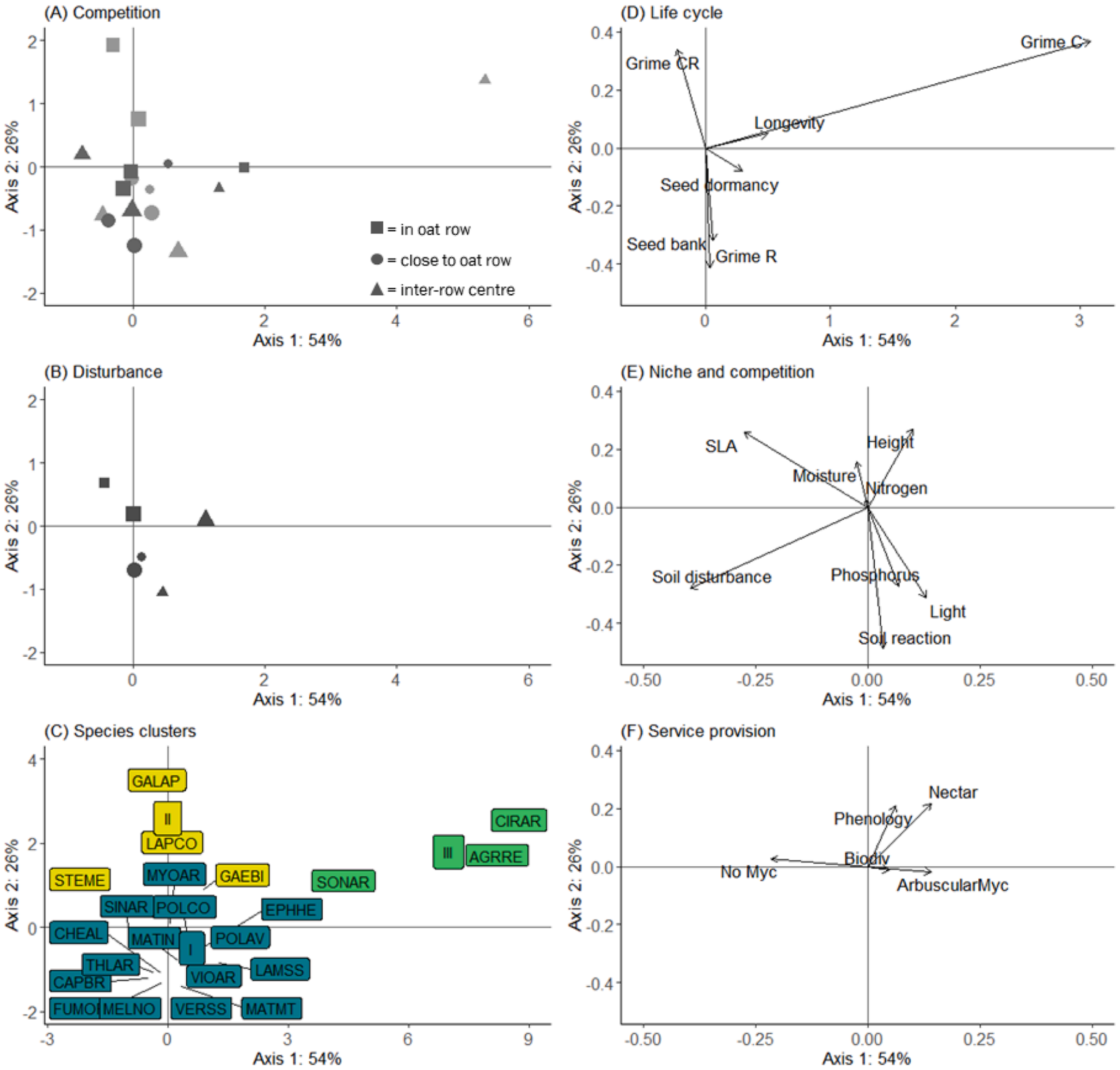

Fig. 2. RLQ-ordination plots divided into environment (A)-(B), species clusters (C) and trait variables (D)-(F). Symbols in the environmental ordinations indicate location, see plot (A). For competition, symbol size indicate oat biomass (low (<8 t ha^{-1}), intermediate (8–13 t ha^{-1}) and high (>13 t ha^{-1})), and light grey indicates low (<0.2 t ha^{-1}) and dark grey high (>0.2 t ha^{-1}) service crop biomass. For disturbance, symbol size indicates row-hoeing intensity (small = 1 and large = 2 row-hoeing events). For species clusters, colours indicate species belonging to each cluster (I, II and III, with the label indicating the centres of each cluster). Abbreviations for traits are explained in Table 2, species are indicated by EPPO codes (https://gd.eppo.int/). Note slightly different scale on the x-axis in the environmental, trait and cluster graphs, for better readability.

number of species gave a wide range of flowering times (Fig. 3H).

