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Why and how we should study field boundary biodiversity in an agrarian landscape context

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Abstract

Field boundaries are generally considered as important semi-natural environments in agrarian landscapes. The aim of this paper is to provide a methodological framework towards a holistic approach for field boundary studies. First, an overview of the successive milestones that have been passed in the history of hedgerow studies is given. These are classified a posteriori and then related to the succession of dominant ecological paradigms. Secondly, we show how former results have been used and integrated into a multiple scale approach involving agronomic and ecological studies in hedgerow network landscapes of western France. The hypothesis is that the main determinants of hedgerow biodiversity are related to farming activities. This hypothesis has been tested in three hedgerow network landscapes differing in their density of hedgerows and their relative abundance of grassland versus crops. The dominant agriculture of the region is dairy production, utilising grassland, maize and cereals. We focus on plant biodiversity and relate it to farming activities described from the boundary up to the landscape. The results show that the composition of the plant assemblages of the herb layer of field boundaries depends upon complex interactions between local structure, herb layer management, field use, farm types and landscape structure. The latter factors are related to the diversity of farming systems. Finally, the advantages of such an approach in terms of fundamental and applied landscape management aspects are discussed, showing how our framework of hedgerow studies expands by successive incorporation, rather than by rejection of former approaches. The main lesson is that it is necessary to capitalise on closer collaboration between ecologists and agronomists in order to stimulate future development of field boundary management and planning. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Biodiversity; Field boundary; Agriculture; Landscape; Ecological paradigms; Plants; Hedgerow

1. Introduction

Conserving and enhancing biological diversity is of great concern to policy makers. Nature conservation policies have traditionally been defensive, focusing on the protection of nature in reserves, on the one hand, and on the preservation of particular species on the other (Franklin, 1993). However, both the strategies have failed to meet their original goal of safeguarding biodiversity in an adequate manner and, even more so, they have failed to reach their objective of sustainability (Duhme et al., 1997). The two main reasons for this are: (i) ecological processes do not recognise the borders of reserve areas; (ii) many species depend

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Nomenclature

Plant species names follow Flora Europae (Tutin et al., 1964–1980)

on man-induced disturbances and are hence not able to survive in "static" protected areas for a long time.

Agricultural modernisation was responsible for considerable changes in both the agricultural practices and landscape structure (Meeus, 1993) in western Europe. Small biotopes (such as woodlots, hedgerows, ditches and grass verges) have largely disappeared from modern agricultural landscapes (Agger and Brandt, 1988). With the increased mechanisation of agriculture, the costs of field boundaries were considered to be greater than the benefits and the number of field boundaries has decreased drastically: 5000 km of field boundaries were removed annually in UK in the late 1960s (Hooper, 1970), 14% of the hedgerow network disappeared from the Northern Ireland landscape between 1976 and 1982 (McAdam et al., 1994), 500 000 km of uncultivated linear features vanished from Finnish agricultural landscapes during the last three decades (Helenius, 1994), and 740 000 km of hedgerows were lost in France during the same period (Pointereau and Bazile, 1995).

In present day arable landscapes, perennial field boundaries are generally considered to have important ecological functions: habitats for farmland wildlife, with special emphasis on game birds (Rands, 1986, 1987); overwintering sites for predatory insects (Harwood et al., 1992; Lys and Nentwik, 1992; Lys, 1994; Zangger, 1994); buffers against erosion and floods (Mérot, 1999) or potential sites for denitrification processes (Haycock et al., 1993). Kaule and Krebs (1989) reported that almost 45% of the species in the flora of different parts of southern Germany grow in edge habitats that cover no more than 8–10% of the landscape.

The wise management of nature and the preservation of its biodiversity depend upon knowledge of the actual forces that maintain biodiversity. It is assumed that, in agricultural landscapes, the main driving factors are related to farming activities. The objectives of the present paper are: (1) to briefly review the history of hedgerow studies following the pathway of shifting ecological paradigms during the last five decades (we do not intend to provide a review, see, e.g. Le Cœur (1996) and Burel (1996), for a more comprehensive contribution); (2) to give methodological insights, together with a few selected results from our studies in Brittany, western France, in order to link biodiversity in hedgerows to various aspects of farming activities, taking place at several spatial scales.

