Impacts of Land Abandonment on Vegetation: Successional Pathways in European Habitats

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Abstract Changes in traditional agricultural systems in Europe in recent decades have led to widespread abandonment and colonization of various habitats by shrubs and trees. We combined several vegetation databases to test whether patterns of changes in plant diversity after land abandonment in different habitats followed similar pathways. The impacts of land abandonment and subsequent woody colonization on vegetation composition and plant traits were studied in five semi-natural open habitats and two arable habitats in six regions of Europe. For each habitat, vegetation surveys were

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carried out in different stages of succession using either permanent or non-permanent plots. Consecutive stages of succession were defined on a physiognomic basis from initial open stages to late woody stages. Changes in vegetation composition, species richness, numbers of species on Red Lists, plant strategy types, Ellenberg indicator values of the vegetation, Grime CSR strategy types and seven ecological traits were assessed for each stage of the successional pathway. Abandonment of agro-pastoral land-use and subsequent woody colonization were associated with changes in floristic composition. Plant richness varied according to the different habitats and stages of succession, but semi-natural habitats differed from arable fields in several ecological traits and vegetation responses. Nevertheless, succession occurred along broadly predictable pathways. Vegetation in abandoned arable fields was characterized by a decreasing importance of R-strategists, annuals, seed plants with overwintering green leaves, insect-pollinated plants with hemi-rosette morphology and plants thriving in nutrient-rich conditions, but an increase in species considered as endangered according to the Red Lists. Conversely, changes in plant traits with succession within the initially-open semi-natural habitats showed an increase in plants thriving in nutrient-rich conditions, stress-tolerant plants and plants with sexual and vegetative reproduction, but a sharp decrease in protected species. In conclusion, our study showed a set of similarities in responses of the vegetation in plant traits after land abandonment, but we also highlighted differences between arable fields and semi-natural habitats, emphasizing the importance of land-use legacy.

Keywords Arable field · Natural forest regeneration · Secondary succession · Semi-natural habitat

Plant nomenclature Jäger and Werner (2002)

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Introduction

Changes in land use over recent decades have influenced habitat and vegetation composition in most regions of Europe (Poschlod et al. 2005; Stoate et al. 2009). After World War II, agriculture intensified in productive areas whereas areas that did not allow mechanized agricultural techniques were abandoned. The most obvious effect of this land abandonment was the colonization of previously open landscapes by trees and shrubs, which were often of high biological and aesthetic value and considerable recreational potential (Young et al. 2005). Thereby, the role of these areas as reservoirs of biodiversity changed. Many plant species restricted to habitats such as grassland, meadow, heathland or dune grassland are dependent on traditional land-use disturbance regimes (Gustavsson et al. 2007; Römermann et al. 2009). The management regime governing these semi-natural habitats is a major factor that affects the reproductive success of single plant species and whole vegetation patterns (Bakker 1989). Different management regimes create particular disturbance regimes in space and time, which in turn provide conditions for a particular set of plant species with a particular set of interactions between species (Bakker 1989; Pykälä 2000). The different management regimes thus represent key drivers for biodiversity in agricultural landscapes (Poschlod et al. 2005).

Abandonment of traditional management can lead to a decrease in species richness by changing habitat conditions and competitive regime within the assemblage of plant species (Grubb 1977; Huston 1979; Bignall and McCracken 1996; Provoost et al. 2004; Dölle et al. 2008; Römermann et al. 2009). However, most studies on the impact of land abandonment on species diversity have focused on a single type of vegetation, stage of succession or region, making it difficult to compare results. Taking the example of grasslands, several studies found a decrease in species diversity with land-use abandonment (e.g., Smith and Rushton 1994; Pettit et al. 1995) while others found the effects, if any, were only minor (e.g., Bossuyt et al. 2006; Peco et al. 2006). Obviously, plant diversity can be more strongly affected by other factors, such as the biogeographic species pool, land-use history, type of management or processes like bush encroachment (e.g., Gustavsson et al. 2007; Stadler et al. 2007).

Species identity differs between regions and/or habitats, making it difficult to run cross-comparisons between studies. Functional traits of plant species offer a way to compare studies even across biogeographic realms. Plant traits are linked to plant function and provide insight into the key processes driving vegetation changes (Lavorel and Garnier 2002; Lavorel et al. 2007).

Our study combined several large databases on vegetation succession after abandonment in various European habitats submitted to traditional agricultural practices: calcareous grassland and heathland (the Netherlands), coastal dune grassland (Belgium), mid-elevation grassland (central France), alpine pasture (Austrian Alps) mainly submitted to grazing, and arable fields annually ploughed (Germany). Successions considered in our study were characterized by former agro-pastoral land use, either intensive (arable fields) or extensive (semi-natural habitats). Land abandonment occurred in the past decades and led to a succession towards natural vegetation. Overall, our study addressed the following questions:

i) What are the main changes in the dynamics, composition and richness of plant community assemblies after abandonment?

ii) Based on functional traits, do post-abandonment plant communities assemble along a broadly repeatable successional pathway or exhibit different pathways (Cramer et al. 2008; Bernhardt-Römermann et al. 2008)?

iii) If so, what are the plant trait changes shared by all types of habitats, and what are those mainly determined by prior land use?

Material and Methods

Database

Our study is based on vegetation surveys performed in six different regions across Europe (Table 1 and Electronic Supplementary Material 1 for sites description). The habitats used for the surveys can be split into semi-natural habitats with a long history of agro-pastoral land use (grassland, heathland), and arable fields. These habitats were traditionally used for crops (arable fields), grazing only or in combination with mowing and sod-cutting (grassland, heathland).

In each of these habitats, vegetation surveys were carried out using either permanent plots (arable fields, alpine grassland) or non-permanent plots (other habitats; Table 1). For each survey, we distinguished stages of succession describing the plant community succession after abandonment of the management regime. We defined four stages of succession according to the dominant life forms, grasses, shrubs and trees:

I.   Initial stage, referring to the community present under traditional land use.
II.   Grass stage, dominated by graminoid species with tree or shrub cover <30%.
III. Scrub stage, dominated by woody phanerophytes 0.5 to 5 m tall, with cover >30% and tree cover remaining below 30%.
IV.   Woodland stage, dominated by trees at least 5 m tall and covering at least 30% of the surface area.

The number of stages of succession for each survey varied between 2 and 4, reflecting the difference in the initial community composition, propagule pressures, site conditions and time elapsed since abandonment.

Analysis of Vegetation Composition

Plot size differed between surveys (Table 1). Furthermore, vascular plants were recorded in each plot and abundance-dominance was estimated by eye using various scales.

