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Original article

Factors affecting plant species composition of hedgerows: relative importance and hierarchy

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Abstract

Although there has been a clear quantitative and qualitative decline in traditional hedgerow network landscapes during last century, hedgerows are crucial for the conservation of rural biodiversity, functioning as an important habitat, refuge and corridor for numerous species. To safeguard this conservation function, insight in the basic organizing principles of hedgerow plant communities is needed. The vegetation composition of 511 individual hedgerows situated within an ancient hedgerow network landscape in Flanders, Belgium was recorded, in combination with a wide range of explanatory variables, including a selection of spatial variables. Non-parametric statistics in combination with multivariate data analysis techniques were used to study the effect of individual explanatory variables. Next, variables were grouped in five distinct subsets and the relative importance of these variable groups was assessed by two related variation partitioning techniques, partial regression and partial canonical correspondence analysis, taking into account explicitly the existence of intercorrelations between variables of different factor groups. Most explanatory variables affected significantly hedgerow species richness and composition. Multivariate analysis showed that, besides adjacent land use, hedgerow management, soil conditions, hedgerow type and origin, the role of other factors such as hedge dimensions, intactness, etc., could certainly not be neglected. Furthermore, both methods revealed the same overall ranking of the five distinct factor groups. Besides a predominant impact of abiotic environmental conditions, it was found that management variables and structural aspects have a relatively larger influence on the distribution of plant species in hedgerows than their historical background or spatial configuration.

Keywords: Agricultural landscapes; Linear semi-natural habitats; Partial CCA; Partial regression; Variation partitioning; Vegetation composition

1. Introduction

With the emergence of the principles of landscape ecology and the parallel increase in interest for the human-shaped rural landscape, scientific attention for the composition, structure and functioning of the different types of farmland habitat constituting the rural landscape mosaic has been growing steadily (Forman, 1995; Marshall and Arnold, 1995; Kleijn and Verbeek, 2000; Freemark et al., 2002). Within these semi-natural habitats, a central place is taken by hedgerows or narrow bands of woody vegetation that separate adjacent fields (Forman and Baudry, 1984; Baudry et al., 2000). Besides recognition of their traditional functions as a boundary delineation structure, fence and source of a variety of wood and non-wood products (Burel and Baudry, 1990; Cherrill, 1996; Baudry et al., 2000), the importance of hedgerows for the maintenance of ecological diversity and the sustainability of agricultural productivity is increasingly emphasized (de Blois et al., 2002).

The linear semi-natural habitats of hedgerows and hedgerow networks found in various agricultural landscapes throughout the world typically form an essential part of the backbone structure of rural biodiversity, carrying a broad range of different fauna and flora species (Dover and Sparks, 2000; Hinsley and Bellamy, 2000; French and Cummins, 2001; Tattersall et al., 2002; Freemark et al., 2002). Moreover, in contemporary landscapes hedgerows often serve as a refuge for numerous species once widespread but now largely restricted to uncultivated field margins due to the process of agricultural intensification, resulting in a marked decline of those species in the surrounding landscape matrix (Stoate et al., 2001; Robinson and Sutherland, 2002). Furthermore, hedgerows can also act as a corridor for species migration from one suitable habitat patch to another in a fragmented landscape (e.g. the movement of forest species

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from one isolated woodlot to another) (Burel and Baudry, 1994; Forman, 1995; Tischendorf et al., 1998; Corbit et al., 1999).

Due to the linear structure and limited width of the concerning habitat patches, hedgerows are typically characterised by a high edge to area ratio and thus consist mainly of edge habitat, strongly affected by the surrounding land use practices (Forman, 1995; Smart et al., 2001). Adjacent agricultural activities (especially tillage and herbicide use), together with hedgerow management routines (trimming, coppicing, pollarding, etc.), result in a high level of disturbances, with serious consequences for the floristic diversity of these semi-natural elements (Jobin et al., 1997; Boutin and Jobin, 1998; Smart et al., 2001). Finally, nutrient enrichment due to fertilizer misplacement and agrochemical drift also affects plant community organization within hedgerow ecosystems (Kleijn and Snoeijing, 1997).

Scientific interest in hedgerow and hedgerow network ecology has been rising steadily during the last few decades (see for instance McCollin (2001) for a comprehensive overview of contemporary publications about hedgerow research in the UK). A substantial fraction of this research is devoted to the analysis of the composition and functioning of hedgerow plant communities in the temperate regions of North America (e.g. Jobin et al., 1997; Corbit et al., 1999; de Blois et al., 2002; Boutin et al., 2002) and Western Europe (e.g. Burel and Baudry, 1990,1994; Le Coeur et al., 1997,2002; McCollin et al., 2000; Moonen and Marshall, 2001). Most of this work however addresses only a limited number of possible influencing factors, often with little attention for spatial and landscape-scale variables, leading to a diverse but fragmented view on the general characteristics and fundamental organizing principles of plant species distribution in hedgerow habitats. Especially the role of spatial variables describing the specific arrangement of individual hedgerows within the surrounding hedgerow network and other nearby natural or semi-natural habitat patches is seldom addressed. With the exception of the work of Le Coeur et al. (1997) and de Blois et al. (2002), little attention is also given to the frequent existence of correlations between different explanatory variables, troubling the interpretation of the role played by each individual factor, and possible statistical techniques to tackle this problem.

Based on a systematic and quantitative approach, this study tries to overcome these shortages by a comprehensive analysis of the role played by a broad range of different potential factors, on both the local and landscape level and with special attention to spatial variables. The following questions are addressed:

1. What are the key variables associated with hedgerow flora or, in other words, which explanatory variables are statistically significant in explaining patterns of plant species richness and composition in hedgerow habitats within traditional agricultural landscapes in Flanders, Belgium?
2. What is the relative importance of distinct groups of factors, more specifically environmental conditions, historical background, management variables, structural aspects and spatial configuration of the hedgerow network, for the process of plant community assembly in hedgerow ecosystems, allowing for intercorrelations between variables of different factor groups?
3. Has the spatial configuration of the hedgerow network an exclusive and statistically significant contribution in explaining plant species distribution patterns?

2. Methods

2.1. Study area

One of the few quasi-intact relics of typical bocage landscapes in Flanders, Belgium in which the basic processes of hedgerow plant community organisation were thought to function undisturbed (Hermy and De Blust, 1997), was selected to conduct our research. The study area, 251 ha in size, is situated in the municipality of Meerhout, in the south of the province of Antwerp and is characterised by the presence of a very dense and intact network of interconnected hedgerows (Fig. 1). As derived from historical land use maps, the site has been in cultivation from at least the end of the 18th century as an ancient hayfield and pasture landscape. Traditional small-scale farming activities resulted in an extremely fine-meshed parcel structure with an average field size of approximately 0.6 ha, bordered with hedgerows and often in conjunction with a system of banks and/or ditches. Present land use is dominated by different types of grassland and corn for silage production. The pedological characteristics of the terrain are mainly typified by moist to moderately dry soils with a sand to sandy loam texture. Furthermore, topographical features are little pronounced with a maximum elevation difference of 5.75 m.

Within the studied hedgerow network, both planted and spontaneous elements are present. Moreover, differences in historical background and former management practices result in various types of hedgerows, with the most frequent ones being coppice, rows of trees and coppice with standards (i.e. a combination of the two former types). An assortment of present day management strategies, often differing from those from the past (abandonment of traditional coppice management), adds to the structural diversity of the linear habitats as well. Besides a substantial fraction of hedgerows that are not managed any longer, hedgerow woody vegetation is at present mostly pruned (yearly mechanical cut), coppiced (rotational cut at ground level) or pollarded (rotational cut at 1–2 m height). The shrub and tree layer is typically dominated by one of the following species: *Quercus robur, Frangula alnus, Alnus glutinosa, Betula pendula* and *Sorbus aucuparia* (nomenclature follows De Langhe et al., 1988). An overview of some key attributes of the studied bocage landscape is given in Table 1.

