Environmental Conservation 32 (1): 20–29 © 2005 Foundation for Environmental Conservation doi:10.1017/S0376892905001840

Long-term spatio-temporal dynamics of a hedgerow network landscape in Flanders, Belgium

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Date submitted: 26 August 2004 Date accepted: 18 January 2005

SUMMARY

Although the importance of hedgerows for sustainable agriculture and conservation of rural biodiversity is increasingly being recognized, obtaining insight into the spatial and temporal dynamics of hedgerow networks remains an important challenge for landscape ecologists, with the key factors driving changes in rural landscape structure especially deserving further attention. The present study analyses the long-term history of a hedgerow network landscape in Flanders, Belgium. A detailed reconstruction of the hedgerow network is made at five points in time, starting at the end of the 18th century until present, for 367 distinct 400 m × 400 m samples. Whilst hedgerows were mainly concentrated around historical village centres and within valleys at the end of 18th century, the network expanded progressively during the 19th century. In the 20th century, the hedgerow network degraded strongly, with hedgerow density and connectivity declining and mesh-size heterogeneity and network fragmentation increasing, although the network recovered slightly during the 1990s. Different trajectories of change in hedgerow network structure were observed depending on landscape position, with both topography and village proximity significantly affecting hedgerow network dynamics. The present network structure was mainly governed by land use, with highly developed networks being predominantly associated with pasture. Three main conclusions arise from the results of this study. First, the role of land use and landscape position as basic factors steering hedgerow network dynamics at the landscape scale is demonstrated. Second, the long-term perspective of the study enabled insight into the poorly known expansion phase of hedgerow networks, linked mainly with the development of small-scale labour-intensive agriculture. Finally, the findings confirm the large-scale degradation of linear semi-natural habitats in European agricultural landscapes during most of the 20th century, and indicate that a pro-active rural policy can halt and even reverse this process.

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Keywords: agricultural landscapes, connectivity, hedgerows, historical reconstruction, landscape structure, network dynamics

INTRODUCTION

In terms of area, agriculture forms the most important type of land use within the temperate regions of the world, especially in densely populated zones such as Western Europe, where more than 50% of the land surface can be classified as agricultural (Rounsevell *et al*. 2003). In Flanders, Belgium, this situation is even more pronounced, with about 63% of the land currently in agricultural use (Nationaal Instituut voor de Statistiek 2004). Whilst the production function formerly dominated, a growing emphasis on the multifunctionality of agricultural landscapes has arisen during recent decades, with increased attention being paid to cultural, environmental and ecological issues (Altieri 1999; Thies & Tscharntke 1999; Franco *et al*. 2003).

Landscape ecology (i.e. the study of the effect of spatial pattern on ecological process, cf. Turner 1989) is characterized by a strong focus on rural landscapes, with the network-matrix model especially offering a useful conceptual framework for analysing the functioning of agricultural ecosystems (Forman 1995). The application of this model to actual landscapes has led to an increased interest in the different semi-natural habitats within the farmland mosaic (for example Marshall & Arnold 1995; Kleijn & Verbeek 2000; Freemark *et al*. 2002; Deckers *et al*. 2005). Hedgerows, linear strips of woody vegetation that separate adjacent fields, often represent an important element in these small-scaled habitat fragments (Forman & Baudry 1984; Baudry *et al*. 2000).

Traditionally, hedgerows have functioned mainly as fences for livestock and sources of a variety of wood and non-wood products (Burel & Baudry 1990*a*; Baudry *et al*. 2000). At present, the importance of hedgerows for agricultural sustainability is becoming increasingly emphasized (de Blois *et al*. 2002). They help to control erosion and reduce pesticide drift and fertilizer misplacement (Ucar & Hall 2001; Marshall & Moonen 2002). They also create a specific, more mesic microenvironment and harbour natural enemies of biological pests (Forman & Baudry 1984; Forman 1995; Thies & Tscharntke 1999). Moreover, hedgerows are crucial for the conservation of rural biodiversity by acting as habitats, corridors or refuges for a variety of plant and animal species

(Le Coeur *et al.* 1997; Hinsley & Bellamy 2000; Dover & Sparks 2000; Thomas *et al.* 2001; Deckers *et al.* 2004).

The various hedgerow networks throughout the world are dynamic landscape structures that have evolved simultaneously with the development of agriculture (Moore *et al.* 1967; Demers *et al.* 1995; Thenail 2002). In Western Europe, most hedgerows originated in the 18th and 19th centuries, when the gradual conversion of open-field systems to enclosed parcels was linked with widespread planting of hedgerows (Pollard *et al.* 1974; Baudry & Jouin 2003). During the 20th century, agricultural intensification and mechanization (with a concurrent need to increase parcel size) on the one hand, and on the other technological innovations, such as the introduction of post and wire fencing, led to a change and subsequent loss of past functions of hedgerows (Baudry *et al.* 2000). This led to much hedgerow removal, either by individual initiatives or within organized land consolidation programmes (Burel & Baudry 1990*b*; Barr & Gillespie 2000; Kesseler & Reif 2002). Recently, the increasing recognition of the ecological and amenity functions of hedgerows and the growing attention to their role in environmental protection and sustainable agriculture has led to initiatives for the conservation and restoration of hedgerow networks through active management and planting programmes (Kristensen & Caspersen 2002; Petit *et al.* 2003; Croxton *et al.* 2004).

Obtaining information over the expansion, disintegration, stabilization and possible recovery of hedgerow networks during history forms an important issue in landscape ecological research. Whilst several authors have analysed the spatial arrangement and temporal dynamics of hedgerow network landscapes since World War II (for example Burel & Baudry 1990*b*; Demers *et al.* 1995; Kristensen & Caspersen 2002; Schmucki *et al.* 2002), no study has yet explicitly addressed the structural evolution of a hedgerow network over a more extended period of time. Hence, information about the expansion phase is largely lacking, especially in the traditional agricultural landscapes of West and Central Europe. Furthermore, the key factors driving changes in a given rural landscape structure also deserve further attention. Although some authors have studied the effect of landscape type on hedgerow network structure and dynamics (Demers *et al.* 1995; Schmucki *et al.* 2002), their relationships with land use and landscape position need further clarification.

Focusing on the long-term history of a typical *bocage* landscape (i.e. a landscape characterized by the presence of a strongly developed hedgerow network, cf. Baudry *et al.* 2000) in Flanders (Belgium), the present study addresses these limitations. More specifically, the spatial and temporal dynamics of the hedgerow network in the region is assessed in relation to land use and landscape position. The objectives are (1) making a detailed reconstruction of the structure of the hedgerow network at five points in time, from the end of the 18th century until present, using a systematic sampling strategy, (2) determining different trajectories of change for distinct types of samples by means of hierarchical cluster analysis and linking them with landscape position using discriminant analysis and (3) assessing the effects of land use and landscape position on the present-day spatial configuration of the hedgerow network using multiple linear regression analysis.