Previous studies had repeatedly shown that analyses of plant traits or indicator values weighted by abundance showed little difference from studies using simple presence-absence data (Schaffers and Sýkora 2000; Dzwonko 2001, but see Cingolani et al. 2007). We therefore recoded all cover-abundance data to presence/absence to enable our analyses to minimize the impact of methodological differences among studies.

Changes in plant composition from stage (I) to a later stage were analyzed as follows:

1.   We selected the species we recorded in more than 5% of the relevés belonging to a particular stage of each survey. This threshold was chosen to exclude rare species.

Table 1 Main characteristics of sampling protocols and successional pathways for the different field case studies

Type of vegetation	Study area: location	Sample* characteristics	Successional pathways: stages sampled Time elapsed since land abandonment (yr) and number of plots (n)				Data sources (references)
			Initial (I)	Grass (II)	Shrub (III)	Woodland (IV)	
Calcareous grasslands	Province of Limburg (NL) 50°50'–5°41' 50°54'–6°09'	n=747 NP s=1–100	Yes n=467	Yes 5–10 yr n=208	Yes 15–20 yr n=72	No	Dutch National Vegetation Database
Low-elevation heathlands	Province of Drenthe (NL) 52°45'–6°13' 52°55'–6°50'	n=1,021 NP s=4–80	Yes n=434	Yes 5–15 yr n=393	No	Yes 30–35 yr n=194	Dutch National Vegetation Database
Dry and moist dune grasslands	Flemish coast Belgium 51°05'–2°32' 51°21'–3°22'	n=1,282 NP s=4–250	Yes n=758	Yes 3–10 yr n=67	Yes 10–30 yr n=404	Yes >30 yr n=53	Vlavedat (INBO-vegetation database from Flanders, Belgium)
Alpine pastures & meadows	Enns Valley, Styria, Austrian Alps 47°38'–14°06'	n=12 P s=50–100	Yes n=6	Yes 3-5 yr n=6	No	No	Not published

Table 1 (continued)

Type of vegetation	Study area: location	Sample* characteristics	Successional pathways: stages sampled Time elapsed since land abandonment (yr) and number of plots (n)				Data sources (references)
			Initial (I)	Grass (II)	Shrub (III)	Woodland (IV)	
Mid-elevation grasslands	Chaîne des Puys (Massif central, France) 45°46′–2°58′	n=340 NP s=25–400	Yes n=125	No	No	Yes 30–35 yr n=215	Coquillard 1993; Prévosto 1999
Arable fields	Halle, Saxony- Anhalt (Germany) 41°30′–12°10′ 51°23′–11°52′	n=125 P s=4	Yes n=65	Yes 3–18 yr n=60	No	No	Stadler et al. 2007

*Sample characteristics (n - number of relevés, P/NP - permanent/non permanent plots, s - size in m^2)

2. We compared with species present in the relevés of the following stage and identified each species according to the following criteria:

   a) 'Extinct': species whose numbers had fallen to <1%.
   b) 'Loser': species whose numbers had fallen by >40%.
   c) 'Stable': species whose numbers had risen or fallen by <40%.
   d) 'Winner': species whose numbers had risen by >40%.
   e) 'Newcomer': species initially absent, now in numbers >5%.

Furthermore, we included the conservation status of species in our analyses using Red Lists (when available). We counted all species of the different stages for each vegetation survey considered as 'critically endangered', 'endangered', 'vulnerable' or 'nearly threatened'. References for the Red Lists used are as follows: for Belgium, Biesbrouck et al. (2001); for Germany, Garve (2004); for Austria, Niklfeld and Schratt-Ehrendorfer (1999); for The Netherlands, van der Meijden et al. (2000); for France, Olivier et al. (1995).

Functional Traits

For comparison across study sites, we used the CSR plant strategy types according to Grime (1977). We used a simple method to rank these strategy types on a linear scale derived from Hill et al. (2002) in three dimensions, using the following convention:

C (competitor)	= (1,0,0);
S (stress tolerator)	= (0,1,0);
R (ruderal)	= (0,0,1);
SR (stress-tolerant ruderal) = (S + R)/2	= (0,0.5,0.5);
CSR (completely intermediate) = (C + S + R)/3	= (0.33,0.33,0.33)

Average C, S and R values were then computed for each relevé. Grime's strategy type was extracted from the BIOLFLOR Database (Klotz et al. 2002).

Ellenberg values (Ellenberg et al. 2001) are well established as surrogates for changes in environmental factors associated with plant communities (e.g., Persson 1980; van der Maarel 1993, Dzwonko and Loster 1997). Available Ellenberg indicator values for light availability (L), soil reaction (R), nitrogen availability (N) and soil moisture (F) for plants in every relevé were used to calculate the average indicator value of each relevé (sum of indicator values of species present in the relevé divided by the number of species for which an indicator value was available). Furthermore, we included seven plant traits extracted from the BIOLFLOR Database:

1. Raunkiaer life form, with five categories: chamaephyte, geophyte, hemi-cryptophyte, phanerophyte = (macrophanerophyte + nanophanerophyte), therophyte.
2. Type of reproduction, with four categories: 's' by seed/spore; 'ssv' mostly by seed and rarely vegetative, 'sv' by seed and vegetative, 'vvs' mostly vegetative, rarely by seed.
3. Vegetative propagation, with four categories: 'runner': lateral shoot with long thin internodes and adventitious roots; 'rhizome': subterranean or close to the

soil surface, mostly thickened shoot with short internodes, adventitious roots and cataphyllary leaves; 'root-shoot': adventitiously-rooted shoot growing from a main or lateral shoot; 'miscellaneous' for all other types.

4. Leaf anatomy, with three categories: 'scleromorphic': firm, stiff leaves with thickened epidermis and cuticula, but with mechanisms promoting water transport under beneficial conditions; 'mesomorphic': between scleromorphic and hygromorphic; and 'hygromorphic': delicate shade and semi-shade plants.

5. Leaf persistence, with four categories: 'v': spring green; 's': summer green; 'w': overwintering green; and 'i': persistent green.

6. Plant morphology, with three categories: 'erosulate': development of long internodes, leaves spaced at roughly equal intervals on the axes; 'hemi-rosette': single or repeated change between phases in which either long or short internodes develop, leaves either scattered or tightly packed at the shoot; and 'rosette': leafy shoots exclusively consisting of short internodes with all foliar leaves basally arranged to form a rosette.

7. Type of pollination, with three categories: 'wi': by wind; 'in': by insects; 'self': different types of self-pollination; 'div': other types of pollination.

Each species of each presence/absence-transformed relevé was assigned one of the trait categories. Frequency of each trait category was then computed per relevé across species. In a second step, the mean of the frequencies of all the relevés included in the given stages was calculated.