2.2. Data collection

An individual hedgerow was defined as a discrete segment between two different nodes of the hedgerow network. If

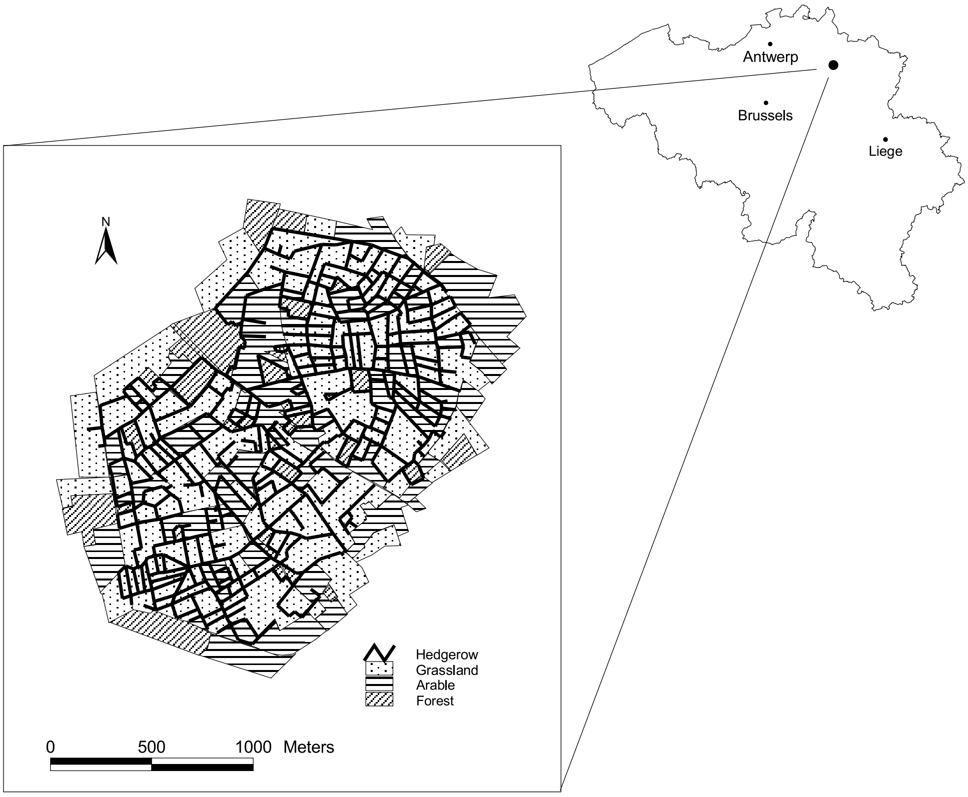

Fig. 1. Schematic representation of the studied hedgerow network landscape in combination with the geographical location of the study area within the country of Belgium.

Table 1
Key attributes of the studied bocage landscape

Attribute	Value
Total surface of study area	251 ha
Total number of hedgerows	511
Total length of hedgerows	36726 m
Hedgerow density	14632 m km^{-2}
Average hedgerow length	71.87 m
Average hedgerow width	7.52 m
Average hedgerow height	10.8 m
Presence of tree layer	89%
Presence of shrub layer	91.4%
Presence of bank	22.9%
Presence of ditch	81.4%
Presence of gaps	27.4%

necessary, these segments were subdivided further to achieve uniformity in adjacent land use, hedgerow management, etc. A total of 511 hedgerows were surveyed, with a total of 27 explanatory variables recorded (see Table 2), besides presence/absence data for all higher plant species. Fieldwork was done from April to June, 2002. Both sides of the hedgerow were inventoried systematically over the entire length of the element with all plant species present being registered. Explanatory variables were determined via both field observations and systematic analyses of digital maps and aerial photographs. All data were integrated in a GIS-environment with ArcView 3.2a (ESRI, 2000). Registered structural variables comprise hedgerow length, average width, variation in width, average height, variation in height, percentage gaps, presence of tree layer, presence of shrub layer, presence of bank and presence of ditch (see also Hegarty et al., 1994; Le Coeur et al., 1997; Moonen and Marshall, 2001). Environmental conditions include soil texture, moisture content and profile development, elevation and ditch water level (analogous to, amongst others, Forman and Baudry, 1984; Hegarty et al., 1994). Current hedgerow management and adjacent land use are grouped as management variables (see also Le Coeur et al., 1997; Boutin and Jobin, 1998; de Blois et al., 2002). Besides hedge origin, hedgerow type is classified as a historical variable, since the present-day appearance of a hedgerow is essentially the result of its historical background and former management practices (Baudry et al., 2000; de Blois et al., 2002). Finally, the spatial position and context of the hedgerow are characterised by its orientation, number of adjacent hedgerows, number of hedgerows within a circle of, respectively, 50, 100 and 250 m, presence of direct connection to forest, distance to nearest forest and density of the surrounding hedgerow network (see also Corbit et al., 1999; Sarlöv-Herlin and Fry, 2000). A summary of the basic characteristics of all recorded variables is provided in Table 2.

2.3. Data analysis

In first instance, individual explanatory variables were related to hedgerow species richness using non-parametric statistics. The specific effect of hedgerow type, origin, management and adjacent land use was studied in more detail by

Table 2
Recorded explanatory variables

Variable	Code	Method	Precision	Range	Group
Hedgerow origin	ORG	FO	/	Planted (P), spontaneous (S), combination of planted and spontaneous elements (C)	HIS
Hedgerow type	TYP	FO	/	Coppice (CP), coppice with standards (CWS), row of trees (RT), spontaneous regeneration (SR) + corresponding double equivalents D(CP), D(CWS), D(RT) and D(SR) (i.e. strips of woody vegetation on both sides of a small pathway, considered as one functional habitat element)	HIS
Hedgerow management	MNG	FO	/	No management (NM), pruning (PN), pollarding (PD), coppicing (CP), combination of different management practices (CB)	MAN
Adjacent land use	ALU	FO	/	Neglected grassland (NG), extensive grassland (EG), intensive grassland (IG), pasture (PT), arable field (AF), paved road (PR), unpaved road (UR), garden (GD), forest (FR)	MAN
Hedgerow length	LT	AP	1 m	10–401 m	STR
Average hedgerow width	AW	AP	0.5 m	1.0–38.0 m	STR
Variation in hedgerow width	VW	AP	1	0/1/2/3 (no/little/moderate/high variation in width)	STR
Average hedgerow height	AH	FO	0.5 m	1.5–27.0 m	STR
Variation in hedgerow height	VH	FO	1	0/1/2/3 (no/little/moderate/high variation in height)	STR
Presence of tree layer	TL	FO	/	0/1 (absence/presence)	STR
Presence of shrub layer	SL	FO	/	0/1 (absence/presence)	STR
Percentage gaps	GP	FO	5%	0–95%	STR
Presence of bank	BK	FO	/	0/1 (absence/presence)	STR
Presence of ditch	DT	FO	/	0/1 (absence/presence)	STR
Ditch water level	WT	FO	1	0/1/2/3 (no water/low/moderate/high water level)	ENV
Elevation	EL	DTM	0.25 m	19.25–25.00 m	ENV
Soil texture	ST	DSM	/	Sand (Z), loamy sand (S), sandy loam (P), other (O) [a]	ENV
Soil moisture	SM	DSM	/	Wet (e), moderately wet (d), moderately dry (c), dry (b), very dry (a), other (o) [a]	ENV
Soil profile	SP	DSM	/	Thick, anthropogenic humic A horizon (m), clear iron and/or humic B horizon (g), less clear iron and/or humic B horizon (f), strongly spotted, disrupted texture B horizon (c), other (o) [a]	ENV
Orientation	ORT	AV	/	North–south (N–S), northeast–southwest (NE–SW), east–west (E–W), southeast–northwest (SE–NW)	SPC
Number of adjacent hedgerows	NAS	AV	1	1–8	SPC
Number of hedgerows within 50 m	NS50	AV	1	2–20	SPC
Number of hedgerows within 100 m	NS100	AV	1	5–41	SPC
Number of hedgerows within 250 m	NS250	AV	1	16–126	SPC
Presence of connection to forest	PCF	AV	/	0/1 (absence/presence)	SPC
Distance to nearest forest	DNF	AV	1 m	0–316 m	SPC
Density of the hedgerow network	DHN	AV	1 m km^{-2}	12117–30073 m km^{-2} [b]	S PC