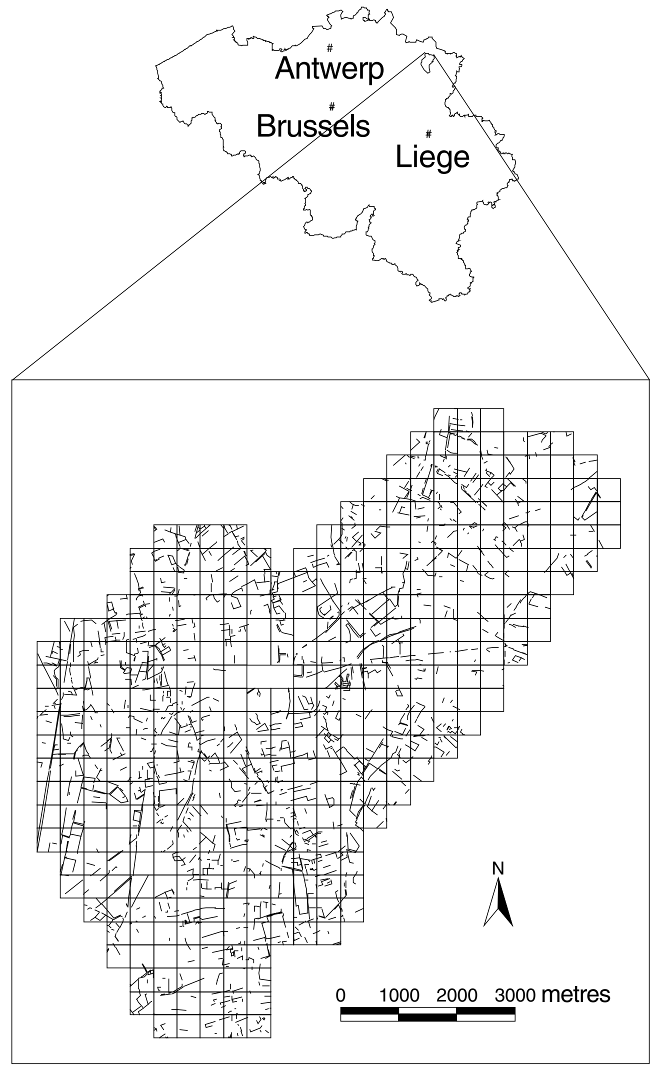

Figure 1 Location of the study area within the country of Belgium, together with the hedgerow network of 2002, where each square represents a 400 m × 400 m sample.

METHODS

Study area

The study area (58.72 km^2) is located in the municipality of Peer, in the north-east of the province of Limburg, Flanders, Belgium (51°7′59″N, 5°27′11″E). It forms part of the Campine plateau and is characterized by a relatively flat landscape, intersected by the Dommel and Abeek stream and tributaries (Fig. 1). The soils vary from sand to sandy loam in texture and the altitude ranges from 50–75 m. The region is mainly agricultural, with the present land use being dominated by fodder crops (mainly intensive grassland

and maize for silage production) and pasture. A scattered network of partially-connected hedgerows is present. As a result of differences in historical background and management practices, distinct types of hedgerows can be found, with coppice and rows of trees being most frequent. *Quercus robur*, *Betula pendula*, *Rhamnus frangula*, *Sorbus aucuparia* and the exotic *Prunus serotina* are the dominant woody species (nomenclature follows De Langhe *et al*. 1988).

Data collection

In accordance with the average scale level of the parcel structure of the landscape (cf. Kerselaers 2003), the study area was divided into 367 samples of 400 m × 400 m (Fig. 1). Using historical maps, aerial photographs and field observations, the hedgerow network was reconstructed for each sample separately at five points in time (1789, 1900, 1950, 1992 and 2002), with a hedgerow defined as a linear habitat fragment with a woody vegetation structure embedded within the agricultural landscape matrix. Data were integrated in a GIS-environment using ArcView 3.2a (ESRI [Environmental Systems Research Institute] 2000).

For each sample, the qualitative and quantitative characteristics of the hedgerow network structure were described by four distinct variables, namely hedgerow density, mesh-size heterogeneity, network connectivity and network fragmentation. Hedgerow density was determined as the total length of hedgerows within the sample divided by its area. Mesh-size heterogeneity was calculated using the Shannon index of diversity (Shannon & Weaver 1949; Legendre & Legendre 1998):

$$H' = -\sum_i P_i \ln(P_i) \tag{1}$$

where P_i represents the proportion of mesh-size class i within the sample. Ten classes of mesh size were used (< 0.1, 0.1–0.5, 0.5–1, 1–2.5, 2.5–5, 5–7.5, 7.5–10, 10–12.5, 12.5–15 and >15 ha), with mesh sizes estimated using Geographic Information Systems (GIS). Network connectivity was assessed by assigning a number to each hedgerow intersection as a function of the total number of connections it provides (Burel & Baudry 1990*b*; Schmucki *et al*. 2002). A T-type intersection, linking three hedgerows, provides six (3 × 2) possible connections, since each of the three hedgerows is connected with two others, while an X-type intersection, linking four hedgerows, offers 12 (4 × 3) possible connections, and an L-type intersection, linking two hedgerows, provides only two (2 × 1) connections. The number of connections per unit area provided a measure of the connectivity of the network. Network fragmentation was assessed by the number of dead ends (i.e. free hedgerow ends not connected with any other hedgerow) per unit area. The landscape position of the samples (percentage valley/plateau and distance to nearest village centre) was quantified using GIS. Present land use (percentage forest, pasture, fodder crops, cereals and built-up land) was determined by the analysis of aerial photographs in combination with field verification.

Overall connectivity of the study area's entire hedgerow network was examined in more detail by means of the following connectivity indices (Cantwell & Forman 1993; Forman 1995):

$$\gamma = \frac{L}{3(V-2)} \tag{2}$$

$$\alpha = \frac{L-V+F}{2V-5} \tag{3}$$

$$\beta = \frac{L}{V} \tag{4}$$

where L = number of linkages (hedgerows), V = number of nodes (hedgerow intersections) and F = number of discrete network fragments. While the γ-index weighs the actual number of linkages against the maximum possible number of linkages, the α-index compares the actual number of loops or circuits within the network with the maximum possible number of circuits. Both the γ- and α-index vary from 0 to 1 with increasing network connectivity. The β-index gives the average number of linkages per node, with a value < 1 indicating a relatively low connectivity and a value > 1 indicating more complex networks.

Data analysis

Sample-based differences in hedgerow network structure between periods were analysed using Friedman tests and non-parametric multiple comparisons (procedure described in Siegel & Castellan 1988). Temporal evolution of the connectivity indices and node type distribution of the entire hedgerow network were examined graphically.