Statistical Analysis

To characterize the general pattern of vegetation dynamics occurring during succession, we used principal components analysis (PCA) employing the correlation matrix. PCA was performed on a data matrix composed of values for each trait category values (31 categories) recorded in the different stages of each site (altogether 21 stages). Calculations were run on ADE-4 software (Thioulouse et al. 1997). The pathway for a given site during succession was then assessed by drawing the pathway within the two-dimensional space from stage to stage.

In addition, comparisons among stages of a given habitat for species richness, mean Ellenberg and Grime values, and ecological trait values were evaluated using ANOVAs followed by a multiple range test (Tukey test). Before each analysis, variance normality and homogeneity were checked, and when these conditions were not met, transformations were applied to approach the ANOVA assumptions. Otherwise, we used non-parametric Kruskall-Wallis tests.

Results

Species Richness and Composition

Species richness (= mean number of species per plot) did not show a consistent pattern of variation with succession (Fig. 1a). Species richness decreased for calcareous grasslands, alpine grasslands and in one case of arable fields (arable field
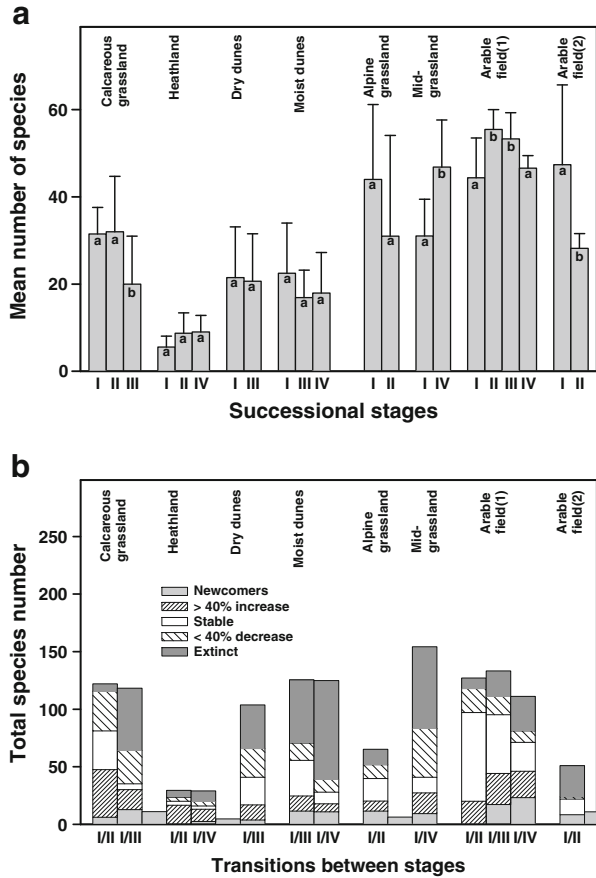
(2)) but increased for heathlands and mid-elevation grasslands. We found a hump-shaped relationship for arable fields (1) and no change in species richness in coastal dune grasslands. Floristic composition was more strongly affected by the transition to later stages of succession (Fig. 1b): the total number of 'stable' species per stage decreased with succession, while the proportion of other categories increased, and major shifts in plant composition occurred with shrub or tree colonization.

Species of the Red Lists

The total number of species on the Red Lists differed between semi-natural habitats and arable fields (Fig. 2). Semi-natural habitats showed a decrease due to disappearance of species dependent on open conditions and management regime, such as *Cirsium acaule*, *Briza media*, *Gentianella germanica* (calcareous grasslands), *Drosera rotundifolia*, *Andromeda polifolia*, *Eriophorum vaginatum* (moist heathlands), *Nardus stricta*, *Trichophorum cespitosum* (dry heathlands), *Blackstonia perfoliata*, *Gentianella amarella*, *Herminium monorchis* (moist dunes), *Koeleria macrantha*, *Thesium humifusum* (dry dunes). In contrast, arable fields showed a moderate increase followed by a decrease in arable fields (1). For instance, *Silene noctiflora* or *Euphrasia*

Fig. 2 Total number of species
of the stages of succession
appearing on Red Lists in the
different habitats
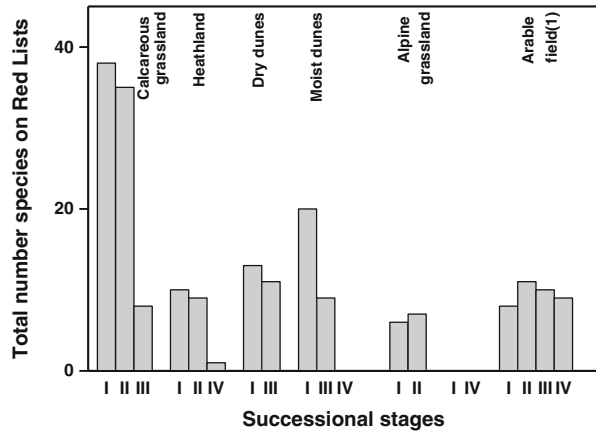
officinalis were found in the first stages but disappeared in the last stage of the succession, whereas species such as *Tanacetum corymbosum* predominantly growing at forest edges or in gaps was a newcomer in the second stage and remained stable throughout the succession. No species of the Red List were encountered in the mid-elevation grasslands of the French Massif Central, despite high species richness.

Functional Traits

Ellenberg Indicator Values

Ellenberg values for light decreased with succession at all sites (Fig. 3). Ellenberg values for nitrogen displayed contrasting responses between semi-natural habitats where values increased during succession, and arable fields where values decreased (arable field (1)) or remained unchanged (arable field (2)). Ellenberg indicators for soil reaction clearly decreased in calcareous grasslands and arable fields (1) but increased or remained stable in other habitats. Responses of Ellenberg values for soil moisture increased with succession in calcareous grasslands, dry coastal dunes grasslands and mid-elevation grasslands, but decreased or remained stable in the other habitats.

Grime CSR Strategy Types

Plant strategies according to Grime's classification differed largely through stages of succession, but showed a consistent response among the different habitats (Fig. 4). The competitors, which concerned more than half of the species of the early stages of succession, increased significantly with succession (except in alpine grasslands, not significant), whereas the ruderals declined with succession and the stress tolerators decreased only in semi-natural habitats.