Method: FO, field observation; AP, aerial photograph; DTM, digital terrain model; DSM, digital soil map; AV, ArcView analysis on digitised network.
Group: HIS, historical background; MAN, management; STR, structure; ENV, environmental conditions; SPC, spatial configuration.
[a] Soil type nomenclature according to the Belgian soil classification system (Tavernier and Maréchal, 1972).
[b] Values represent total length of hedgerow per area unit, calculated for a 250 m buffer around each hedgerow element.

non-parametric multiple comparisons (procedure described in Siegel and Castellan, 1988). Furthermore, the fraction of variation in species data explained by single explanatory variables was obtained by canonical correspondence analysis (CCA) (ter Braak, 1986). For each individual variable a separate CCA was done using that variable, or for nominal variables their corresponding zero/one dummy variables, as the only constraining variable(s). The significance of the fraction of variation explained by a variable, given by the ratio of the sum of all constrained or canonical eigenvalues to the total inertia of the species data, was tested with a Monte-Carlo permutation test (999 unrestricted permutations). Additional insight in the functioning of hedgerow plant communities was obtained by means of an overall CCA with all explanatory variables. The forward selection option was used to exclude non-significant variables. Based on the results of this overall CCA, a species–environment biplot was constructed.

Two different methods were used to determine the relative importance of the five distinct groups of variables: partial regression analysis (Legendre and Legendre, 1998; Lichstein et al., 2002) and partial CCA (Borcard et al., 1992; Økland and Eilertsen, 1994; Le Coeur et al., 1997; Legendre and Legendre, 1998; de Blois et al., 2002; Cushman and McGarigal, 2002). Both methods explicitly account for the intrinsic existence of correlations between variables of different factor groups, resulting in a shared component of variance explained by the corresponding factor groups.

With reference to the partial regression approach the following procedure was adopted, repeated for all species with a frequency of occurrence above 5% and for all variable groups separately. First, a stepwise logistic regression was done with all explanatory variables. Next, a multiple logistic regression was performed with all significant variables, except those of the studied factor group. The unique contribution of the concerning factor group is then given by its partial R^2, calculated as the difference in R^2 between the full model, containing all significant variables, and the corresponding reduced model, lacking the variables of the concerning factor group. A measure of the relative importance of the five distinct factor groups for a particular plant species is then given by a comparison of their respective partial R^2-values for this species. Finally, the average partial R^2-value for all examined species together gives an overall measure of the relative importance of a certain factor group for the process of vegetation organisation in hedgerow habitats.

Partial CCA is the extension of partial regression analysis for multivariate response data (Legendre and Legendre, 1998). Rather than examining plant species one by one separately, this technique considers all present plant species together. Similar to the partial regression approach, the partial CCA-approach partitions the variance in species data explained by all explanatory variables over different subsets of variables. In first instance, the total fraction of variance explained by a variable set was obtained by CCA with forward selection of variables from this set. Variables were added stepwise and their significance was tested with a Monte-Carlo permutation test. The selection procedure was stopped when the first non-significant variable (at the $P = 0.05$ level) was encountered. Next, the unique fraction of variance explained by one set of variables and not shared with other sets was obtained by partial CCA, in which the significant member variables of the concerning group are used as constraining variables, while the significant variables of all other sets are treated as covariables of which the effect is removed a priori by multiple regression (Borcard et al., 1992; Økland and Eilertsen, 1994). Again, significance of the separate variance fractions was tested with a Monte-Carlo permutation test (999 unrestricted permutations).

Logistic regression and non-parametric statistical analyses were performed with SPSS 11.0 for Windows (SPSS, 2002). Canoco for Windows (ter Braak and Smilauer, 1998) was used for direct gradient analysis. For the different CCA-analyses, nominal variables were coded as series of zero/one dummy variables. Besides a downweighting of rare species, standard options were selected.

3. Results

3.1. General characteristics hedgerow flora

Within the 511 individual hedgerows of the surveyed hedgerow network, a total of 198 different plant species were recorded (see Appendix A), of which 57 (or 29%) have a woody and 141 (or 71%) an herbaceous character. A single hedgerow contains on average 24 plant species, with the mean number of woody species being equal to seven and the mean number of herbaceous species summing up to 17. Of these species, approximately 80% (158 species) are native, while about 20% (40 species) are of introduced origin. Native flora consists mainly of common, widespread species that are currently not endangered (147 out of 158 species or 93%), although some declining (10 species or 6%) and a single moderately rare species (less than 1% of the native vegetation) are present as well.

3.2. Effects of individual explanatory variables

Most explanatory variables are significantly associated with the woody, herbaceous and total number of plant species in hedgerow habitats, although some clear differences between the three species groups can be observed (Table 3, column 2–4). Hedgerow origin, type, management and adjacent land use significantly influence all of the three species groups. Hedge dimensions are also mostly significant, with length, average width and variation in width positively correlated with hedgerow species richness. While the presence of a shrub layer is important for all three species groups, the presence of a tree layer has no influence on the number of herbaceous species. The percentage gaps exert a more differentiated influence on hedgerow species richness with the number of herbaceous species positively and the number of woody species negatively correlated with this variable. The same pattern can be observed for the water level of the ditch. Orientation is significant for none of the three species groups. The number of adjacent hedgerows and the number of hedgerows within 50 and 100 m are typically positively correlated with hedgerow species richness. For the number of hedgerows within 250 m this correlation is no longer significant. Presence of connection to forest and distance to the nearest forest are only important for the number of woody species in hedgerow habitats. Finally, no significant relationship with hedgerow species richness could be found for the density of the hedgerow network.

The species richness of planted hedgerows is shown to be significantly lower than that of spontaneous hedgerows (Fig. 2(a)). Hedgerows with a combination of planted and spontaneous elements harbor the highest number of plant species. Furthermore, obvious differences in species richness can be observed for different hedgerow types (Fig. 2(b)), with rows of trees and spontaneous regeneration characterised by low species richness, while coppice and coppice with standards carry a higher number of plant species. The hedgerows with the highest species richness, however, are the double equivalents of the former types, i.e. strips of woody vegetation on both sides of a small pathway (width < 1 m), acting as one functional habitat element. For hedgerow management, the number of plant species increases from hedgerows with no management over pruning, pollarding and coppicing to hedgerows subjected to a combination of different management practices (Fig. 2(c)). Regarding the effects

Table 3
Relationships of individual explanatory variables with herbaceous, woody and total hedgerow species richness and fraction of total variation in species data explained by these variables