Different groups of samples with distinct hedgerow network structural characteristics were determined using cluster analysis, considering the observations of the different periods as separate samples (i.e. working with a data matrix of 367 × 5 = 1835 samples by 4 structural variables). First, Gower's similarity coefficient (Gower 1971) was employed to obtain sample similarities. Next, samples were clustered hierarchically using Ward's method (Ward 1963). Calculation of similarities and clustering were done with ClustanGraphics 5.08 (Clustan 2001). The optimal number of clusters was established by interpretation of the clustering dendrogram. Differences between clusters were analysed with Kruskal-Wallis tests.

Combining the observations of the different periods (i.e. working with a data matrix of 367 samples by 4 × 5 = 20 structural variables), different groups of samples with distinct trajectories of change in hedgerow network structure were determined using hierarchical cluster analysis, with the followed methodology analogous to that described above. Next, multiple group discriminant analysis (Legendre & Legendre 1998) was used to assess the effect of landscape position on sample

Table 1 Hedgerow network structural characteristics in 1789, 1990, 1950, 1992 and 2002. Significance of differences among periods tested with Friedman test (*** $p < 0.001$). Values are means, with superscript characters indicating groups separated by non-parametric multiple comparisons ($p < 0.05$).

Characteristic	*1789*	*1900*	*1950*	*1992*	*2002*	*p*
Hedgerow density ($m\ ha^{-1}$)	75.17^b	86.85^a	48.05^c	35.38^d	39.69^c	***
Mesh size heterogeneity (Shannon index H′)	0.99^a	1.24^b	1.55^c	1.80^{cd}	1.96^d	***
Network connectivity ($connections\ ha^{-1}$)	2.73^b	2.84^a	1.02^c	0.38^d	0.46^d	***
Network fragmentation ($dead\text{-}ends\ ha^{-1}$)	0.06^a	0.17^b	0.24^c	0.32^d	0.38^e	***

trajectory membership. Relationships between landscape position and canonical discriminant functions were assessed by means of Pearson correlation coefficients. Differences in landscape position between sample trajectories were examined in more detail using one-way ANOVA and Bonferroni multiple comparisons.

Multiple linear regression was employed to analyse the effect of both land use and landscape position on present hedgerow network structure. Using the 2002 data, a separate regression model was constructed for each of the four structural variables (i.e. hedgerow density, mesh-size heterogeneity, network connectivity and network fragmentation). Except if stated otherwise, all analyses were done in Statistical Package for the Social Sciences, SPSS 11.0 for Windows (SPSS 2002).

RESULTS

Hedgerow network structure

There were significant differences between periods for all hedgerow network structural characteristics (Table 1). While the hedgerow density increased from 1789 to 1900, it more than halved between 1900 and 1992, then increased again slightly by 2002, resulting in the present average of $40\ m\ ha^{-1}$. The same pattern was observed for hedgerow network connectivity, with an increase during the 19th century, a substantial decrease throughout most of the 20th century and a stabilization in the last decade. In 2002, the study area harboured approximately 0.5 hedgerow connections ha^{-1}. Both mesh-size heterogeneity and network fragmentation progressively increased between 1789 and 2002. The Shannon index of mesh-size diversity was nearly 2 and the corresponding network contained on average 0.4 dead ends ha^{-1} in 2002. Visual inspection of the study area's hedgerow network in 2002 (Fig. 1) confirmed the presence of a heterogeneous and fragmented network with a relatively low connectivity.

Further insight into the temporal evolution of the network is provided by the connectivity indices (Fig. 2). Whilst a value above 1.00 indicates a relatively high connectivity for the networks of 1789 and 1900, the β-index strongly declined between 1900 and 1992. After 1992 the index rose slightly, to reach the value of 0.65 in 2002. Both the γ- and α-indices

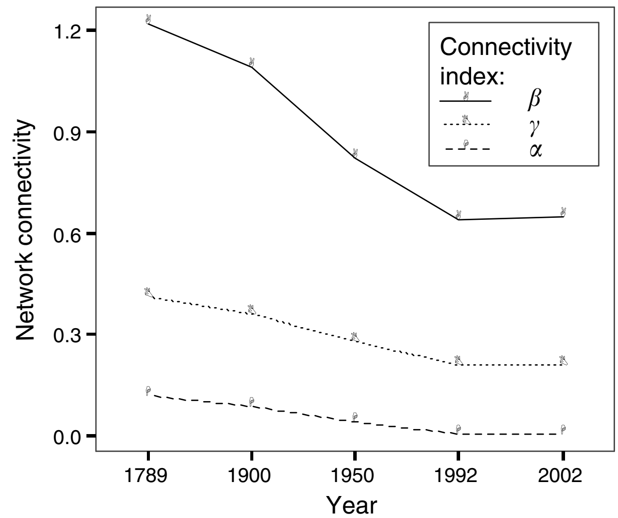

Figure 2 Plot of the hedgerow network connectivity indices for the entire hedgerow network as a function of time.

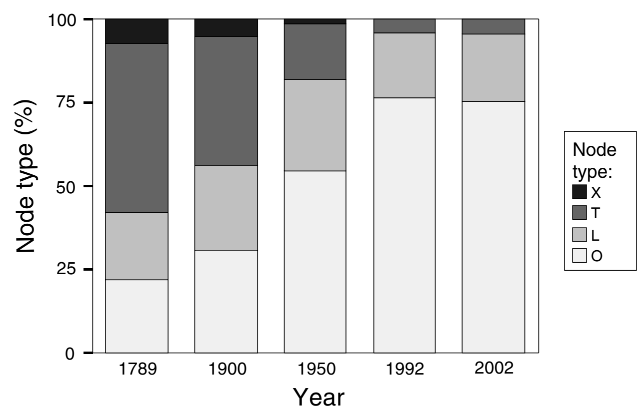

Figure 3 Plot of the hedgerow network node type distribution (fraction of O, L, T and X-type nodes) as a function of time.

were already rather low at the end of the 18th century and decreased steadily throughout the studied period. Only during 1992–2002 has this decline been partially reversed by a limited recovery, with the γ- and α-indices currently amounting to values of 0.21 and 0.03, respectively.

The relative frequency of the different node types as a function of time allowed further insight into the quality of the hedgerow network connections and confirmed the patterns described above (Fig. 3). The importance of X- and T-type nodes indicates a complex hedgerow network with a high connectivity in 1789 and 1900. However, X-type nodes almost disappeared and T-type nodes strongly declined over time, while the fraction of L-type nodes remained approximately constant and O-type nodes strongly increased in importance. In 2002, the landscape was characterized by a preponderance of O- and, to a lesser extent, L-type nodes, indicative of a strongly fragmented hedgerow network (Fig. 3).