Other Traits

Hemicryptophytes decreased with succession in semi-natural habitats, while phanerophytes logically increased in all habitats (Table 2). Therophytes, which are
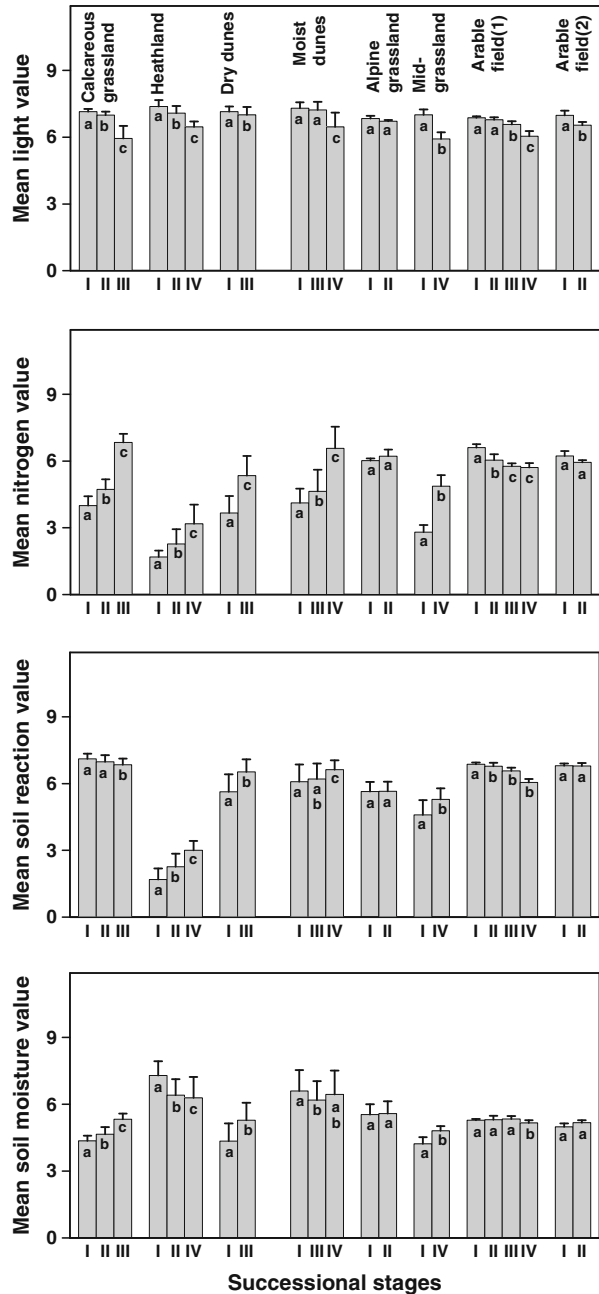
rare in semi-natural habitats, were common in the initial stages of arable lands, but fell sharply after land abandonment. Plants reproducing only by seeds increased with succession in semi-natural habitats but decreased in arable fields. Responses of the other reproduction groups were more variable. Vegetative propagation by lateral

Fig. 4 Plant strategies according to Grime's classification. We present average plot values for competitiveness (C), stress-tolerance (S) and ruderal type (R) for the different stages of succession. For a given habitat, different lowercase letters indicate statistical differences among stages (*P*<0.05). Bars indicate standard deviations
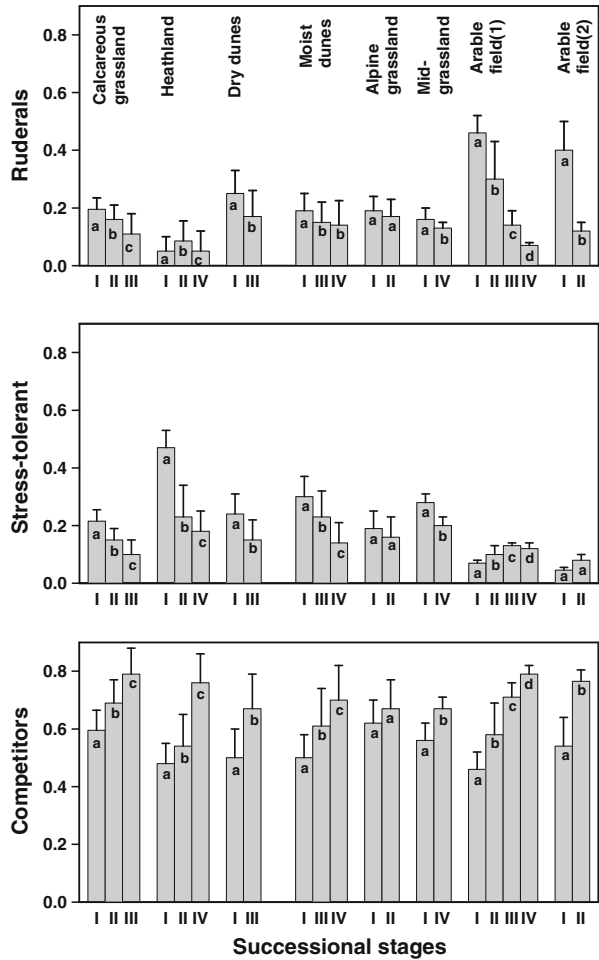
shoots with long thin internodes (runners) declined or remained stable with succession in semi-natural habitats, but increased in arable fields. Propagation by rhizomes was more common in semi-natural habitats, whereas root-shoot propagation became more frequent as succession progressed in all habitats. Mesomorphic leaf anatomy was clearly dominant in all the habitats and generally increased with succession (except for calcareous grasslands), whereas scleromorphic anatomy showed the opposite pattern. Hygromorphic leaf anatomy was of minor importance in initial stages but its importance increased in semi-natural habitats (calcareous grasslands), while it remained stable in arable fields. The relative number of species with persistent leaves decreased with succession in semi-natural habitats, whereas they peaked in intermediate stages in arable fields. Species with summer green leaves increased significantly in every habitat. In all the habitats, semi-basal species decreased with succession whereas basal leaf species decreased only in semi-natural habitats. Relative numbers of erosulate species increased with succession, sometimes remarkably, except in arable fields (1). The proportion of plants pollinated by wind

Table 2 Plant trait mean values (%) for the stages of succession in different habitats. For a given habitat, different lower case letters indicate statistical differences between the stages (P<0.05)