Variable	Relationship with Number of herbaceous species	Number of Woody species	Total number of plant species	Fraction of total variation in species data explained [a]
Hedgerow origin	11 .147 [b,*]	75.212 [b,**]	43.935 [b,**]	0.017 *
Hedgerow type	91.686 [b,**]	103.130 [b,**]	102.126 [b,**]	0.035 *
Hedgerow management	44.786 [b,**]	73.748 [b,**]	84.463 [b,**]	0.019 *
Adjacent land use	111.240 [b,**]	57.834 [b,**]	75.372 [b,**]	0.050 *
Hedgerow length	0.389 [c,**]	0.322 [c,**]	0.509 [c,**]	0.005 *
Average hedgerow width	0.071 [c,***]	0.218 [c,**]	0.099 [c,*]	0.013 *
Variation in hedgerow width	0.162 [c,***]	0.069 [c,***]	0.166 [c,**]	0.003 *
Average hedgerow height	–0.147 [c,**]	0.233 [c,**]	-0.001 [c,ns]	0.014 *
Variation in hedgerow height	0.036 [c,ns]	0.246 [c,**]	0.164 [c,**]	0.003 *
Presence of tree layer	0.440 [d,ns]	5.095 [d,**]	2.164 [d,***]	0.006 *
Presence of shrub layer	3.569 [d,**]	8.898 [d,**]	7.580 [d,**]	0.007 *
Percentage gaps	0.100 [c,*]	–0.329 [c,**]	–0.080 [c,***]	0.011 *
Presence of bank	1.930 [d,ns]	4.140 [d,**]	3.825 [d,**]	0.007 *
Presence of ditch	7.084 [d,**]	1.550 [d,ns]	4.459 [d,**]	0.013 *
Ditch water level	0.214 [c,**]	–0.081 [c,***]	0.125 [c,**]	0.015 *
Elevation	0.043 [c,ns]	–0.134 [c,**]	–0.030 [c,ns]	0.015 *
Soil texture	3.308 [b,ns]	28.530 [b,**]	5.977 [b,ns]	0.020 *
Soil moisture	14.137 [b,***]	8.648 [b,ns]	9.411 [b,ns]	0.032 *
Soil profile	8.420 [b,ns]	33.656 [b,**]	13.538 [b,*]	0.020 *
Orientation	1.153 [b,ns]	3.717 [b,ns]	0.391 [b,ns]	0.003 [ns]
Number of adjacent hedgerows	0.079 [c,***]	0.179 [c,**]	0.146 [c,**]	0.004 *
Number of hedgerows within 50 m	0.080 [c,***]	0.178 [c,**]	0.153 [c,**]	0.008 *
Number of hedgerows within 100 m	0.058 [c,ns]	0.141 [c,**]	0.116 [c,**]	0.013 *
Number of hedgerows within 250 m	0.032 [c,ns]	0.051 [c,ns]	0.048 [c,ns]	0.014 *
Presence of connection to forest	2.250 [d,***]	4.032 [d,**]	0.042 [d,ns]	0.004 *
Distance to nearest forest	0.013 [c,ns]	–0.106 [c,*]	–0.038 [c,ns]	0.005 *
Density of the hedgerow network	0.048 [c,ns]	0.006 [c,ns]	0.053 [c,ns]	0.011 *

ns, not significant.
* $P \leq 0.01$. ** $P \leq 0.001$. *** $P \leq 0.05$.
[a] Determined via CCA, in each case using the concerning individual variable (or its corresponding zero/one dummy variables) as the only constraining variable(s), significance tested with the Monte-Carlo permutation test (999 unrestricted permutations).
[b] Kruskal–Wallis Chi^2-value.
[c] Spearman rank correlation.
[d] Wilcoxon/Mann–Whitney Z.

of adjacent land use on hedgerow species richness, the low number of plant species present in hedgerows bordered by gardens or paved roads and the high species richness of hedgerows contiguous to extensive or neglected grasslands and unpaved roads deserve mention (Fig. 2(d)).

All but one variable (i.e. orientation) explain a significant fraction of the variation in species composition, with percentages of variation explained ranging from 0.3% to 5% (Table 3, column 5). Especially adjacent land use (5%), hedgerow type (3.5%), soil moisture content (3.2%), soil texture (2%), soil profile development (2%), hedgerow management (1.9%) and hedgerow origin (1.7% of the variation explained) seem to be important factors for the process of plant community assembly in hedgerow ecosystems.

Using all explanatory variables, a CCA with forward selection retained 41 significant variables out of the total of 63 different variables (variable number inflated by recoding of nominal variable classes as zero/one dummy variables), explaining about 18% of the variation in species data. The corresponding species–environment biplot visualizes the relationships between hedgerow species and environmental variables (Fig. 3). While the first ordination axis is strongly associated with management, history and spatial configuration, the second axis is more closely linked with structural variables. Abiotic environmental conditions are related with both axes. The first axis separates species of coppiced hedgerows with a strongly developed shrub layer on wet soils besides extensive or neglected grassland within a dense hedgerow network (e.g. *A. glutinosa, Salix caprea, Lychnis flos-cuculi, Lysimachia vulgaris*) on the left side from species of planted rows of trees with a poorly developed shrub layer on dry soils besides roads or arable fields within a less dense hedgerow network (e.g. *Castanea sativa, Plantago major, Hypericum perforatum, Chaerophyllum temulum*) on the right side. The second axis differentiates species of wide, large hedgerows without gaps and often in association with

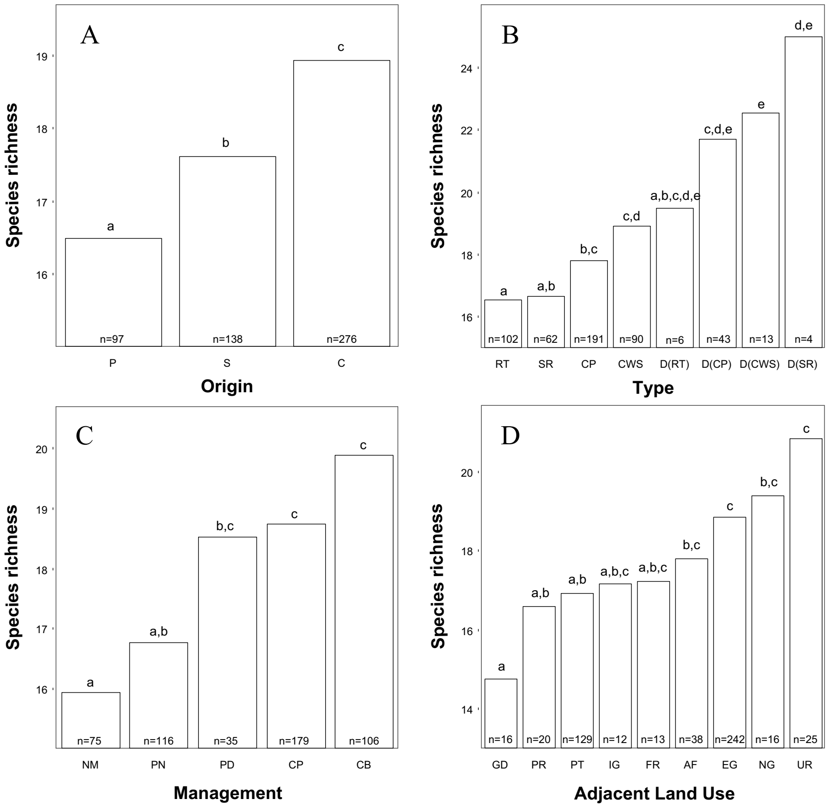

Fig. 2. Effect of hedgerow origin (A), type (B), management (C) and adjacent land use (D) on the species richness (i.e. total number of higher plant species) of hedgerow habitats. (Bars show means, characters above indicate groups separated by non-parametric multiple comparisons. Abbreviations of variable classes according to Table 2.)

an earthen bank (e.g. *Corylus avellana, Ranunculus ficaria, Descampsia flexuosa*) from species of narrow, small hedgerows with gaps and without a bank (e.g. *Stellaria graminea, Lotus corniculatus, Myosotis arvensis*).

3.3. Relative importance of variable groups

Clear differences among species in overall performance of regression models (expressed by the respective total R^2-values) and relative importance of variable groups (deducible from the corresponding partial R^2-values) can be observed (Fig. 4). Stepwise logistic regressions of individual hedgerow species on all explanatory variables yield total R^2-values ranging from 0.086 to 0.587, with an average number of 0.291 (Table 4). In other words, percentages of variation in species presence/absence data accounted for by the constructed regression models approximately vary between 9% and 59%, with an average percentage of variation explained of about 29%. Species with high partial R^2-values for abiotic environmental conditions are for instance *Lemna minor* (0.414), *Cardamine hirsuta* (0.338) and *Callitriche platycarpa* (0.258) (Fig. 4). While *P. major* and *Plantago lanceolata* are affected strongly by management variables (partial R^2 0.256 and 0.208), *Crataegus monogyna* and *Quercus rubra* are mainly governed by structural variables (partial R^2 0.151 and 0.129). The historical background was important, amongst others, for *Aegopodium podagraria* (partial R^2 0.240) and the spatial configuration of the hedgerow network for *S. aucuparia* (partial R^2 0.068) (Fig. 4).