The fourth-corner analysis did not reveal any strong correlations between environmental variables and species traits (data not shown). This indicates that many of the environments shared the same species, and hence species traits, or that many of the species had similar traits, or both.

Discussion

Micro-habitats characterised by low crop biomass or high disturbance rate favoured a small group of tall-growing perennial species with competitive life strategies (cluster III), all being problematic weeds in agricultural fields. Two of three species were characterised by modest or high nectar production and all had the ability to form arbuscular mycorrhiza associations. Another group of species with competitive traits, the competitive-ruderals, where on the other hand found where competition was the highest, within the oat row. This group was characterised by high SLA, ability to form arbuscular mycorrhiza associations and rather low nectar production (cluster II). A larger group of relatively low-growing species with mainly ruderal life strategy (cluster I), mainly found between crop rows, was associated with micro-habitats with intermediate disturbance and intermediate to high competition, primarily from the main crop but also from the service crop. The service crop had the clearest effect within the oat row.

Environment-trait associations

The arable plant species found in the oat row (the micro-habitat with the lowest disturbance and relatively high competition) had lower requirements for soil disturbance and light, and higher requirements for moisture, than species commonly found between oat rows, i.e. encountering intermediate disturbance (Figs. 2 and 3, cluster II). The arable plant community shifted gradually with distance from the row, a shift that was greater with more intensive disturbance, towards more light-demanding species. The difference in soil moisture demand could be due to that species which establish between crop rows established later in the season, after row-hoeing, when the soil generally has dried out more. These findings reflected characteristics expected for species