Three different groups of samples with distinct hedgerow network structural characteristics were obtained using hierarchical cluster analysis (Table 2). The first cluster ($n =$

Table 2 Mean hedgerow network structural characteristics for the sample clusters obtained using hierarchical cluster analysis, treating the observations of the different periods as separate samples ($n_t = 1835$). Significance of differences among clusters tested with Kruskal-Wallis test (*** $p < 0.001$), values are cluster means, with superscript characters indicating groups separated by non-parametric multiple comparisons ($p < 0.05$).

Hedgerow network structural characteristics	*Cluster 1*	*Cluster 2*	*Cluster 3*	*p*
Hedgerow density (m ha^{-1})	21.63^{a}	67.74^{b}	131.11^{c}	***
Mesh size heterogeneity (Shannon index H′)	1.24^{a}	1.89^{c}	1.54^{b}	***
Network connectivity (connections ha^{-1})	0.26^{a}	1.32^{b}	5.03^{c}	***
Network fragmentation (dead-ends ha^{-1})	0.20^{a}	0.31^{b}	0.18^{a}	***
n	888	611	336	

888), containing samples with a poorly-developed hedgerow network, was characterized by low hedgerow density and connectivity. Mesh-size heterogeneity and network fragmentation were small as well. The second cluster ($n = 611$), with a partially-developed hedgerow network, had an intermediate hedgerow density and connectivity in combination with a high mesh-size heterogeneity and network fragmentation. The third cluster ($n = 336$), with a highly developed hedgerow network, had a high hedgerow density and connectivity together with a low mesh-size heterogeneity and network fragmentation. Samples with a highly developed hedgerow network prevailed in 1789 and 1900 with, respectively, 37% and 44% of the samples belonging to cluster 3 (Fig. 4*a*, *b*). Between 1900 and 1992, samples with a less developed hedgerow network strongly increased in importance, with the cluster 1 fraction rising from 23–70% (Fig. 4*b*–*d*). During 1992–2002, the hedgerow network recovered slightly, with a small increase in samples of cluster 2 (from 29% to 36%) and 3 (from 1% to 2%) (Fig. 4*d*–*e*).

Hierarchical cluster analysis of the combined dataset revealed three distinct trajectories of change in hedgerow network structure (Fig. 5). Samples of trajectory 1 ($n = 114$) began with a very low hedgerow density at the end of the 18th century, which increased over time (Fig. 5*a*). In contrast, samples of trajectory 2 ($n = 61$) started with an intermediate hedgerow density that decreased over time, whereas samples of trajectory 3 ($n = 192$) had a high initial hedgerow density, which also gradually decreased. Mesh-size heterogeneity progressively increased over time for trajectories 1 and 3, but remained more or less constant for trajectory 2 (Fig. 5*b*). With the exception of 1900, hedgerow network connectivity was generally low for trajectory 1 (Fig. 5*c*). Samples of trajectories 2 and 3 had, respectively, an intermediate and a high network connectivity at the start, which decreased over time. Network fragmentation gradually increased for all three trajectories (Fig. 5*d*).

Effects of land use and landscape position

A strong relationship between landscape position (percentage valley, distance to nearest village centre) and sample trajectory membership was demonstrated using discriminant analysis. Both canonical discriminant functions (CDFs) were

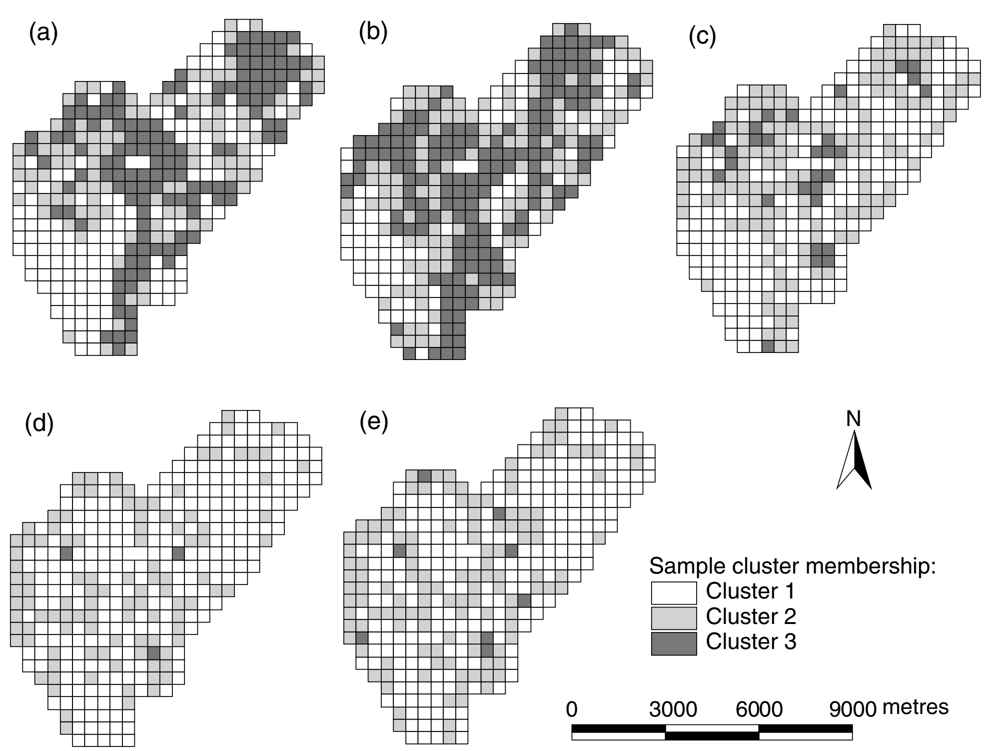

Figure 4 Spatial distribution of the three structural groups of samples, obtained using hierarchical cluster analysis, for the five periods studied: (*a*) 1789, (*b*) 1900, (*c*) 1950, (*d*) 1992 and (*e*) 2002. A detailed description of cluster attributes can be found in Table 2.

https://doi.org/10.1017/S0376892905001840 Published online by Cambridge University Press

