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Trajectories of weed communities explained by traits associated with species' response to management practices

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ABSTRACT

Two large-scale weed surveys conducted on winter wheat crops in France in the 1970s and the 2000s were used to determine the influence of management on weed communities. A trait-based approach was used to identify the mechanisms associated with the changing status of arable weeds over a 30 year period.

A three-table ordination method (RLQ analysis) of the data set was performed to relate the environmental table to the species trait table using a species composition table to extract the joint structure (synchronic analysis). We then conducted a diachronic analysis to investigate the relationship between traits, alone or in combination, and the changing status of weeds.

The synchronic analysis showed that tillage intensity filtered weeds according to height, seed weight, life forms and dispersal. Conversely, herbicides selected for species with delayed germination, which allows them to escape herbicide treatments. The diachronic analysis showed that successful weeds that have expanded were small plants, with rather light seeds, that can germinate over a long time frame during the vegetative period. This trait syndrome was probably favoured by profound changes in crop rotation and by increasing herbicide pressure. Our approach provides an excellent example of how future shifts in weed communities can be predicted and hence how weed management can be adapted so as to avoid promoting selection of problematic weeds.

1. Introduction

The dramatic changes in composition and richness of arable weed communities following changes in crop husbandry since the 1950s are now well documented in Europe (Baessler and Klotz, 2006; Fried et al., 2009a). Following the review by Booth and Swanton (2002), who proposed to use community assembly rules as a tool in weed science, recent efforts have aimed to characterise specific management practices that act as filters, selecting for weeds according to their functional traits that respond negatively or positively to selection pressure. For instance, in winter wheat fields, a trait syndrome of short stature, large seed and late flowering has been identified as typical of species in decline since the 19th century (Storkey et al., 2010). In the flora of sunflower fields in France, changes since the 1970s are marked by the increase of tall, nitrophilous, late germinating and late flowering species (Fried et al., 2009b). In glyphosate-resistant cropping systems, perennial species and annuals with late germination and short intervals between recruitment and anthesis are more frequent (Gulden et al., 2010). Although studies using trait-based approaches in arable agroecosystems have increased in recent years (Lososová et al., 2006; Storkey, 2006; Gunton et al., 2011), to date, only a small number of traits have been tested on large spatial and temporal scales. Traits are measurable properties of individuals that relate to their functioning and modulate their fitness (Violle et al., 2009); they therefore help to capture the interactions between organisms and their environment (both abiotic and biotic) and bring a functional perspective to the study of biodiversity and how functional biodiversity affects processes at higher levels of organisation (Garnier and Navas, 2012).

In this study, the response of weeds to agricultural practices was investigated by quantifying the relationships between weed traits and environment in winter wheat fields. In this synchronic analysis, we focused particularly on the relative impact of tillage systems, herbicide management and crop rotation. In a second step, we asked to which extent species with the same status (increasing

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vs. decreasing) share the same traits using a 30-year diachronic analysis. The hypothesis here is that the frequency of weeds with response traits (*sensu* Lavorel and Garnier, 2002) adapted to management factors will increase, while the frequency of weeds with one or more response traits not adapted to these management factors will decrease. To summarise, the following questions were addressed: (1) What are the links between management practices and weed traits? (2) Are there any trait syndromes associated with the increase or decrease of certain weed species in response to management practices? (3) Can this (these) trait syndrome(s) explain the changes that have been observed in the weed flora of winter wheat fields in France since the 1970s?

2. Materials and methods

Vegetation data were extracted from two national large-scale weed surveys conducted in France during the 1970s and the 2000s. The first survey was done between 1973 and 1976 and sampled a total of 2170 fields (Barralis, 1977), of which 768 were winter wheat fields representative of the main production areas under oceanic climate in north-western France (cf. Appendix A in Supplementary Materials). In this dataset, only the frequency and mean abundance of the 32 most frequent weed species were available. Data from the *Biovigilance Flore* survey (Fried et al., 2008) were used for the 2003–2006 period which involved 816 winter wheat fields out of the 2773 fields available and 206 weed species.

The weed sampling strategy was similar in both surveys (for more details, see Barralis, 1977 and Fried et al., 2008). In each surveyed field, a comprehensive vegetation record was carried out on a 2000 m^2 plot (50 × 40 m), positioned at least 20 m from field boundaries to avoid field edge effects. For each record, two or more trained persons walked across the surveyed area for a minimum of 20 min recording all species observed until no new species were found. Species abundance was recorded using six cover abundance classes, adapted from Barralis (1976), i.e.+ = 1 individual/2000 m^2; 1 = <1; 2 = 1–2; 3 = 3–20; 4 = 21–50; 5 = >50 individuals/m^2. The frequency of individual species for each period was the ratio between the number of fields where a species was found and the total number of fields sampled in the survey.