2. Field boundaries as isolated features

Initially, field boundaries were considered as isolated and elongated pieces of semi-natural habitat between two adjacent landscape elements. Most of the early studies essentially concerned woody field boundaries or hedgerows. In this approach, the hedgerow was regarded as a linear forest, acting as a habitat or a refuge in which ecological processes occurred with no or few interaction with the surrounding land. The 1960s and 1970s were the times of rapid agricultural changes, which led to massive hedgerow removal. The question addressed by ecologists was, most of the time, simply: what will be lost if we continue removing hedgerows? The way to answer it was, very often, no more elaborate than: let us go and census what lives in hedgerows. These investigations provided amounts of empirical evidence, showing the overall importance of hedgerows as habitats for plants (Richards, 1928; Helliwell, 1975; Hegarty et al., 1994; Mountford et al., 1994), breeding birds (Yahner, 1982; O'Connor, 1987; Parish et al., 1994a,b, 1995), small mammals (Boone and Tinklin, 1988) and invertebrates (Lewis, 1969a,b).

Concerning plants, the central tenet of common ecological thought was that they were organised in communities and associations, and the first step in vegetation science was to describe them without questioning their theoretical foundation. The alternative continuum concept had not yet reached the continent (Austin, 1985). So, in France, e.g. there were many studies on field boundaries, mainly restricted to woody ones, i.e. hedgerows, which aimed to try to recognise, often with limited success, plant associations previously described in forest edges (Rozé, 1976; Delelis-Dusollier, 1973).

The ecology of hedgerow network landscapes was still limited to phenomenological community ecology, at the very local scale of the hedgerow itself. There were few attempts to relate floral diversity to farming activities, despite the fact that the primary motivation for the studies was driven by landscape changes related to agricultural modernisation. From a methodological viewpoint, field boundaries were essentially seen as wild places to sample vegetation and fauna and had most of the time no clear spatial definition. A section of hedgerow was sampled, without asking where the hedgerow started or ended, where the sampling area should be placed or considering why these matters were important. Thus farming activities, taking place in the adjacent field, were not taken into account to explain patterns of biodiversity in field boundaries, neither was the place of the boundary in the landscape considered.

3. Field boundaries and adjacent fields

A second way to look at a hedgerow was to consider it as a field boundary, the border, the outer part, the woody limit of a field. Most farmers, historians and agronomists of the 1950–1970s shared this approach and, as demonstrated below, this ecologically judicious viewpoint. Hedgerows are generally man-made, they were built by rural societies between Neolithic times and World War II (Rackham, 1986; Morgan Evans, 1994), and the motivation for planting them was precisely to enclose fields. This viewpoint resulted in a series of agronomic works focusing on the positive effects of hedgerows for crop protection (Barloy et al., 1976; Lemaire et al., 1976), wind speed reduction (Cabom, 1957; Caborn, 1976; Olesen, 1976), or soil erosion prevention (Carnet, 1976; Soltner, 1985). Most of the latter scientific works concerned the hedgerow and adjacent field. Ecologists showed that hedgerows influence insect distribution in adjacent fields (Lewis, 1969a,b), but they did not analyse the effects of fields on hedgerow species.

Relating a field to its boundary (implicitly in latter studies, a woody one and a hedgerow), constituted a first step toward integrating ecological and agronomic viewpoints. Although many authors used the term "bocage" (hedgerow network landscape), few of them carried out studies at larger scales than one field, and addressed processes that are relevant to a landscape approach.