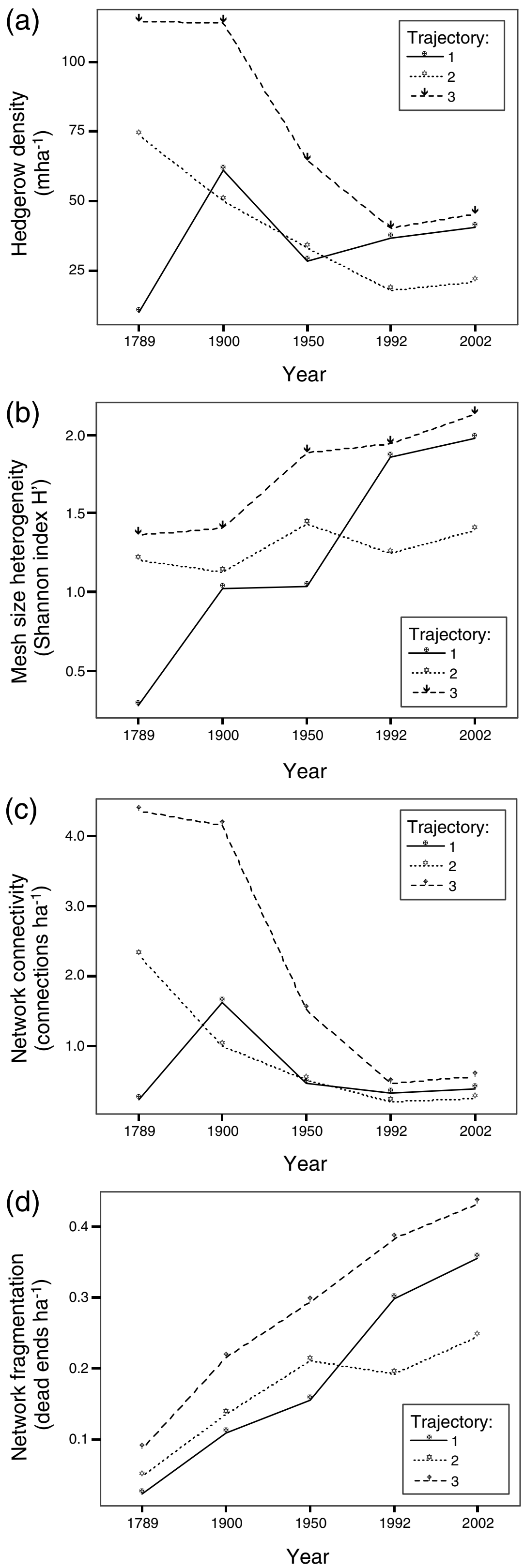

Figure 5 Hedgerow network structural characteristics of the sample trajectories obtained using hierarchical cluster analysis: (*a*) hedgerow density, (*b*) mesh-size heterogeneity, (*c*) network connectivity and (*d*) network fragmentation.

highly significant (Wilk's $\lambda = 0.62$ and 0.85, respectively, $p < 0.001$, Table 3). While distance to nearest village centre was significantly correlated with the first CDF ($r_p = 0.86$, $p < 0.001$), percentage valley was strongly linked with the second CDF ($r_p = 0.78$, $p < 0.001$) (Table 4). Based on the landscape position of the samples, trajectory membership could be efficiently predicted, with an overall classification success > 67% (Table 3). Interpretation of variable means showed that trajectory 1 was followed mainly by samples with a plateau position further away from the village centre, whilst samples with the same position but close to the village centre mostly adhered to trajectory 2 (Table 4). Samples with a valley position predominantly followed trajectory 3.

The effect of land use and landscape position on the 2002 hedgerow network structure was analysed with multiple linear regression (Table 5). Hedgerow density was positively related to the percentage of pasture and fodder crops within the sample and negatively related to the percentage of forest ($R^2 = 0.39$, $p < 0.001$). Mesh-size heterogeneity was negatively related to the percentage of pasture and positively related to the percentage of forest and fodder crops ($R^2 = 0.49$, $p < 0.001$). Network connectivity was positively related to the percentage of pasture and negatively related to the percentage of built-up land ($R^2 = 0.34$, $p < 0.001$). Network fragmentation was positively linked with the percentage of fodder crops and built-up land and negatively linked with the percentage of pasture ($R^2 = 0.45$, $p < 0.001$). In contrast with the strong relationships with current land use, none of the 2002 structural characteristics was significantly affected by the landscape position of the samples.

DISCUSSION

The study presented here is the first one addressing the long-term history of hedgerow network landscapes using a systematic and quantitative approach. Analysis of historical maps allowed a detailed reconstruction of the hedgerow network to be made over an extended period of time, also covering the period before World War II. With both the total amount of hedgerows within the landscape and the quality of the hedgerow network connections being important for hedgerow network functioning, the recorded variables (hedgerow density, mesh-size heterogeneity, network connectivity and fragmentation) describe key aspects of hedgerow network structure.

Hedgerow network dynamics

The structural evolution of the hedgerow network over the last two centuries can be divided into three distinct phases. The first phase, extending from the end of the 18th to the end of the 19th century, was a period of net hedgerow network development, with an increase in average hedgerow density and connectivity and a spatial expansion of the network (Table 1, Fig. 4). The observed change in landscape structure during this period was linked mainly to the reclamation of

Table 3 Results of multiple group discriminant analysis predicting trajectory membership based on the sample's landscape position. Both canonical discriminant functions (CDF) and classification success of the model obtained are shown.

Canonical discriminant function	*Eigen-value*	*Percentage of variance*	*Canonical correlation*	*Wilks' λ*	χ^2	*df*	*p*
CDF 1	0.37	67.9	0.52	0.62	172.45	14	< 0.001
CDF 2	0.17	32.1	0.39	0.85	58.36	6	< 0.001
Classification success (percentage of samples correctly classified):			*Trajectory 1*	*Trajectory 2*	*Trajectory 3*	*Total*	
			66.7	36.1	77.6	67.3	

Table 4 Correlation coefficients between original variables and canonical discriminant functions (CDF) as well as variable means for the different trajectories. Significance of differences between means tested with one-way ANOVA ($p < 0.001$ for both variables), superscript characters indicate groups separated by Bonferroni multiple comparisons ($p < 0.05$). $^{***}p < 0.001$, $^{**}0.001 < p < 0.01$, $^{*}0.01 < p < 0.05$, ^{ns} not significant.

Pearson correlation coefficient (r_p)		*CDF 1*	*CDF 2*
Distance to nearest village centre (km)		0.86^{***}	0.19^{ns}
Valley (%)		-0.32^{*}	0.78^{***}
Variable means	*Trajectory 1*	*Trajectory 2*	*Trajectory 3*
Distance to nearest village centre (km)	3.16^{a}	1.93^{b}	1.88^{b}
Valley (%)	29^{a}	33^{a}	64^{b}
n	114	61	192

heathland for agricultural expansion, triggered by the rising population pressure within the region and governed by specific legislation (Ulenaers 1986). An analysis of land-use patterns on historical maps confirmed the large-scale conversion of heathland into arable land during the 19th century, which resulted in a fine-meshed parcel structure for most of the study area at the start of the 20th century. Comparison with other studies, however, is difficult, because most authors have only studied hedgerow network dynamics over the last 50 years. Nevertheless, Pollard *et al.* (1974) and Baudry and Jouin (2003) mentioned the importance of the 18th and 19th century for hedgerow network expansion in Western Europe. In England, the process of 'Parliamentary Enclosure' by specific private enclosure acts led to widespread hedgerow planting during the period 1750–1850 (Hoskins 1955; Mingay 1997). Furthermore, the fact that hedgerow density reached its maximum at the end of the 19th century is confirmed by Braekevelt (1988), who provided a tritemporal inventory of a hedgerow network landscape in the Houtland region of north-west Belgium.