Semi-natural habitats

	Calcareous grass.			Dry & moist heath.			Dry dunes		Moist dunes			Alpine grass.		Mid-elev. grass.	
	I	II	III	I	II	IV	I	III	I	III	IV	I	II	I	IV
Life form															
Chamaephyte	2.3 (a)	2.3 (a)	1.6 (b)	0 (a)	3.3 (b)	1.9 (b)	7.3 (a)	8.2 (a)	1.0 (a)	1.2 (a)	3.2 (b)	5.7 (a)	4.0 (a)	17.3 (a)	9.8 (b)
Geophyte	8.6 (a)	8.7 (a)	7.1 (b)	6.0 (a)	4.6 (b)	1.7 (c)	11.7 (a)	12.8 (a)	20.3 (a)	20.4 (a)	9.7 (b)	5.0 (a)	9.3 (a)	3.3 (a)	10.9 (b)
Hemicryptophyte	81.1 (a)	75.8 (b)	43.3 (c)	43.6 (a)	47.8 (a)	22.2 (b)	72.2 (a)	52.6 (b)	62.2 (a)	53.5 (b)	49.0 (c)	83.7 (a)	78.3 (a)	67.9 (a)	48.7 (b)
Phanerophyte	4.4 (a)	10.6 (b)	45.2 (c)	29.0 (a)	31.5 (a)	68.2 (b)	6.3 (a)	23.0 (b)	9.8 (a)	19.8 (b)	27.4 (c)	3.3 (a)	4.3 (a)	11.3 (a)	29.8 (b)
Therophyte	2.5 (a)	2.6 (a)	1.5 (b)	0 (a)	2.0 (b)	3.8 (b)	2.1 (a)	1.6 (a)	2.5 (a)	0.5 (b)	1.3 (a,b)	1.7 (a)	3.7 (a)	0.2 (a)	0.8 (a)
Sexual reproduction															
Seed/spore	37.1 (b)	39.7 (b)	43.7 (c)	11.5 (a)	23.4 (b)	59.1 (c)	29.7 (a)	30.5 (a)	15.7 (a)	18.8 (a)	27.1 (b)	24.0 (a)	22.2 (a)	26.7 (a)	35.8 (b)
Mostly seed	21.0 (a)	21.0 (a)	12.7 (b)	35.9 (a)	27.5 (b)	13.7 (c)	15.1 (a)	10.8 (b)	8.91 (a)	7.67 (a)	18.2 (b)	16.8 (a)	21.4 (a)	16.0 (a)	9.1 (b)
Seed, vegetatively	38.5 (a)	36.9 (a)	40.7 (b)	44.5 (a)	44.5 (a)	23.9 (b)	49.3 (a)	53.3 (b)	68.4 (a)	65.6 (a)	48.5 (b)	53.8 (a)	49.6 (a)	49.4 (a)	50.6 (a)
Mostly vegetatively	3.3 (a)	2.2 (b)	2.7 (b)	8.0 (a)	4.5 (b)	3.2 (b)	5.44 (a)	3.84 (b)	6.81 (a,b)	7.34 (b)	4.60 (a)	4.7 (a)	5.4 (a)	3.0 (a)	2.6 (a)
Vegetative reproduction															
runners	46.8 (a)	44.2 (a)	46.6 (a)	57.0 (a)	47.6 (b)	35.7 (c)	49.3 (a)	44.5 (b)	54.3 (a)	52.2 (a)	38.4 (b)	55.3 (a)	52.3 (a)	41.8 (a)	29.4 (b)
rhizome	15.7 (a)	12.5 (b)	14.7 (c)	38.5 (a)	35.3 (a)	16.5 (b)	8.84 (a)	9.37 (a)	17.1 (a)	14.4 (b)	7.96 (c)	29.7 (a)	26. (a)	14.9 (a)	14.4 (a)
root shoot	12.8 (a)	18.1 (a)	26.2 (b)	2.8 (a)	17.0 (b)	47.7 (b)	5.21 (a)	10.1 (b)	4.84 (a)	8.82 (b)	12.0 (c)	3.4 (a)	4.2 (a)	5.5 (a)	7.2 (b)
Leaf anatomy															
Mesomorphic	75.0 (a)	78.5 (a)	65.9 (b)	22.8 (a)	42.7 (b)	77.0 (c)	53.4 (a)	65.4 (b)	54.4 (a)	60.8 (b)	71.7 (c)	71.5 (a)	71.8 (a)	50.1 (a)	67.1 (b)
Scleromorphic	22.0 (a)	15.8 (b)	8.4 (c)	47.6 (a)	34.8 (b)	13.7 (c)	41.6 (a)	24.5 (b)	22.5 (a)	23.0 (a)	9.13 (b)	11.4 (a)	10.4 (a)	42.1 (a)	23.0 (b)
Hygromorphic	1.4 (a)	4.2 (b)	25.0 (c)	0.0 (a)	1.7 (b)	2.5 (c)	1.01 (a)	4.69 (b)	8.24 (a,b)	5.68 (a)	9.27 (b)	12.7 (a)	13.2 (a)	0.2 (a)	5.3 (b)
Leaf persistence															
Persistent green	42.0 (a)	30.0 (b)	18.3 (c)	70.2 (a)	55.0 (b)	30.7 (c)	45.8 (a)	31.9 (b)	50.3 (a)	40.7 (b)	33.0 (c)	51.3 (a)	40.2 (a)	54.0 (a)	38.7 (b)
Summer green	55.5 (a)	67.2 (b)	70.9 (c)	29.8 (a)	45.0 (b)	69.2 (c)	39.1 (a)	53.9 (b)	41.0 (a)	49.7 (b)	54.6 (c)	44.7 (a)	52.0 (a)	39.9 (a)	56.0 (b)
Overwintering green	0.8 (a)	2.0 (b)	9.6 (c)	0.0 (a)	0.0 (a)	0.0 (a)	11.8 (a)	12.2 (a)	5.51 (a)	6.58 (a)	10.0 (b)	2.9 (a)	2.5 (a)	0.1 (a)	2.2 (b)
Plant morphology															
Rosette	11.2 (a)	4.2 (b)	2.6 (c)	18.6 (a)	17.6 (a)	7.8 (b)	11.2 (a)	8.54 (b)	10.5 (a)	12.7 (b)	8.81 (a)	9.5 (a)	9.5 (a)	5.7 (a)	7.1 (a)
Hemirosette	65.4 (a)	60.8 (b)	23.2 (c)	27.3 (a)	34.1 (b)	18.6 (c)	54.1 (a)	40.7 (b)	46.1 (a)	41.8 (b)	33.7 (c)	61.7 (a)	56.4 (a)	45.2 (a)	31.5 (b)
Erosulate	23.4 (a)	34.9 (b)	74.3 (c)	54.0 (a)	48.3 (a)	73.4 (b)	34.2 (a)	49.6 (b)	43.1 (a)	44.9 (a)	56.2 (b)	28.8 (a)	34.1 (a)	44.2 (a)	59.5 (b)
Pollination															
Insects	48.0 (a)	50.1 (b)	47.9 (a)	22.3 (a)	23.1 (a)	31.2 (b)	22.3 (a)	21.9 (a)	26.4 (a)	28.0 (a)	17.6 (b)	49.4 (a)	52.3 (a)	62.7 (a)	53.4 (b)
Self	18.2 (a)	20.4 (b)	26.7 (c)	12.1 (a)	9.1 (a)	10.0 (a)	31.4 (a)	43.0 (b)	31.1 (a)	32.4 (a)	39.4 (b)	20.9 (a)	20.0 (a)	5.6 (a)	14.9 (b)
Wind	31.3 (a)	26.2 (a)	21.7 (b)	63.6 (a)	66.6 (a)	58.7 (b)	45.3 (a)	32.8 (b)	41.0 (a)	38.0 (a)	39.3 (a)	20.2 (a)	19.1 (a)	31.8 (a)	31.7 (a)