The overall importance of the different variable groups for hedgerow plant community organization can be assessed by the corresponding average partial R^2-values for all examined species, as found in Table 4. The most important factor group determining plant species presence in hedgerow habitats seems to be the environmental conditions, with a mean partial R^2-value of 0.078. Next come successively, management variables, structural aspects and historical background, with average partial R^2-values of 0.065, 0.047 and 0.034, respectively. The variable set describing the spatial configuration of the hedgerow network appears to be less influential with a mean partial R^2-value of only 0.020.

Comparable results are found by the partial CCA-approach with the same relative order of importance generated for the five distinct factor groups (Table 5). A comparison of the unique amount of variance explained by a variable group controlled for covariation with variables from other groups, with the total amount of variance explained by that variable group (respectively, the CEV- and TEV-values in Table 5) shows that about half (on average 48%) of the total variance explained by a variable group is shared by variables from other groups. Nevertheless, the individual effect of each variable group separately is significant at the $P = 0.01$ level

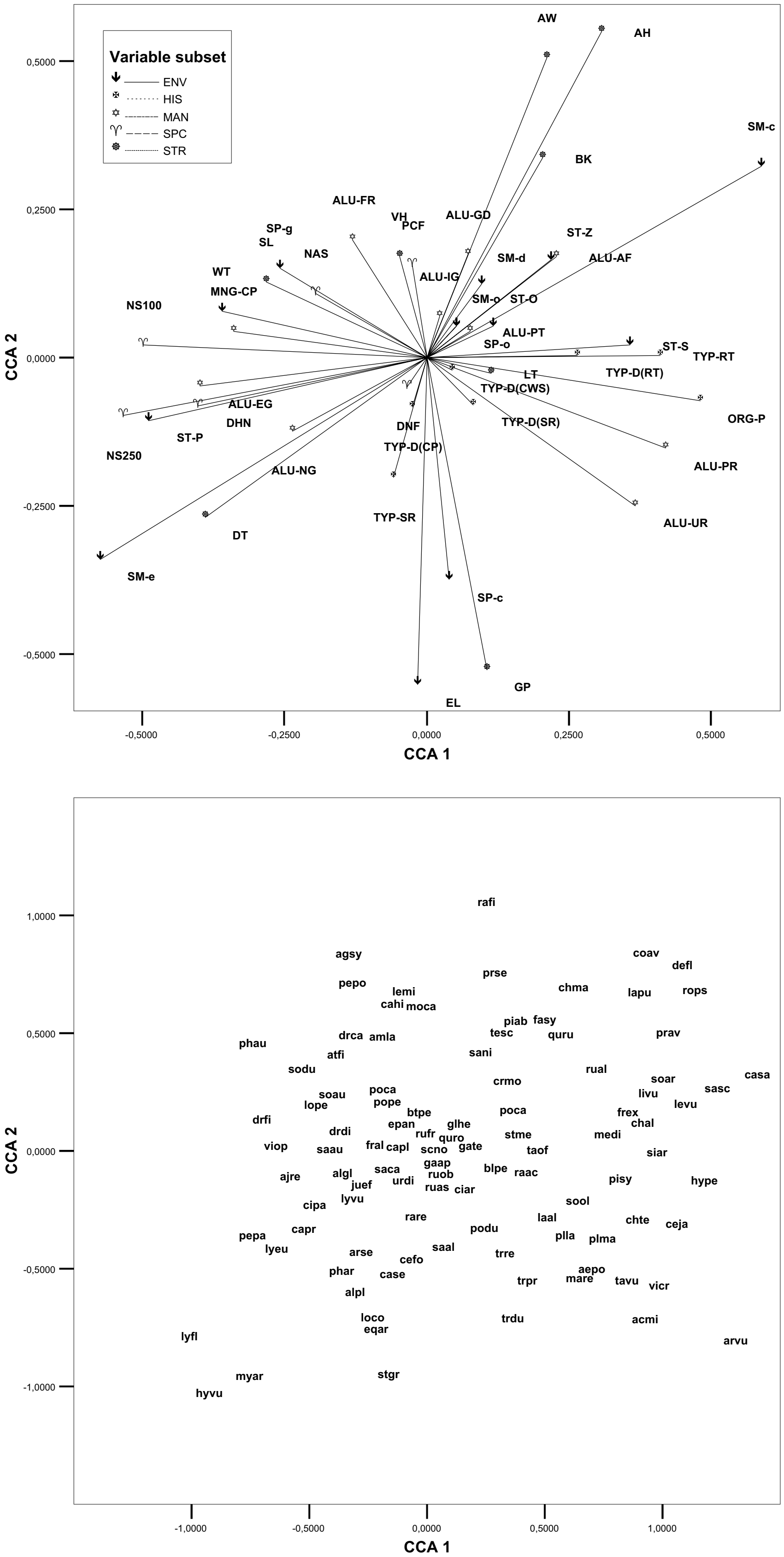

Fig. 3. Species–environment biplot, presenting the results of the overall CCA with forward selection using all explanatory variables. For reasons of clarity, two separate graphs are used for the species and environmental variables. Only significant variables and the 100 most frequent species are shown (abbreviations of environmental variables and variable groups cf. Table 2, species abbreviations cf. Appendix A).