The second phase in hedgerow network dynamics covers most of the 20th century, and is characterized by extensive degradation of the hedgerow network, with a decrease in hedgerow density and connectivity and an increase in mesh-size heterogeneity and network fragmentation (Table 1, Figs. 2–4). The introduction of barbed-wire fences for pasture enclosure in conjunction with an increase in economically optimal parcel size, linked to the process of agricultural intensification and mechanization, were the main factors causing hedgerow removal within the study area during this period (Vandevoort *et al.* 2000; Kerselaers 2003). A major decline in hedgerow network structure throughout the 20th century has been observed in several West European countries, such as Belgium (Braekevelt 1988), France (Burel & Baudry 1990*b*; Pointereau 2001; Kesseler & Reif 2002) and Great Britain (Barr & Gillespie 2000; Petit *et al.* 2003). Denmark differs from this general pattern, with periods of both hedgerow expansion and degeneration, mainly because of a long history of shelterbelt planting programmes (Kristensen & Caspersen 2002; Busck 2003). North America is characterized by a fundamentally

Table 5 Results of the multiple linear regression analyses modelling the present hedgerow network structure as a function of land use and landscape position, based on the dataset of 2002. Both estimated regression coefficients and model R^2 values are shown. $^{***}p < 0.001$; $^{**}0.001 < p < 0.01$; $^{*}0.01 < p < 0.05$; ns = not significant.

Results		*Hedgerow density*	*Mesh size heterogeneity*	*Network connectivity*	*Network fragmentation*
Standardized regression coefficient (β)					
Landscape position	Valley (%)	ns	ns	ns	ns
	Distance to nearest village centre (km)	ns	ns	ns	ns
Land use	Forest (%)	-0.25^{*}	0.29^{**}	ns	ns
	Pasture (%)	0.36^{***}	-0.35^{***}	0.28^{**}	-0.23^{*}
	Fodder crops (%)	0.26^{*}	0.24^{*}	ns	0.38^{***}
	Cereals (%)	ns	ns	ns	ns
	Built-up land (%)	ns	ns	-0.21^{*}	0.24^{*}
Regression model R^2		0.39^{***}	0.49^{***}	0.34^{***}	0.45^{***}

different land-use history and shows a differential evolution in hedgerow network structure, with both increases and decreases in hedgerow density during the last century depending on landscape type and geology (Demers *et al*. 1995; Schmucki *et al*. 2002).

The last decade of the 20th century forms the third phase in the evolution of the landscape structure of the study area, with a slight recovery in hedgerow density and connectivity (Table 1, Fig. 4). In this period, there was a change in rural policy, with increased legal restrictions for hedgerow removal (which allowed felling only by permit) and the installation of a subsidy scheme for hedgerow planting and management. These changes, in combination with a growing awareness of the recreational, ecological and environmental functions of hedges, halted the process of hedgerow-network disintegration (Kerselaers 2003). Stabilization and even recovery of the landscape ecological network during the last decade of the 20th century also occurred in France and Britain (Pointereau 2001; Petit *et al*. 2001, 2003). Although hedgerow degradation has mostly stopped in quantitative terms, a qualitative decline often continued to occur, with old species-rich hedgerows being replaced by newly-planted monospecific hedges or rows of trees (Petit *et al*. 2001; Kesseler & Reif 2002; Kerselaers 2003).

Trajectories of change

Hedgerow-network structural dynamics is strongly linked with landscape position, with samples following distinct trajectories of change as a function of topography and village proximity (Tables 3 and 4, Fig. 5). Located at the plateau further away from the historical village centres, samples adhering to trajectory 1 formed mainly part of the extensive heathlands at the end of the 18th century and were therefore characterized by a very low initial hedgerow density. During the 19th century, these heathlands were progressively taken into cultivation, explaining the major increase in hedgerow density. On the plateau close to the village centres, samples followed trajectory 2 and mainly consisted of ancient arable fields around historical built-up land. These samples had a fairly well-developed hedgerow network already at the end of the 18th century that gradually decreased with time due to agricultural intensification. Situated in the valley complex, samples of trajectory 3 predominantly consisted of old hayfields and pastures, with a small-scale parcel structure and strongly developed hedgerow network at the end of the 18th century. The loss of the function of hedgerows as livestock fences with the introduction of barbed wire in the first half of the 20th century played a central role in the major decline in the hedgerow network of trajectory 3 samples during the last century.

While Reif *et al*. (1982), Demers *et al*. (1995) and Schmucki *et al*. (2002) have demonstrated strong differences in hedgerow network dynamics between landscape types with distinct geological characteristics, the present study shows that the topographical position within a given landscape also strongly affects the structural evolution of the hedgerow network. Furthermore, the importance of the location of the site with respect to nuclei of human habitation confirms the observations of Burel *et al*. (1990*b*) that distinct patterns of change in network structure occur with different types of human occupation, with a clear distinction between villages and less-populated areas.

Present network structure

Both the 2002 hedgerow density (40 m ha^{-1}) and connectivity (0.5 connections ha^{-1}) of the study area lie between values obtained for typical bocage landscapes in France on the one hand (Burel *et al*. 1990*b*; Kesseler & Reif 2002) and shelter-belt landscapes in Denmark and Canada on the other hand (Kristensen & Caspersen 2002; Schmucki *et al*. 2002). Furthermore, the small fraction of complex node types, with only 4% T-type and $< 1\%$ X-type nodes (Fig. 3), is comparable with findings for hedgerow networks in Britain and Denmark (Barr & Gillespie 2000; Kristensen & Caspersen 2002).

Land use strongly affected present hedgerow network structure (Table 5). Highly developed networks were predominantly associated with pastureland. Zones dominated by fodder-crop production typically carried a relatively dense, but heterogeneous and fragmented hedgerow network. The observation that grassland-dominated landscapes are characterized by a strongly developed hedgerow network confirms the results of Cherrill (1996). Schmucki *et al*. (2002) further demonstrated that the conversion of dairy farms, with a high percentage of pasture and fodder crops, into cereal-crop farms led to a clear decrease in hedgerow density. Thenail (2002) and Kantelhardt *et al*. (2003) studied the effect of farm characteristics and agricultural-site conditions on landscape structure and also found relationships between production type and hedgerow network structure. Severely fragmented networks with a low connectivity characterized built-up areas, whereas the presence of forest resulted in sparse, heterogeneous networks of linear semi-natural habitat (Table 5). In a similar way, Schmucki *et al*. (2002) found that the abandonment of agricultural fields followed by spontaneous afforestation led to a reduction in hedgerow density. Whilst landscape position affected hedgerow network structure through effects on land-use patterns in the past, the absence of a net effect of landscape position in 2002 (Table 5) was probably linked with a decoupling of land use from landscape position because of recent developments in agriculture, such as large-scale drainage and re-allotment programmes (Reif *et al*. 1982; Burel 1984).