Table 2 (continued)

Arable fields

	Arable fields (1)				Arable fields (2)	
	I	II	III	IV	I	II
Life form						
Chamaephyte	0.5 (a)	2.1 (b)	2.0 (b)	1.3 (c)	1.4 (a)	1.7 (a)
Geophyte	6.8 (a,b)	6.9 (b)	8.5 (a,c)	8.3 (a,c)	5.4 (a)	10.8 (b)
Hemicryptophyte	48.8 (a)	60.6 (b)	57.2 (c)	43.4 (a)	49.7 (a)	54.9 (b)
Phanerophyte	9.4 (a)	12.7 (a)	25.6 (b)	41.3 (c)	11.3 (a)	25.4 (b)
Therophyte	33.9 (a)	16.4 (b)	4.5 (c)	1.8 (d)	32.3 (a)	6.1 (b)
Sexual reproduction						
Seed/spore	65.4 (a)	49.1 (b)	37.4 (c)	40.4 (d)	71.2 (a)	41.0 (b)
Mostly seed	6.5 (a)	8.3 (a,b)	9.5 (b,c)	11.7 (c)	3.9 (a)	8.7 (b)
Seed, vegetatively	25.5 (a)	40.4 (b)	51.0 (c)	45.9 (d)	22.2 (a)	46.4 (b)
Mostly vegetatively	0.8 (a,b)	0.8 (b)	0.8 (b)	0.3 (a)	1.4 (a)	3.8 (b)
Vegetative reproduction						
runners	16.2 (a)	27.2 (b)	36.0 (c)	34.6 (c)	12.7 (a)	33.6 (b)
rhizome	2.5 (a)	4.7 (b,c)	4.5 (b)	5.9 (c)	0.4 (a)	6.5 (b)
root shoot	5.6 (a)	9.0 (b)	13.0 (c)	15.7 (d)	6.9 (a)	7.6 (a)
Leaf anatomy						
Mesomorphic	65.5 (a)	70.0 (b)	71.0 (b,c)	71.9 (c)	70.4 (a)	70.7 (a)
Scleromorphic	12.3 (a)	11.2 (a,b)	11.0 (a,b)	10.1 (b)	17.2 (a)	17.9 (a)
Hygromorphic	13.8 (a)	10.4 (b)	9.9 (b)	12.4 (a)	9.6 (a)	8.4 (a)
Leaf persistence						
Persistent green	19.7 (a,)	30.9 (b)	25.9 (a)	15.6 (c)	23.7 (a)	23.7 (a)
Summer green	47.7 (a)	48.7 (a)	66.2 (b)	78.6 (c)	47.8 (a)	67.0 (b)
Overwintering green	32.1 (a)	18.2 (b)	4.9 (c)	2.7 (d)	28.5 (a)	9.3 (b)
Plant morphology						
Rosette	46.1 (a)	40.9 (a)	52.6 (b)	67.1 (c)	4.6 (a)	3.6 (a)
Hemirosette	46.8 (a,b)	52.4 (a)	41.3 (b)	27.8 (c)	54.3 (a)	44.3 (a)
Erosulate	6.6 (a)	5.5 (a)	4.8 (a)	3.4 (b)	41.1 (a)	52.0 (b)
Pollination						
Insects	52.6 (a)	44.5 (b)	39.5 (c)	36.2 (d)	34.5 (a)	34.4 (a)
Self	32.8 (a)	39.4 (b)	42.3 (b)	39.9 (b)	49.0 (a)	40.7 (a)
Wind	11.1 (a,b)	12.4 (a)	14.9 (b)	19.7 (c)	16.5 (a)	29.0 (b)

generally decreased with succession in semi-natural habitats, whereas it decreased in arable fields. In contrast, the proportion of plants pollinated by insects decreased or remained stable in arable fields and showed a variable response in semi-natural habitats. Finally, self-pollination exhibited a more varied response depending on habitat type.

Succession and Changes in Plant Functional Traits

Results of PCA show that on its positive segment the first axis gathered plants with persistent, scleromorphic leaves, "runner" or "rhizome" types for vegetative reproduction, seeds as main type for sexual reproduction and pollinated by wind. In contrast, the negative segment of the first axis gathered plants with mesomorphic overwintering leaves, reproduction by seeds exclusively, and high Ellenberg values for soil reaction and nitrogen availability (Fig. 5a). This axis thus reflected a trophic gradient and a gradient of "naturalness" (land-use intensity), as it clearly separated the formerly extensively used, nutrient-poor heathlands from the intensively used, nutrient-rich arable fields. The second axis separated plants dominated by hemi-rosette morphology, hemicryptophyte form, ruderals and high Ellenberg light values (positive segment, Fig. 5a) from plants characterized mainly (negative segment) by an erosulate morphology, phanerophyte form, "root-shoot" vegetative reproduction, summer green leaves and competitors according to Grime's classification. Therefore, this second axis was linked to vegetation dynamics from open to woody stages, as it opposed the initial stages against the later, more mature stages.

Successional pathways taken as a whole were parallel for all semi-natural habitats along a direction from the top right to the bottom left corner (Fig. 5b), i.e., from an open to a more woody and nutrient-demanding vegetation. Pathways of arable fields showed a contrasting pattern, following a direction from the top left to the bottom left corner.