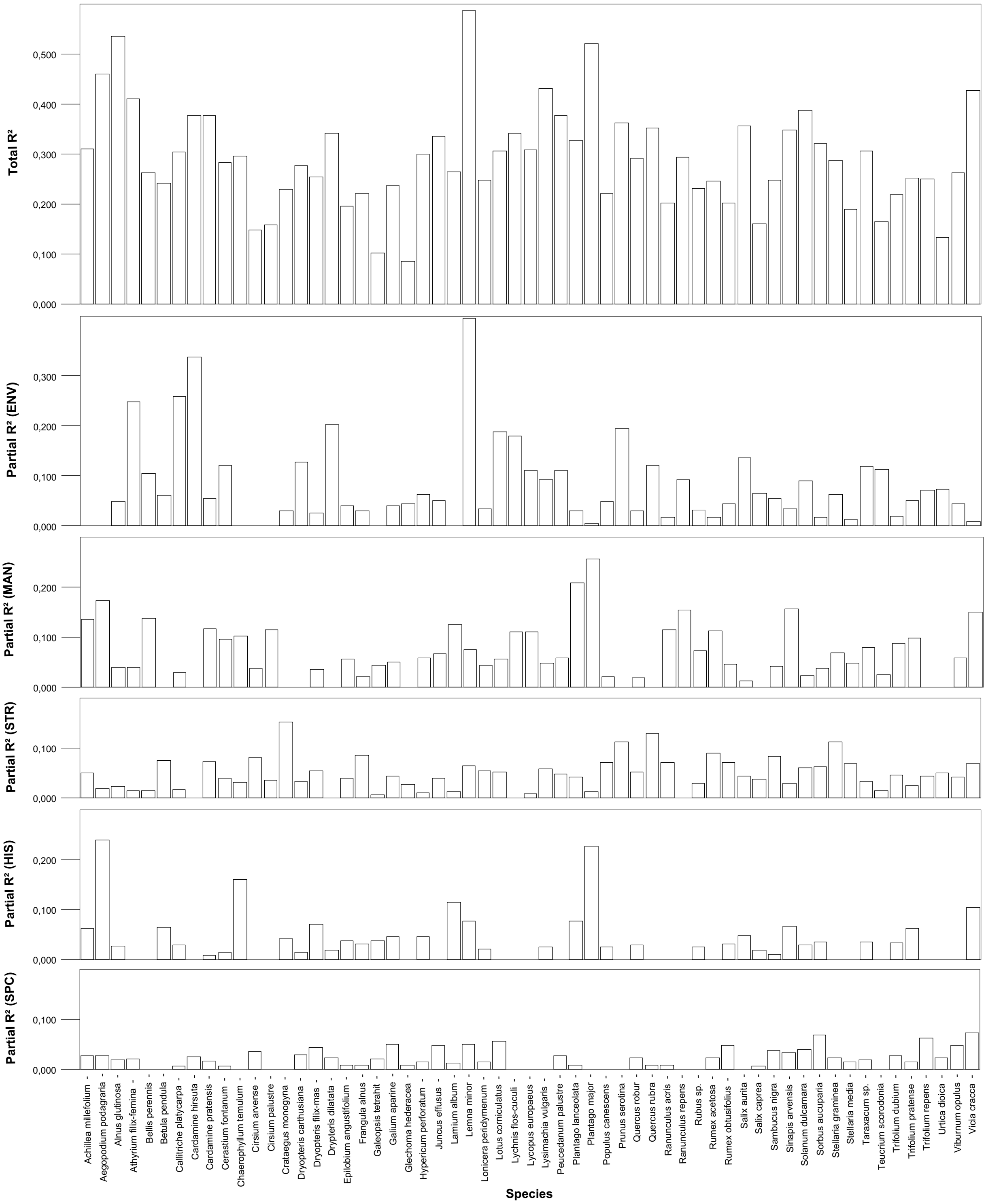

Fig. 4. Total R^2-values and partial R^2-values for the five distinct variable groups for all 59 species with a frequency of occurrence >5%, based on partial regression analysis (variable groups: ENV, environmental conditions; MAN, management; STR, structure; HIS, history; SPC, spatial configuration).

(Monte-Carlo permutation test of first constrained axis). All explanatory variables together explain 19.5% of the variation in species data, of which 21% is uniquely accounted for by environmental conditions, 19% by management variables, 13% by structural variables, 10% by the historical background and 9% by spatial variables.

4. Discussion

4.1. Methodology

While partial CCA is appropriate to study the overall importance of factor groups for the entire species pool, par-

Table 4
Summary of the results of the partial regression approach (based on 59 different partial regression analyses for all species with a frequency of occurrence >5%)

Variable group	Partial R^2		
	Minimum	Maximum	Mean
ENV	0.000	0.414	0.078
MAN	0.000	0.256	0.065
STR	0.000	0.151	0.047
HIS	0.000	0.240	0.034
SPC	0.000	0.072	0.020
Total R^2	0.086	0.587	0.291

Variable group: ENV, environmental conditions; MAN, management; STR, structure; HIS, history; SPC, spatial configuration.

tial regression analysis considers individual plant species separately, enabling differences in relative importance of factor groups between distinct species or species groups to be detected. By an exact quantification of the variation explained by different sets of variables, the partial regression and partial CCA-approach provide quantitative information on the relative importance of competing sets of explanatory variables as possible primary causes of variation in hedgerow species composition. The strength of both methods lies in the fact that the frequent existence of correlations between explanatory variables of different subsets is explicitly accounted for by partialling out shared components of variation explained by the various factor groups.

4.2. Organizing principles of hedgerow plant communities

4.2.1. Relative importance of variable groups—general order

Both methods reveal the same overall ranking of the five factor groups with, in decreasing order of importance, environmental conditions, management variables, structural aspects, historical background and spatial variables each affecting significantly hedgerow species composition (Tables 4 and 5). Although the partial CCA approach was also used by Le Coeur et al. (1997) and de Blois et al. (2002), a detailed comparison with their results is problematic since different explanatory variables were recorded and the grouping of them in discrete subsets varies greatly between these studies. Nevertheless, some general observations can be made. Besides a confirmation of the effect of management variables (i.e. adjacent land use and management of the hedgerow itself) and, still stronger, structural variables, the study of Le Coeur et al. (1997) additionally showed a significant effect of landscape type, a factor not examined here since our work is limited to a single study area. Also in agreement with the results of our work, the study of de Blois et al. (2002) stressed the importance of environmental conditions, management variables and historical background. Moreover, a significant spatial component in species variation was demonstrated using different polynomial combinations of *x* and *y* geographic coordinates, indicating that other spatially structured variables not measured in their study do influence species distribution patterns (cf. Borcard et al., 1992). This hypothesis is confirmed by the results of our study showing a significant effect of additional spatial variables not included in the analysis of de Blois et al. (2002), such as distance to nearest forest, number of adjacent hedgerows, etc.

4.2.2. Relative importance of variable groups—species-specific differences

Although a detailed analysis of dissimilarities between different functional groups of species falls beyond the scope of this paper, some general inferences about species-specific differences can be made, based on the results of the partial regression analyses (Fig. 4). A comparison of the relative contribution of the five factor groups for individual plant species shows that environmental conditions are especially influential for aquatic plants (e.g. *Callitriche platycarpa* and *L. minor*) and phreatophytes (e.g. *L. flos-cuculi*), as well as for species associated with specific soil nutrient conditions, such as *Teucrium scorodonia* and *Urtica dioica*. Management variables appear to be important mostly for grassland species (e.g. *Achillea millefolium, Bellis perennis* and *Ranunculus acris*) and trampling tolerant plants or species of road verges (e.g. *P. lanceolata* and *P. major*). This is probably due to the fact that the occurrence of these species is strongly linked with the type of adjacent land use (respectively, grassland and road), classified here as a management variable. Tree and shrub species, such as *C. monogyna,*

Table 5
Summary of the results of the partial CCA approach (for each variable group TEV-values were obtained via CCA-analyses with forward selection of variables from this group and CEV-values via partial CCA-analyses with significant member variables as constraining variables and all other significant variables as covariables)

Variable group	Absolute amount		Fraction of total inertia		Fraction of total variance explained	
	TEV	CEV	TEV	CEV	TEV	CEV
ENV	0.183	0.100	0.075	0.041	0.384	0.210
MAN	0.160	0.092	0.065	0.038	0.336	0.193
STR	0.132	0.063	0.054	0.026	0.277	0.132
HIS	0.101	0.048	0.041	0.020	0.212	0.101
SPC	0.079	0.041	0.032	0.017	0.166	0.086
ALL	0.476	0.476	0.195	0.195	1.000	1.000

TEV, total amount of variance explained by variable group; CEV, amount of variance explained by variable group, controlled for covariation with variables from other groups; ENV, environmental conditions; MAN, management; STR, structure; HIS, history; SPC, spatial configuration; ALL, all variables.

Prunus serotina and *Q. rubra*, are mainly affected by structural factors, whereas historical variables seem to influence the presence of species typical of ancient cultural landscapes (e.g. *A. podagraria* and *Lamium album*). Although the overall effect of spatial variables is rather limited, the proportionally larger weight of this factor group for zoochores (e.g. *Galium aparine, S. aucuparia* and *Viburnum opulus*) is worth mentioning.

4.2.3. Management variables

Besides the primary impact of abiotic environmental conditions as fundamental steering factors of all types of plant communities (Borcard et al., 1992; Økland and Eilertsen, 1994), management variables turned out to be the most important factor group governing the plant species composition of hedgerows. Within this variable group, the central role of adjacent land use can be explained by the fact that this factor determines to a great extent the level of human-induced disturbances by more or less frequent practices of tillage, mowing, harvesting, etc. (Boutin and Jobin, 1998) and alters plant competitive interactions in hedgerow ecosystems by processes of pesticide drift and nutrient enrichment (Jobin et al., 1997; Tsiouris and Marshall, 1998). Although the importance of adjacent land use is clearly confirmed by existing evidence (see for instance Le Coeur et al., 1997; Boutin and Jobin, 1998; Mercer et al., 1999; de Blois et al., 2002), the assumed negative relationship between hedgerow species richness and intensity of neighbouring agricultural practices as mentioned by Bunce et al. (1994) and Hegarty et al. (1994), is only partially supported by the results of this study (see Fig. 2).