The decoupling of the hedgerow network structure from topography and village proximity will mainly lead to a more uniform spread of hedgerows over the entire rural landscape, while the net effect on the absolute amount of semi-natural habitat might be relatively small. The strong impact of land use indicates that an encouragement of production systems based on pasture or grassland could help to conserve and restore a high-quality hedgerow network.

CONCLUSIONS

The hedgerow network structure of the studied landscape strongly changed over time. At the end of the 18th century, hedgerows were mainly concentrated around historical village centres and within valleys. Agricultural expansion and the reclamation of former heathland caused the network to expand progressively to the more remote parts of the plateau in the course of the 19th century. Then followed a period of extensive degradation, linked with the development of large-scale, mechanized agriculture. During the last decade of the 20th century, the hedgerow network recovered slightly, attributable to a change in rural policy and a growing awareness of the functional significance of linear, semi-natural habitat fragments in agricultural landscapes.

Hedgerow network structure was affected by land use and landscape position. Formerly, landscape position controlled to a large extent the allocation of different types of land use, with strong effects on hedgerow density and connectivity. Distinct trajectories of change in hedgerow network structure were observed in relation to topography and village proximity. At the end of the 20th century, the link between land use and landscape position was less strong. The 2002 hedgerow network structure was mainly affected by land use *per se*, with pastoral landscapes especially being characterized by a well-developed network.

ACKNOWLEDGEMENTS

A Research Assistant Grant from the Fund for Scientific Research, Flanders (FWO), supported Bart Deckers. We are grateful to the Limburgse Intercommunale voor Milieubeheer (LIM) for permission to use the 1992 inventory and for assistance with fieldwork in 2002. The environmental administration of the town of Peer provided financial support and housing during periods of fieldwork. Useful comments and linguistic corrections by N. Polunin and two anonymous referees greatly improved the manuscript.

References

Altieri, M.A. (1999) The ecological role of biodiversity in agro-ecosystems. *Agriculture, Ecosystems and Environment* **74**: 19–31.

Barr, C.J. & Gillespie, M.K. (2000) Estimating hedgerow length and pattern characteristics in Great Britain using Countryside Survey data. *Journal of Environmental Management* **60**: 23–32.

Baudry, J., Bunce, R.G.H. & Burel, F. (2000) Hedgerows: An international perspective on their origin, function and management. *Journal of Environmental Management* **60**: 7–22.

Baudry, J. & Jouin, A. (2003) *De la haie aux bocages – organisation, dynamique et gestion*. Paris, France: INRA.

Braekevelt, A. (1988) Evolution of the spatial structure of the hedgerows in the Houtland (NW-Belgium). In: *Connectivity in Landscape Ecology – Proceedings of the 2nd International Seminar of the International Association for Landscape Ecology*, ed. K.-F. Schreiber, pp. 153–155. Münster, Germany: Münstersche Geographische Arbeiten.

Burel, F. (1984) Use of landscape ecology for the management of rural hedgerow network areas in western France. In: *Methodology in Landscape Ecological Research and Planning – Proceedings of the 1st International Seminar of the International Association for Landscape Ecology*, ed. J. Brandt & P. Agger, pp. 73–81. Roskilde, Denmark: Roskilde University Centre.

Burel, F. & Baudry, J. (1990*a*) Hedgerow network patterns and processes in France. In: *Changing Landscapes: an Ecological Perspective*, ed. I.S. Zonneveld & R.T.T. Forman, pp. 99–120. New York, USA: Springer-Verlag.

Burel, F. & Baudry, J. (1990*b*) Structural dynamic of a hedgerow network landscape in Brittany, France. *Landscape Ecology* **4**: 197–210.

Busck, A.G. (2003) Hedgerow planting analysed as a social system – interaction between farmers and other actors in Denmark. *Journal of Environmental Management* **68**: 161–171.

Cantwell, M.D. & Forman, R.T.T. (1993) Landscape graphs: ecological modeling with graph theory to detect configurations common to diverse landscapes. *Landscape Ecology* **8**: 239–255.

Cherrill, A. (1996) Landscapes, land covers and linear features in a river catchment in northern England. *Landscape Research* **21**: 109–122.

Clustan (2001) *ClustanGraphics 5.08*. Edinburgh, UK: Clustan Ltd.

Croxton, P.J., Franssen, W., Myhill, D.G. & Sparks, T.H. (2004) The restoration of neglected hedges: a comparison of management treatments. *Biological Conservation* **117**: 19–23.

de Blois, S., Domon, G. & Bouchard, A. (2002) Factors affecting plant species distribution in hedgerows of southern Quebec. *Biological Conservation* **105**: 355–367.

De Langhe, J.E., Delvosalle, L., Duvigneaud, J., Lambinon, J. & Vanden Berghen, C. (1988) *Flora van België, het Groothertogdom Luxemburg, Noord-Frankrijk en de aangrenzende gebieden*. Meise, Belgium: Patrimonium van de Nationale Plantentuin van België.

Deckers, B., De Becker, P., Honnay, O., Hermy, M. & Muys, B. (2005) Sunken roads as habitats for forest plant species in a dynamic agricultural landscape: effects of age and isolation. *Journal of Biogeography* **32**: 99–109.

Deckers, B., Hermy, M. & Muys, B. (2004) Factors affecting plant species composition of hedgerows: relative importance and hierarchy. *Acta Oecologica* **26**: 23–37.

Demers, M.N., Simpson, J.W., Boerner, R.E.J., Silva, A., Berns, L. & Artigas, F. (1995) Fencerows, edges, and implications of changing connectivity illustrated by two contiguous Ohio landscapes. *Conservation Biology* **9**: 1159–1168.

Dover, J. & Sparks, T. (2000) A review of the ecology of butterflies in British hedgerows. *Journal of Environmental Management* **60**: 51–63.

ESRI (2000) *ArcView 3.2a*. Redlands, USA: Environmental Systems Research Institute Inc.

Forman, R.T.T. (1995) *Land Mosaics – The Ecology of Landscapes and Regions*. Cambridge, UK: Cambridge University Press.

Forman, R.T.T. & Baudry, J. (1984) Hedgerows and hedgerow networks in landscape ecology. *Environmental Management* **8**: 495–510.