Discussion

Methodological Constraints

This study combined vegetation data from habitats largely differing in soil, climate and land-use history. Furthermore, the methods used to collect basic data differed considerably among studies. An important constraint is that we merged permanent and non-permanent plot studies that by nature provide information at different temporal and spatial scales. Nevertheless, both approaches provide information on the main patterns in the structure and dynamics of the development of the vegetation. The main criticism on the use of space-for-time substitution or chronosequencing is the assumption that each site in the chronosequence differs only in age and has experienced the same history in its biotic and abiotic components (Glenn-Lewin and van der Maarel 1992; Johnson and Miyanishi 2008). Although this is not always true, chronosequences provide a valuable approach for inferring many aspects of successional change (Foster and Tilman 2000). To handle the issues of combining permanent and non-permanent plots, we first divided the succession into stages based on physiognomy so that permanent and non-permanent plots provided a comparable level of information. Second, we tried to minimize the limitations associated with chronosequences (see Pickett 1989) by studying succession for each habitat on rather limited areas having comparable ecological characteristics, i.e., the same climatic and edaphic conditions and, to a large extent, similar history. With such precautions, permanent plots and chronosequences are comparable (Bakker et

al. 1996). A second constraint was the differences in protocols used to collect vegetation data like the number and size of plots. The use of different plot sizes – which is currently observed in most studies like ours gathering many relevés made by different authors at different times – can generate problems in vegetation patterns analysis (e.g., Otýpková and Chytrý 2006; Dengler et al. 2009). However, the use of different plot sizes to study successional changes is a function of the system studied. Smaller plots were used to sample vegetation in open habitats and larger ones are necessary to sample the woody vegetation (Chytrý and Otýpková 2003). To minimize the influence of variations of plot size, we have chosen to analyze the data at the stage level instead at the more variable plot level. Moreover it must be noted that plot size has often no influence on patterns of vegetation composition: Otýpková and Chytrý (2006) showed that patterns resulting from the ordination analyses of vegetation data patterns were not affected by large fluctuations of plot size, particularly in the analysis of heterogeneous vegetation types.

The use of plant functional traits allowed us to perform a global analysis combining habitats to detect general trends (Díaz et al. 2001). Nevertheless, the results can be influenced by the way plant traits are computed. We only used presence/absence of species and therefore we considered a first-level filtering process: species have a certain probability of being present or not (occurrence). This approach ignores a second-level filtering process that considers the probability of becoming dominant in cover abundance. We acknowledge that these two different ways of analyzing a trait-environment relationship do not always lead to similar results (Cingolani et al. 2007).

Species Composition and Richness: Profound Changes Due to Abandonment and Woody Colonization

As expected, land abandonment and subsequent colonization by woody species were associated with changes in floristic composition in all habitats studied. High species turnover has frequently been described after land abandonment through the different stages of succession, in particular when woody colonization has occurred (see for instance Harmer et al. 2001).

Initially species-rich, semi-natural habitats were more strongly affected by land abandonment, as illustrated with calcareous grasslands that showed a strong decrease in plant richness. This is in agreement with previous studies emphasizing the importance of land abandonment as a major cause for plant diversity decline.
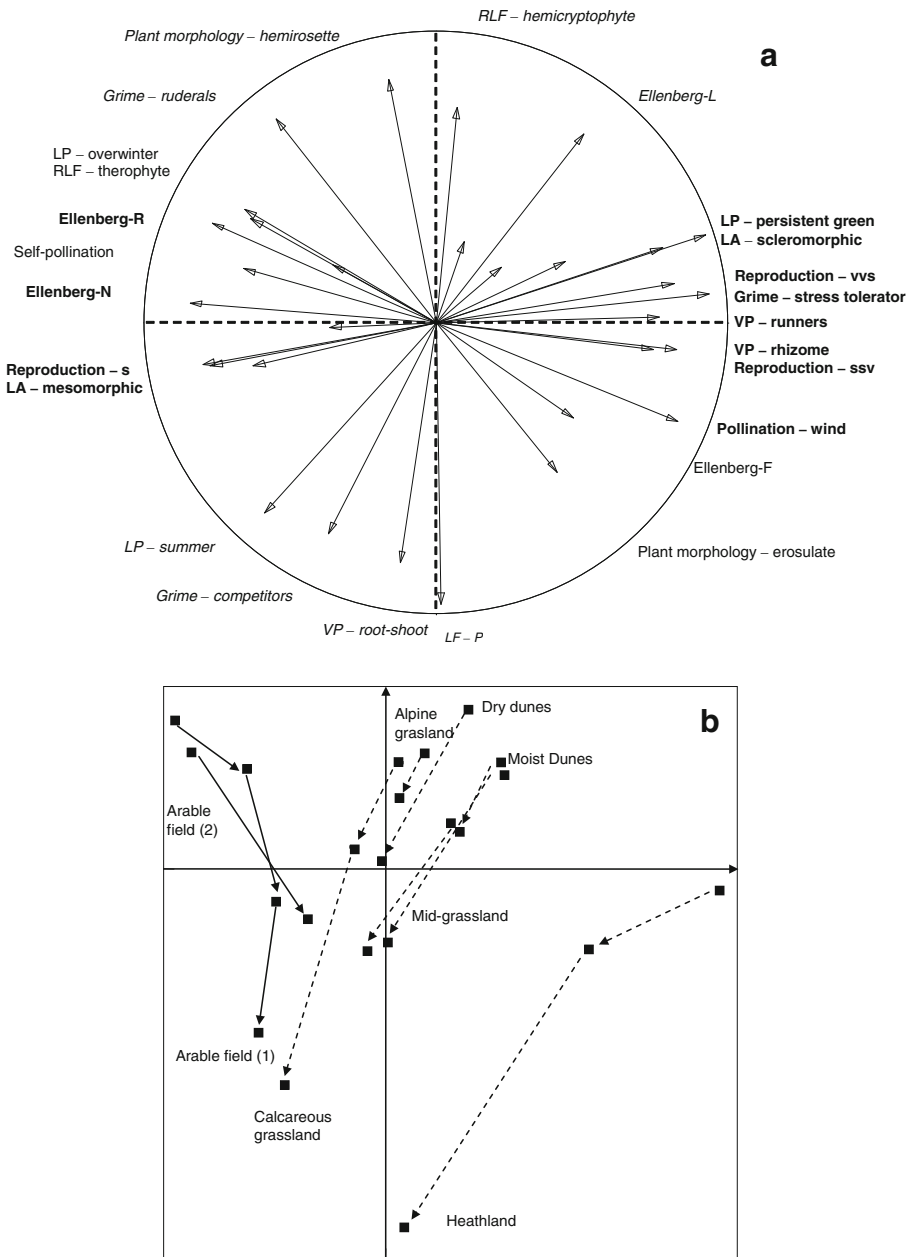
Cessation of traditional management practices (grazing, mowing) can lead to the accumulation of litter, which impedes seed germination and the establishment of seedlings (Foster and Gross 1997; Tilman 1997; Pärtel et al. 2005). The decrease in species richness in open meadow is also due to the increasing importance of nitrophilous, tall herbs and grasses that benefit from the increased nutrient availability after grazing abandonment (Krahulec et al. 2001). In contrast, in habitats

of low initial species richness (heathland, coastal grassland), the extinction of initial-stage species was counterbalanced by colonization by new species during later stages of succession leading to a stable trajectory of species richness in these habitats. Finally, the increase in species richness in mid-elevation grasslands may be explained by the high light availability in woody stages composed of birch or Scots pine facilitating the coexistence of semi-shade-tolerant species as well as heathland species (Prévosto 1999; Curt et al. 2003). Similarly, in arable field (1), the peak of species richness at mid- stages of succession before tree canopy closure was also due to the coexistence of different life forms and dispersal strategies (Harmer et al. 2001; Bonet and Pausas 2004; Dölle et al. 2008). In contrast, the decline of species richness in arable field (2) may be explained by the establishment of highly competitive non-woody species, which also prevented tree or shrub encroachment. Consequently, the idiosyncratic trajectories of species appear to be influenced by the species pool with its functional traits as well as local habitat conditions.