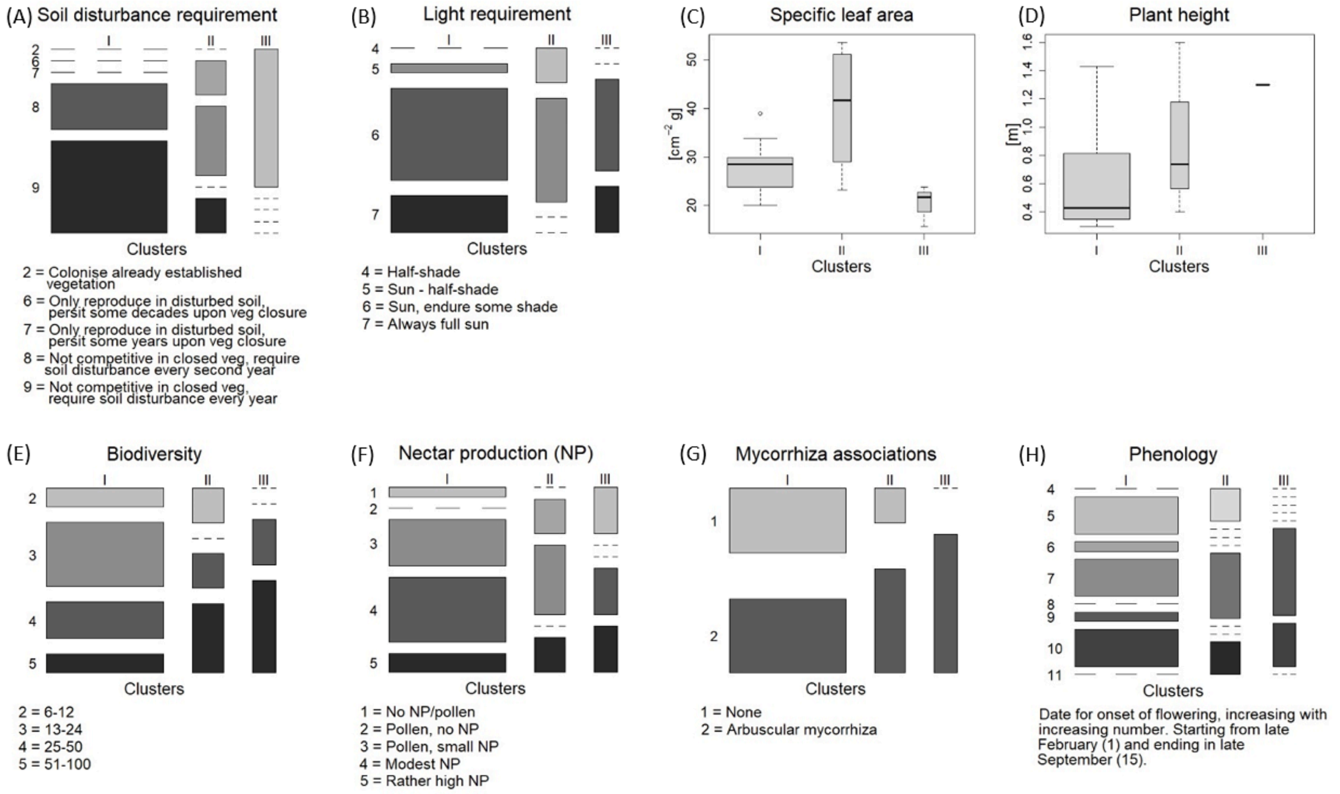

Fig. 3. Composition of species traits in the three species clusters (I-III) identified in RLQ analysis (see Fig. 2C). Same shade of grey indicates same category value within a plot, box length indicates proportion of the species with a certain score, and box width indicates the size of the cluster.

growing in these different locations. The most disturbed environment, i.e. inter-row centre, was an outlier with regard to soil disturbance, showing a strong association with competitive perennial species (Figs. 2 and 3, cluster III). These species commonly associated with undisturbed soils (Trichard et al., 2013) and have been shown to be suppressed by repeated low-intensity mechanical disturbance in standing crops (Bergkvist et al., 2017; Thomsen et al., 2015). However, the row-hoeing performed in the present study, operating just below the soil surface, may have stimulated production of new shoots, as the deeper roots or rhizomes, which store much energy, were not affected and could have supported regrowth. More frequent in-season disturbance would probably have been needed to reduce shoots of perennials, as shown by Thomsen et al. (2015). Our results suggest that shallow in-season disturbance has a greater effect on annual than perennial species in the short-term.

With increasing competition from oats, micro-habitats became less associated with the small cluster of competitive species (cluster III) and mainly associated with the more species-rich cluster I. This supports previous findings that increased competition from the main crop mainly suppresses dominant arable plants (Gaba et al., 2018). Similarly, intercropping with a service crop has been shown to greatly reduce biomass of the most dominant arable plants, with less effect on rarer species (Taab et al., 2023). Competition also efficiently suppresses perennials (Brandsæter et al., 2012; Ringselle et al., 2017), such as those found in cluster III. In our study, low to intermediate crop growth was mainly seen in the dry year of 2018, and at one site the year after. This could also explain why the perennial species had an advantage, potentially sourcing for water at greater depths. The effect of inclusion of a service crop was mainly seen within the oat row, where species in cluster II dominated (squares in Fig. 2A) and to some extent at low oat biomass (small symbols in Fig. 2A), indicating that the service crop used niche spaces mainly occupied by competitive and competitive-ruderal species. Poor crop growth could also be a result of high competition from arable plants. Our analysis only show which environmental factors are associated with which arable plant traits, but explains less about what is the cause and response relationship.

Micro-habitat selection for desired arable plants

No species cluster simultaneously scored low on traits associated with competition and high on traits associated with ecosystem services (Fig. A1). Instead, the cluster with perennial competitive species (III), which are considered problematic in crop fields, scored highest on the assessed service traits. However, all species detected in the experimental plots scored high on at least one service-providing trait, supporting the claim that higher diversity of species provides more services to the agroecosystem (Gaba et al., 2020). In the present study, all micro-habitats associated with cluster I species do not necessarily have high diversity, it only indicates that a wider range of species were found in locations with similar environment. Moreover, the results provide an indication of whether species with potential for service provision were favoured or not, but actual provision of services is more complex and would require in-field determination of traits and service provision (e.g. Storkey, 2006).

All species identified scored intermediate or high on nutrient demand, including species such as *Stellaria media* L. (STEME), *Viola arvensis* Murr. (VIOAR) and *Veronica* sp. (VERSS) that cause small, if any, crop yield losses. This implies that traits other than high nutrient demand, such as plant size and growth rate, need to be taken into account to gain a better understanding of species competitiveness, specifically traits associated with access to light (DeMalach et al., 2016) and competition for water (Sauter et al., 2021).