Franco, D., Franco, D., Mannino, I. & Zanetto, G. (2003) The impact of agroforestry networks on scenic beauty estimation – the role of a landscape ecological network on a socio-cultural process. *Landscape and Urban Planning* **62**: 119–138.

Freemark, K.E., Boutin, C. & Keddy, C.J. (2002) Importance of farmland habitats for conservation of plant species. *Conservation Biology* **16**: 399–412.

Gower, J.C. (1971) A general coefficient of similarity and some of its properties. *Biometrics* **27**: 857–874.

Hinsley, S.A. & Bellamy, P.E. (2000) The influence of hedge structure, management and landscape context on the value of hedgerows to birds: a review. *Journal of Environmental Management* **60**: 33–49.

Hoskins, W.G. (1955) *The Making of the English Landscape*. London, UK: Hodder & Stoughton.

Kantelhardt, J., Osinski, E. & Heissenhuber, A. (2003) Is there a reliable correlation between hedgerow density and agricultural site conditions? *Agriculture, Ecosystems and Environment* **98**: 517–527.

Kerselaers, E. (2003) Ruimtelijke en temporele dynamiek van het landschapsecologisch netwerk in Peer. Master's thesis, Laboratory of Forest, Nature and Landscape Research, Katholieke Universiteit Leuven, Leuven, Belgium.

Kesseler, B. & Reif, A. (2002) Wandel der Heckenlandschaft, Heckenstructuren und Heckengehölzvegetation im Brionnais. *Naturschutz und Landschaftsplanung* **34**: 309–316.

Kleijn, D. & Verbeek, M. (2000) Factors affecting the species composition of arable field boundary vegetation. *Journal of Applied Ecology* **37**: 256–266.

Kristensen, S.P. & Caspersen, O.H. (2002) Analysis of changes in a shelterbelt network landscape in central Jutland, Denmark. *Journal of Environmental Management* **66**: 171–183.

Le Coeur, D., Baudry, J. & Burel, F. (1997) Field margins plant assemblages: variation partitioning between local and landscape factors. *Landscape and Urban Planning* **37**: 57–71.

Legendre, P. & Legendre, L. (1998) *Numerical Ecology*. Amsterdam, the Netherlands: Elsevier Science.

Marshall, E.J.P. & Arnold, G.M. (1995) Factors affecting field weed and margin flora on a farm in Essex, UK. *Landscape and Urban Planning* **31**: 205–216.

Marshall, E.J.P. & Moonen, A.C. (2002) Field margins in northern Europe: their functions and interactions with agriculture. *Agriculture, Ecosystems and Environment* **89**: 5–21.

Mingay, G.E. (1997) *Parliamentary Enclosure in England*. London, UK: Longman.

Moore, N.W., Hooper, M.D. & Davis, B.N.K. (1967) Hedges I. Introduction and reconnaissance studies. *Journal of Applied Ecology* **4**: 201–220.

Nationaal Instituut voor de Statistiek (2004) *Landbouwstatistieken*. Brussels, Belgium: FOD Economie, KMO, Middenstand en Energie.

Petit, S., Stuart, R.C., Gillespie, M.K. & Barr, C.J. (2001) Woody field boundaries in Great Britain: stock and change between 1990 and 1998. In: *Hedgerows of the World: Their Ecological Functions in Different Landscapes – Proceedings of the 2001 Annual IALE (UK) Conference*, ed. C. Barr & S. Petit, pp. 111–116. Birmingham, UK: University of Birmingham.

Petit, S., Stuart, R.C., Gillespie, M.K. & Barr, C.J. (2003) Field boundaries in Great Britain: stock and change between 1984, 1990 and 1998. *Journal of Environmental Management* **67**: 229–238.

Pointereau, P. (2001) Development of the space occupied by hedgerows in France over the past 40 years: the contribution and limits of statistical data. In: *Hedgerows of the World: Their Ecological Functions in Different Landscapes – Proceedings of the 2001 Annual IALE (UK) Conference*, ed. C. Barr & S. Petit, pp. 117–122. Birmingham, UK: University of Birmingham.

Pollard, E., Hooper, M.D. & Moore, N.W. (1974) *Hedges*. London, UK:W. Collins & Sons.

Reif, A., Schulze, E.-D. & Zahner, K. (1982) Der Einfluss des geologischen Untergrundes, der Hangneigung, der Feldgrösse und der Flurbereinigung auf die Heckendichte in Oberfranken. *Berichte der Bayerische Akademie für Naturschutz und Landschaftspflege* **6**: 231–253.

Rounsevell, M.D.A., Annetts, J.E., Audsley, E., Mayr, T. & Reginster, I. (2003) Modelling the spatial distribution of agricultural land use at the regional scale. *Agriculture, Ecosystems and Environment* **95**: 465–479.

Schmucki, R., de Blois, S. & Bouchard, A. (2002) Spatial and temporal dynamics of hedgerows in three agricultural landscapes of Southern Quebec, Canada. *Environmental Management* **30**: 651–664.

Shannon, C.E. & Weaver, W. (1949) *The Mathematical Theory of Communication*. Urbana, USA: University of Illinois Press.

Siegel, S. & Castellan, N.J. (1988) *Nonparametric Statistics for the Behavioral Sciences*. New York, USA: McGraw-Hill.

SPSS (2002) *SPSS 11.0 for Windows*. Chicago, USA: SPSS Inc.

Thenail, C. (2002) Relationships between farm characteristics and the variation of the density of hedgerows at the level of a micro-region of bocage landscape. Study case in Brittany, France. *Agricultural Systems* **71**: 207–230.

Thies, C. & Tscharntke, T. (1999) Landscape structure and biological control in agroecosystems. *Science* **285**: 893–895.

Thomas, C.F.G., Parkinson, L., Griffiths, G.J.K., Fernandez Garcia, A. & Marshall, E.J.P. (2001) Aggregation and temporal stability of carabid beetle distributions in field and hedgerow habitats. *Journal of Applied Ecology* **38**: 100–116.

Turner, M.G. (1989) Landscape ecology: the effect of pattern on process. *Annual Review of Ecology and Systematics* **20**: 171–197.

Ucar, T. & Hall, F.R. (2001) Windbreaks as a pesticide drift mitigation strategy: a review. *Pest Management Science* **57**: 663–675.

Ulenaers, J. (1986) De bevolkingsevolutie van Peer en zijn fusiegemeenten in de negentiende eeuw. *De Zeven Torens* **1**: 3–6.

Vandevoort, C., Van Orshoven, J., Smis, K., Gellynck, X. & Viaene, J. (2000) *Gemeentelijk landbouwontwikkelingsplan Peer*. Leuven, Belgium: Afdeling Agro-Marketing, Universiteit Gent and Ground for GIS, KULeuven Research and Development.

Ward, J.H. (1963) Hierarchical grouping to optimize an objective function. *Journal of the American Statistical Association* **58**: 236–244.