2.1. Management practices and environmental data

Seven management variables were included in the analysis. The ‘Preceding Crop’ included winter cereals (mainly *Triticum aestivum*, *T. durum* and *Hordeum vulgaris*), winter oilseed rape (*Brassica napus*), sugar beet (*Beta vulgaris*), spring pea (*Pisum sativum*), maize (*Zea mays*) and sunflower (*Helianthus annuus*). Herbicide use was described by three variables: the treatment frequency index (TFI) that corresponds to the sum of the ratio of the applied dose to the recommended dose of all the treatments applied in a year, the number of active ingredients and the number of HRAC groups (herbicide classification according to primary site of action). Three kinds of tillage systems were distinguished: no tillage (NT, i.e. implementing direct drilling), minimum tillage (MT), which consists in only chiselling the soil, and conventional tillage (CT), including tilling the soil with mouldboard plough followed by one or more harrow and/or cover-crop passage(s). Tillage depth and sowing date were the two final management variables.

Environmental conditions were described by four variables representing two categories: (1) the soil condition group incorporated soil pH and soil texture (clay, clay loam, sandy clay, silt loam, silty clay, sandy loam and sand) and (2) the climatic conditions which included the mean annual temperature and rainfall over the 30 years separating the two surveys.

2.2. Trait data

Eight traits and two functional types were chosen to differentiate the response of weeds pertaining to various aspects of plant functioning in agricultural fields (Table 1). The traits include the three traits of the Leaf–Height–Seed (L-H-S) strategy scheme (Westoby, 1998): (a) Specific Leaf Area (SLA, the ratio of leaf surface to leaf dry mass) is particularly important because it is directly related to plant resource economy (Wright et al., 2004); (b) plant height (Ph) depicts species’ carbon gain with respect to the plants’ ability to compete for light (Westoby et al., 2002), explaining most of the variation in growth reduction observed in competing individuals (Violle et al., 2009) and (c) seed weight (Sw) is the result of a trade-off between producing a few large seeds, each with a high probability of a successful establishment, and producing many small seeds, each with a low probability of establishing (Moles and Westoby, 2006). Traits associated with persistence in disturbed habitats, such as the mode of species dispersal and phenological traits (Noble and Gitay, 1996; Gunton et al., 2011), were also included: germination start (Germ. st.), germination duration (Germ. rg.), flowering onset (Flow. on.) and flowering duration (Flow. dr.). Together with these eight traits, Raunkiaer’s life forms (therophytes: Th., geophytes: Geo., hemicryptophytes: Hcr.) were considered because this plant classification has been successfully used to illustrate the response of weeds to the level of soil disturbance by tilling systems (Zanin et al., 1997). Finally, the classical distinction made in weed science between broadleaf (Bl.) and grass (Gr.) weeds was included.

Phenological traits were coded using month as a unit. Since the germination date of weeds is related to the sowing date of winter wheat (Gunton et al., 2011), it was coded from 1 corresponding to October, when winter wheat is sown, to 12 corresponding to September, just before the next crop is seeded. The same month-scale unit was used for germination duration. Flowering phenology was coded from 1 (January) to 12 (December). Three broad classes of seed dispersal were distinguished: by animals, by gravity or by wind. To avoid unbalanced classes, all the different types of animal dispersal modes were merged into one animal dispersal class. This grouping did not significantly change the results (data not shown). The units of the traits are given in Table 1. Missing values were replaced by average value of the traits (for nine species for Sw and for two species for SLA).

2.3. Data analyses

First, the direct relationship between management practices and weed species traits was investigated using a modern ordination method: the RLQ approach. The RLQ analysis was developed to study environmental filtering in ecological communities (Doledec et al., 1996) by elucidating combinations of traits that have the highest covariances with combinations of environmental characteristics. Recent applications of the RLQ approach include the analysis of community response to grazing (Saatkamp et al., 2010), land-use intensity (Lienin and Kleyer, 2011), or the effect of changes in agro-pastoral management on calcareous grassland communities (Drobnik et al., 2011).

The RLQ analysis is an extension of co-inertia analysis that performs a double inertia analysis of two arrays: the R-table (the sites described by the environmental descriptors table) and the Q-table (the species described by the ‘traits’ table) with a link expressed by a contingency table: the L-table (the sites described by species table). For this analysis, we used a subsample of 218 fields of the *Biovigilance Flore* survey, for which all environmental and management practices were available. The representativeness of these 218 subsamples was assessed based on their geographical distribution (cf. Appendix A in Supplementary Materials) and on the relative