The importance of hedgerow management is also linked with the fact that current management practices, typically characterised by a specific frequency and intensity of (cyclic) interventions in the hedgerow habitat, strongly affect the level of human-induced disturbances, resulting in changes in physical and biological environment and resource availability. Confirming evidence regarding the effect of management on hedgerow vegetation is provided by, amongst others, McAdam et al. (1994), Moonen and Marshall (2001), de Blois et al. (2002) and Garbutt and Sparks (2002). The assumption that the adoption of a set of different management strategies results in a high species richness and diversity, as stated by Moonen and Marshall (2001), is clearly supported by the results of this study (Fig. 2). The basic reason for the observed relationship is thought to be the high level of spatio-temporal variability in environmental conditions created under a combination of various management practices. The lower species richness of neglected hedgerows lacking any form of (recent) management in comparison with actively managed hedgerows, as found by McAdam et al. (1994), is also neatly confirmed by the findings of this work (Fig. 2).

4.2.4. Structural variables

Within this variable group, a central place is taken by the three spatial dimensions of the hedgerow formation, affecting possibilities for niche differentiation and controlling the extent to which the narrow linear habitat patches with a small interior to edge ratio are buffered against intruding effects of the surrounding agricultural landscape matrix. Regarding the impact of hedge dimensions on hedgerow flora, the positive correlations between species richness on the one hand and hedgerow length and width on the other hand (cf. Table 3) confirm the results of Helliwell (1975), Forman and Baudry (1984), Burel and Baudry (1994) and Hegarty et al. (1994). Although Boatman et al. (1994) and Hegarty et al. (1994) mention the role of hedgerow height specifically, no supporting evidence could be found in the literature for the observed contrasting relationships of this variable with the herbaceous and woody species richness, respectively (Table 3).

The same is true for the effect of gaps in the hedge on plant species richness. In general, our results show a small but significant negative correlation of the percentage gaps with the total hedgerow species richness, in correspondence with the findings of Hegarty et al. (1994), McAdam et al. (1994) and Moonen and Marshall (2001). But this overall picture conceals a more complex situation with gapped hedges carrying a significantly higher number of herbaceous and lower numbers of woody species (Table 3). Additional habitat niches resulting from the creation of gaps in the hedgerow formation probably account for the higher herbaceous species richness, while the establishment of tree and shrub species is possibly impeded by an invasion of fast-growing, competitive grassland species.

Furthermore, the fact that the herbaceous species richness was strongly associated with the presence of a shrub layer and not with the presence of a tree layer (cf. Table 3) probably reflects the greater role of a good developed shrub layer instead of a simple row of more widely spaced trees in creating a temperate forest-like microclimate within the hedgerow habitat. Similarly, Le Coeur et al. (1997) found a proportionally larger impact of the shrub layer in comparison with the tree layer affecting hedgerow plant communities.

4.2.5. Historical variables

The collection of historical data typically being difficult and time consuming, this variable class comprises only hedge type and origin in our study. The observed effect of hedgerow type on plant species richness and composition, supported by the results of Marshall and Arnold (1995) and Boutin et al. (2002), is linked with the fact that the present day appearance of a hedgerow is largely the result of its historical background and former management practices, affecting contemporary distribution patterns of plant species in hedgerow habitats as the outcome of a succession process strongly embedded in history. The specific effect of former management practices is addressed explicitly by de Blois et al. (2002), who showed a unique and significant contribution of this variable to hedgerow species variation.

Authors quoting hedgerow origin as an essential organizing principle of hedgerow vegetation include Pollard (1973), Forman and Baudry (1984), Burel and Baudry (1990) and

Boutin et al. (2002). Our results shows that planted hedgerows are characterised by significantly lower plant species richness than spontaneous hedgerows (Fig. 2), as found by Pollard (1973) and Boutin et al. (2002). This pattern is assumed to be caused by the frequent presence of single species equal-aged dominants in combination with a more uniform and intensive management strategy resulting in a lower level of spatial heterogeneity and temporal stability for planted hedgerows in comparison with natural hedgerows.

4.2.6. Spatial variables

The decreasing impact of the surrounding hedgerows with increasing buffer dimensions (Table 3) indicates that it is mainly the habitat patches in the immediate surroundings of a hedgerow that influence its plant community. Furthermore, the fact that hedgerow species richness was not significantly related with the density of the hedgerow network is probably linked with the low variability of this variable within studied landscape (Table 3). In contrast, Le Coeur et al. (1997) found a strong effect of grain size on species richness examining three hedgerow network landscapes in Brittany, France.

The study presented here is, to our knowledge, the first one addressing explicitly the relative importance of spatial variables, describing the specific arrangement of the individual hedgerow within the surrounding hedgerow network and other nearby natural or semi-natural habitat patches (especially forests), in relative comparison with other explanatory variable groups. Although the results of the partial regression (Table 4) and partial CCA approach (Table 5) show that spatial variables seem to be the least important factor group, the concerning variable set nevertheless explains a significant fraction of the variation in species data ($P < 0.01$, Monte-Carlo permutation test of first constrained axis) and can therefore be considered as an essential steering component of hedgerow vegetation.

The limited contribution of spatial variables in comparison with other variable groups is probably linked with the large fraction of widespread, easy dispersing species occurring in the studied hedgerow network, corroborating the results of Forman and Baudry (1984), Sarlöv-Herlin and Fry (2000) and French and Cummins (2001). Moreover, most of the forests present within the study area are relatively young, planted, homogeneous forest stands and are, therefore, unlikely to function as a source of forest plants for the gradual colonization of surrounding hedgerows (Peterken and Game, 1981), except for some common woody species (Boots, 2001). This is confirmed by a stronger relationship of the forest related variables with hedgerow woody in comparison with herbaceous species richness (Table 3). Finally, it is possible that the specific effect of spatial variables is partially masked due to the high density and intactness of the network under study and would come to expression more clearly in less dense and more degraded hedgerow networks.

5. Conclusion

In first instance, the findings of this work demonstrate that hedgerow vegetation organization is a complex process with a wide range of different factors significantly affecting hedgerow species richness and composition. Besides a strong impact of adjacent land use, hedgerow management, soil conditions, hedgerow type and origin, the role of other factors such as hedge dimensions, intactness, etc. can certainly not be neglected. The grouping of explanatory variables in ecologically meaningful subsets provided further insight within this complexity. Clear differences in relative importance of variable groups could be observed. Besides a predominant impact of abiotic environmental conditions, it was found that management variables and structural aspects have a relatively larger influence on the distribution of plant species in hedgerows than their historical background or spatial configuration. Nevertheless, it is demonstrated that the subset of spatial variables, describing the specific arrangement of individual hedgerows within the surrounding hedgerow network and other nearby natural or semi-natural habitat patches, has a statistically significant effect on plant species distribution patterns within hedgerow habitats.

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Appendix A

Overview of the species recorded in our study, their abbreviation and frequency of occurrence within the studied hedgerow network (i.e. percentage of hedgerows occupied)