Micro-habitats had a greater effect on specific species than on trait composition

Specific species (Fig. 2C) showed more pronounced associations with micro-habitat characteristics than species traits did (Fig. 2D-F), indicating that management had a greater effect on species composition than on trait composition. The similarities in traits may be a result of strong previous selection for traits in the intensively managed crop fields, surrounded by other crop fields and hence low diversity in terms other habitats, at the experimental sites. Strong selection pressure such as soil tillage and herbicide application have a great impact on arable plant community trait composition over time (Bàrberi et al., 2018; Fried et al., 2012). Only species with life cycles, reproductive strategies and habitat requirements (light, nutrients and soil moisture) that fit with crop management practices can establish viable populations in crop fields (Alignier et al., 2020; Fried et al., 2009). The species found in the present study are well-known in crop fields in Europe (Goerke et al., 2008; Salonen et al., 2001), and generally showed high affinity to nutrient-rich soils and high light requirements. In the database of 240 arable plants found in Europe (Bàrberi et al., 2018), only two, 10 and 12 species are classified as having a stress tolerant, competitive-stress tolerant and stress tolerant-ruderal life strategy, respectively, while 30, 60 and 85 species are classified as having a competitive, ruderal and competitive-ruderal life strategy, respectively. This over-representation of competitive and especially ruderal species in crop fields in general, could explain the proportions of life strategies found among species in this study. Re-establishing rare species in crop fields might require other conditions than those in our studied fields. Lang et al. (2021) concluded that rare species established best on low fertility land and land with low competition from the crop and other arable plants.

The three species clusters were well separated according to Grime's life strategies. This indicates filtering in relation to species characteristics, but that combinations of different traits rather than specific ones were important for which type of species that were favoured in different micro-habitat. However, the division of species according to six life strategies does not fully separate between species that are problematic in agricultural fields and those that are not, e.g. *Tripleurospermum inodorum* (L.) (MATIN) that can cause great yield losses and *V. arvensis* (VIOAR) with small impact on yield are both ruderals. Grouping of species on a finer scale with focus on their impact on crops would be useful in analysing agroecosystems.

Traits such as height and SLA might vary among individual plants as a consequence of environment, e.g. competition, or ecotype of a species and hence database trait data has to be interpreted with caution. For the purpose of this study, these general traits were considered satisfying, but assessing the effect of crop competition and/or mechanical disturbance on actual trait expression would provide a deeper understanding of how the species community trait composition can be modified.

Conclusion

We used RLQ analysis to assess how management-induced niche heterogeneity, posed by differences in crop competition and soil disturbance, influenced the arable plant community in terms of species and their traits. RLQ analysis is a multivariate method that connect predefined environmental variables and traits, either numerical or factorial, through data on species abundance (numbers of individuals, cover or biomass). The analysis revealed logical associations between some species traits and the defined micro-habitats, e.g. high SLA associated with species in the crop row and more light demanding species between crop rows. The species were clustered according to the different management pressures, which were well separated by Grime's life strategies; characteristics based on combinations of traits. The grouping of Grime's life strategies used in this paper are, however, too broad with regards to the species they include, especially the ruderals, to be a good indicator of if less harmful species are selected for. Intermediate levels of both competition and disturbance mainly reduced the occurrence of few but competitive species and was instead associated with a larger group of ruderal species, which is in line with other studies on arable plant communities. These findings suggest that competition from crops and intermediate in-season disturbance appear to be promising measures to shape the arable plant community towards less competitive species. However, the low variation in species traits found in this study, indicates that to achieve greater changes in the trait composition of arable plant communities, low-intensity management should be combined with management of the surrounding environment, which has a large effect on the species occurring in crop fields (Alignier et al., 2020), to enhance species pool diversity.

Multivariate analysis is often used when analysing the impact of management practices on the arable plant community, and including trait data already in the analysis would help in interpreting the results. More specific species characteristics based on trait combinations and their impact on crops would, however, improve the usefulness of this method in an agricultural context.

CRediT authorship contribution statement

Elsa Lagerquist: Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Göran Bergkvist:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization. **Alexander Menegat:** Writing – review & editing, Supervision, Methodology, Conceptualization.

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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Data availability statement

Data are available via Zenodo https://doi.org/10.5281/zenodo.10054561 and https://doi.org/10.5281/zenodo.15667616.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.baae.2025.06.004.

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