Species of the Red Lists: a Marked Decline in Semi-Natural Habitats

Semi-natural habitats were characterized by a major loss of biodiversity, highlighting the need for conservation of habitats with low-intensity land use (former agro-pastoral land use or some type of suitable replacement management practice), as already indicated by Provoost et al. (2004) for dry coastal dune grasslands. The increase in tree and shrub cover due to either natural regeneration or afforestation is recognized as one of the main threats to rare grassland species (Provoost et al. 2004; Pykäla et al. 2005).

By contrast, the low number of species on the Red Lists in arable fields may be explained by the rapid colonization of these habitats by perennial and woody plants, by the composition of the soil seed bank and by specific soil characteristics leaving little opportunity for patrimonial species to establish.

Plant Indicator Values and Plant Trait Changes with Succession: Similarities and Differences

The ecosystems studied here showed various succession pathways after land abandonment. Despite this variability, our results suggest that changes in plant traits and indicator values followed a similar general pattern (Fig. 5).

Similarities in Indicator and Trait Value Changes with Succession

Some plant trait changes are closely associated with response to vegetation dynamics following land abandonment, whatever the type of habitat. An obvious illustration is the expected increase in phanerophytes with succession due to tree or shrub establishment (e.g., Grime 1979; McIntyre et al. 1995; Bernhardt-Römermann et al. 2008). We also found a consistent response of leaf anatomy and persistence with succession as a result of shading conditions in late succession stages, in contrast to the full-light conditions of the initial stages.

Similarities can also be found in the changes in Ellenberg's and Grime's indicator values. Ellenberg values for light decreased during succession for all habitats, thus

quantifying the canopy closure by shrubs or trees that leads to a decrease in heliophilous plants and to an increase of semi-shade- and shade-tolerant species (Dölle et al. 2008).

Analysis of plant-strategy types according to Grime's CSR classification showed an increase in competitors and a decrease in ruderal species during succession in all the habitats. These changes were related to the decrease of disturbances after land abandonment, as disturbances are known to favour short-lifespan plants that reproduce rapidly, such as ruderals (e.g., Grime 1979; Noy-Meir 1995; Huisman et al. 1999).

Differences Between Semi-Natural Habitats and Arable Fields

Arable fields differed from semi-natural habitats by the relative importance of therophytes (mainly weeds). Reproductive strategies also differed between these two types of habitat: semi-natural habitats initially harboured more species reproducing vegetatively than arable fields. Vegetative reproduction may be an advantage for long-term persistence in undisturbed or moderately disturbed sites (Noble and Slatyer 1980; McIntyre et al. 1995). After land abandonment, species reproducing by seeds increased only in grazed sites and decreased in arable sites. Arable fields generally benefited from greater nutrient availability, thus sharpening competition in the course of succession. This would likely promote a strategy of vegetative reproduction favouring local spreading and devoting more resources to competing with neighbours (Bernhardt-Römermann et al. 2008; Dölle et al. 2008). This argument could also explain why runner species increased in arable fields but decreased in the semi-natural habitat succession.

Plant architecture plays an important role in the response of herbaceous species to disturbance (Lavorel et al. 1999; Römermann et al. 2009). Taxa that tend to have a basal position of leaves (rosette, hemi-rosette) are favoured by grazing and so regress in semi-natural habitats after land abandonment but progress in arable fields. In contrast, species characterized by leaves that are evenly spaced along the stem (erosulate) are generally grazing-intolerant (Dupré and Diekmann 2001) and therefore increase after land abandonment in semi-natural habitats.

The decrease in the importance of wind pollination with succession in semi-natural habitats was fully expected, given the shift from an initial open landscape to a closed woody landscape in which conditions are less favourable for wind pollination but better geared to self-pollination or insect pollinators (Culley et al. 2002). Arable fields exhibited a different response, but this difference from the semi-natural habitats may not be of great significance, as wind pollination is a minor process and is also affected by phylogeny (annual species are generally mostly self-pollinating (Aarssen 2000)).

Ellenberg and Grime's indicator values also showed contrasting responses depending on type of habitat. The increase in Ellenberg values for nitrogen, noted only for semi-natural habitats, can be explained by litter accumulation and subsequent mineralization, as well as by possible changes in mass and species composition of the soil biota after land abandonment (Archer et al. 2001; Ehrenfeld 2003). In contrast, decreasing N-Ellenberg values through the consecutive stages of succession in arable fields reflect the decrease in nutrient availability due to

cessation of the application of fertilizer or manure and subsequent natural soil acidification processes (Glatzel 1991).

Stress-tolerators sharply declined in semi-natural habitats but not in arable fields, highlighting the more intense competition regime in the arable habitats due to greater nutrient availability.

Variations in Plant Traits Among the Semi-Natural Habitats

As shown in Fig. 5b, semi-natural habitats show large variations among successional pathways, although the pathways are all oriented along the same direction. This result is the consequence of major differences in environmental factors and communities in these habitats. A clear illustration is given by successional pathway of heathlands, which differs strongly from the other semi-natural habitat pathways. Heathland vegetation actually shows more wind-dispersed species with scleromorphic persistent green leaves and phanerophytes than the other semi-natural habitats. These specificities reflect the impacts of specific disturbance regimes (extensive grazing) and specific environmental factors (particularly soils characterized by marked acidity and low fertility, as reflected by the corresponding mean Ellenberg indicator values).

Conclusion

Our study showed that succession occurred along a broadly predictable pathway, all habitats sharing a common set of plant traits and indicator values. The importance of land-use legacies is also highlighted, as we found some contrasting responses of the vegetation to land abandonment between initially semi-natural habitats – despite harbouring various ecosystems – and initially arable habitats. These differences in traits of plant species and their changes through succession reflect fundamentally different successional drivers between arable fields and semi-natural habitats. The vegetation assembly of most of the open semi-natural habitats is the result of a long co-evolution of plants and grazers leading to a set of plant species that can sustain ecological conditions of life in open areas subjected to regular disturbances (Zobel 1992). In contrast, the species pool of formerly arable lands was shaped by other types of disturbance and was deeply influenced by the nature and frequency of the agricultural management practices.

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