Species	AB	FR	Species	AB	FR	Species	AB	FR
Abies grandis	abgr	0.1	*Geranium dissectum*	gedi	0.3	*Prunus domestica*	prdo	0.5
Acer pseudoplatanus	acps	1.7	*Geranium molle*	gemo	2.5	*Prunus laurocerasus*	prla	0.2
Achillea millefolium	acmi	13.2	*Geranium robertianum*	gero	0.2	*Prunus serotina*	prse	33.5
Achillea ptarmica	acpt	0.1	*Glechoma hederacea*	glhe	11.6	*Prunus spinosa*	prsp	0.4
Aegopodium podagraria	aepo	8.1	*Hedera helix*	hehe	0.6	*Pteridium aquilinum*	ptaq	0.6
Ajuga reptans	ajre	1.2	*Heracleum mantegazzianum*	hema	0.2	*Pyrus communis*	pyco	0.1
Alisma plantago-aquatica	alpl	1.4	*Heracleum sphondylium*	hesp	0.9	*Quercus robur*	quro	76.8
Alliaria petiolata	alpe	0.1	*Hieracium laevigatum*	hila	0.7	*Quercus rubra*	quru	23.0
Alnus glutinosa	algl	59.4	*Hieracium pilosella*	hipi	0.2	*Ranunculus acris*	raac	34.4
Alnus incana	alin	0.2	*Hordeum murinum*	homu	0.2	*Ranunculus ficaria*	rafi	2.8
Amelanchier lamarckii	amla	1.3	*Humulus lupulus*	hulu	0.9	*Ranunculus flammula*	rafl	0.1
Angelica sylvestris	agsy	2.6	*Hydrocotyle vulgaris*	hyvu	1.7	*Ranunculus repens*	rare	79.1
Anthriscus cerefolium	ance	0.3	*Hypericum perforatum*	hype	6.0	*Rhododendron ponticum*	rhpo	0.1
Anthriscus sylvestris	atsy	0.5	*Ilex aquifolium*	ilaq	0.3	*Rhus typhina*	rhty	0.1
Aphanes inexpectata	apin	0.3	*Iris pseudacorus*	irps	0.8	*Ribes rubrum*	riru	0.7
Arctium lappa	arla	0.1	*Juglans regia*	jure	0.8	*Ribes uva-crispa*	riuv	0.1
Arctium minus	armi	0.7	*Juncus effusus*	juef	57.7	*Robinia pseudoacacia*	rops	2.8
Arenaria serpyllifolia	arse	3.0	*Kerria japonica*	keja	0.1	*Rosa canina*	roca	0.1
Artemisia vulgaris	arvu	2.2	*Lamium album*	laal	6.1	*Rubus fruticosus*	rufr	86.8
Athyrium filix-femina	atfi	22.9	*Lamium purpureum*	lapu	4.9	*Rumex acetosa*	ruas	53.4
Bellis perennis	blpe	6.9	*Lapsana communis*	laco	0.2	*Rumex acetosella*	rual	1.9
Betula pendula	btpe	56.9	*Lemna minor*	lemi	5.3	*Rumex crispus*	rucr	0.4
Brassica napus	brna	0.8	*Leucanthemum vulgare*	levu	1.2	*Rumex obtusifolius*	ruob	61.4
Callitriche platycarpa	capl	8.4	*Ligustrum vulgare*	lgvu	0.2	*Salix alba*	saal	4.9
Calluna vulgaris	cavu	0.5	*Linaria vulgaris*	lnvu	3.5	*Salix aurita*	saau	39.7
Calystegia sepium	case	1.4	*Lonicera periclymenum*	lope	35.4	*Salix caprea*	saca	19.5
Capsella bursa-pastoris	cabu	0.3	*Lotus corniculatus*	loco	9.5	*Sambucus nigra*	sani	30.5
Cardamine flexuosa	cafl	0.1	*Lupinus polyphyllus*	lupo	0.1	*Sarothamnus scoparius*	sasc	5.0
Cardamine hirsuta	cahi	5.6	*Lychnis flos-cuculi*	lyfl	6.3	*Scrophularia nodosa*	scno	2.2
Cardamine pratensis	capr	18.6	*Lycopus europaeus*	lyeu	15.0	*Senecio jacobaea*	seja	0.4
Carex sp.	casp	0.3	*Lysimachia vulgaris*	lyvu	59.5	*Senecio vulgaris*	sevu	0.8
Carpinus betulus	cabe	0.3	*Mahonia aquifolium*	maaq	0.1	*Sinapis arvensis*	siar	5.4
Castanea sativa	casa	1.9	*Malus sylvestris*	masy	0.7	*Solanum dulcamara*	sodu	18.7
Centaurea jacea	ceja	3.5	*Matricaria recutita*	mare	4.2	*Solanum tuberosum*	sotu	0.7
Cerastium fontanum	cefo	33.0	*Melandrium album*	meal	0.1	*Sonchus arvensis*	soar	2.4
Chaerophyllum temulum	chte	6.7	*Melandrium dioicum*	medi	2.3	*Sonchus oleraceus*	sool	2.8
Chamaecyparis lawsoniana	chla	0.8	*Molinia caerulea*	moca	2.3	*Sorbus aucuparia*	soau	50.1
Chelidonium majus	chma	1.3	*Myosotis arvensis*	myar	2.1	*Spergula arvensis*	spar	0.1
Chenopodium album	chal	1.8	*Nymphaea alba*	nyal	0.1	*Spiraea alba*	spal	0.2
Cirsium arvense	ciar	28.0	*Ornithogalum umbellatum*	orum	0.9	*Stachys sylvatica*	stsy	0.2
Cirsium palustre	cipa	10.0	*Ornithopus perpusillus*	orpe	0.1	*Stellaria graminea*	stgr	8.0
Comarum palustre	copa	0.2	*Peplis portula*	pepo	1.2	*Stellaria holostea*	stho	0.5
Convolvulus arvensis	coar	0.2	*Petasites hybridus*	pehy	0.1	*Stellaria media*	stme	59.7
Cornus sanguinea	cosa	0.1	*Peucedanum palustre*	pepa	17.9	*Stellaria uliginosa*	stul	0.3
Corylus avellana	coav	3.0	*Phalaris arundinacea*	phar	4.6	*Symphytum officinale*	syof	0.4
Crataegus monogyna	crmo	13.3	*Phragmites australis*	phau	1.9	*Syringa vulgaris*	syvu	0.7
Deschampsia cespitosa	dece	0.6	*Picea abies*	piab	2.0	*Tanacetum vulgare*	tavu	3.1
Deschampsia flexuosa	defl	1.2	*Pinus nigra*	pini	0.7	*Taraxacum officinale*	taof	56.6
Digitalis purpurea	dipu	0.2	*Pinus strobus*	pist	0.4	*Teucrium scorodonia*	tesc	17.8
Dryopteris carthusiana	drca	20.0	*Pinus sylvestris*	pisy	1.3	*Tilia platyphyllos*	tipl	1.4
Dryopteris dilatata	drdi	14.5	*Plantago lanceolata*	plla	21.4	*Trifolium dubium*	trdu	5.1
Dryopteris filix-mas	drfi	6.0	*Plantago major*	plma	19.1	*Trifolium pratense*	trpr	21.8
Echium vulgare	ecvu	0.2	*Polygonatum multiflorum*	pomu	0.2	*Trifolium repens*	trre	9.4
Epilobium angustifolium	epan	13.6	*Polygonum amphibium*	poam	1.0	*Tussilago farfara*	tufa	0.4

(continued on next page)

Species	AB	FR	Species	AB	FR	Species	AB	FR
Epilobium hirsutum	ephi	0.7	*Polygonum aviculare*	poav	0.2	*Ulmus minor*	ulmi	0.7
Epilobium parviflorum	eppa	0.2	*Polygonum dumetorum*	podu	1.1	*Urtica dioica*	urdi	78.3
Equisetum arvense	eqar	2.7	*Polygonum hydropiper*	pohy	0.1	*Veronica arvensis*	vear	0.5
Erodium cicutarium	erci	0.2	*Polygonum persicaria*	pope	1.4	*Veronica chamaedrys*	vech	0.8
Eupatorium cannabinum	euca	0.3	*Populus tremula*	potr	16.8	*Veronica persica*	vepe	0.3
Fagus sylvatica	fasy	1.9	*Populus nigra cv pyramidalis*	poni	0.2	*Veronica scutellata*	vesc	0.1
Forsythia suspense	fosu	0.1	*Populus x canadensis*	poca	2.7	*Viburnum opulus*	viop	6.6
Frangula alnus	fral	60.9	*Potamogeton natans*	pona	0.7	*Vicia cracca*	vicr	14.4
Fraxinus excelsior	frex	1.4	*Potentilla anserina*	poan	0.5	*Vicia hirsute*	vihi	0.6
Galeopsis tetrahit	gate	29.9	*Potentilla erecta*	poer	0.9	*Vinca minor*	vimi	0.3
Galium aparine	gaap	57.9	*Prunus avium*	prav	2.4	*Viola arvensis*	viar	0.5
Genista anglica	gean	0.1	*Prunus cerasus*	prce	0.3	*Viola tricolor*	vitr	0.3

Species: Nomenclature follows De Langhe et al. (1988); AB, abbreviation; FR, frequency of occurrence (%).

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