4. Field boundaries as part of a corridor network

In 1980s, with the emergence of landscape ecology, ecologists started to describe landscapes within the conceptual framework of the "patch-matrix-corridor" paradigm (Forman and Godron, 1986). Because of the prevailing weight of both the island biogeography theory (MacArthur and Wilson, 1967) and metapopulation theory (Levins, 1970), the early research carried out on animal movements focused on species in woodlots and forests or woody corridors (Forman et al., 1976; Bennet, 1990a; Verboom and van Apeldoorm, 1990). The development of both the landscape ecology (Forman and Godron, 1986) and of theoretical foundations for assembly rules in communities (Tilman, 1994) emphasised how the dynamics and diversity of a community depend not only on neighbourhood interactions, but also on the dispersal of organisms among neighbourhoods. A species may be absent from a locality not because of local biotic interactions, but because none of its propagules has yet arrived at that site. Such recruitment limitation has often been cited as an important factor determining successional dynamics and community diversity and composition in the context of prairie ecosystems (Platt and Weis, 1977; Gross and Werner, 1982), forest environments (Davis, 1981), or within a more general and theoretical approach (Huston and Smith, 1987). From a landscape ecological viewpoint, agricultural landscapes were often described as patches of suitable habitats, often remnant woodlots of historical interest (Hooper, 1976; Peterken and Game, 1981; Rackham, 1985), embedded in a hostile, or at best neutral, sea of agriculture, but fortunately more or less connected by a network of hedgerows. These hedgerows were thought to play a major role as corridors for forest species (Forman, 1983), enhancing their movements between patches of suitable habitats (Merriam, 1984; Bennett, 1990b). In this respect, studies on hedgerows were central to the establishment of hypotheses and development of early landscape ecology (Forman and Baudry, 1984).

The two following examples illustrate some of the studies carried out on the importance of hedgerows

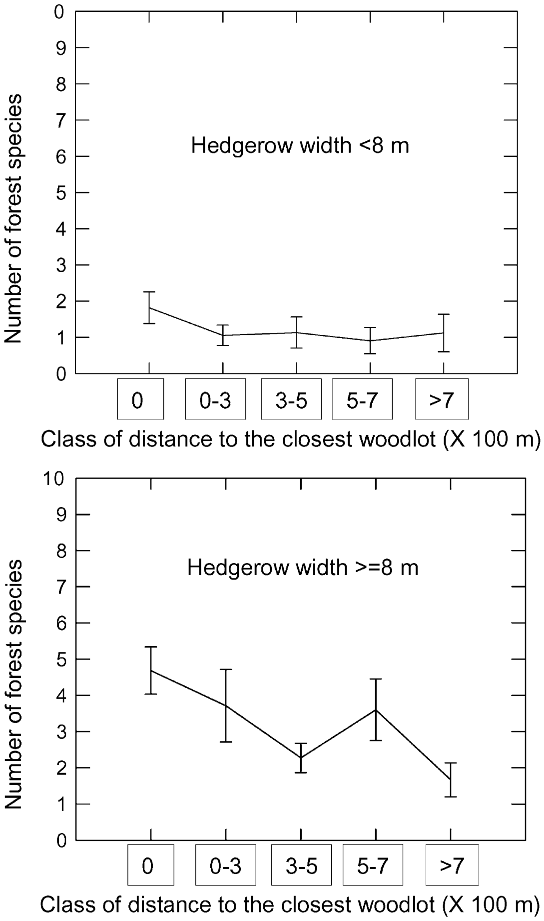

Fig. 1. Relationships between the average number of forest plant species found in hedgerows in New Jersey, hedgerow width and distance to woodlots; bars are standard error (after Baudry, 1985).

for species dispersal. Fig. 1 shows the relationship between the average number of forest plant species found in hedgerows in New Jersey, and the distance to woodlots (Baudry, 1985). First, the number of forest species is lower for narrow hedgerows as compared with wide ones; thence, the quality of the corridor, here in terms of a relationship between width and intensity of forest atmosphere, influences plant species colonisation. Second, it appears that for wide hedgerows the number of forest species decreases with increasing distance to woodlots. As woodlots were older than the hedgerows connected to them, and contained all the forest species found in the hedgerows, Baudry (1985) considered that woodlots behaved as sources of forest species. Hedgerows in this environment were about 50 years old and comprised spontaneous rows of shrubs and trees. So, this pattern of decreasing number of species, as distance to woodlots increases, was interpreted as a pattern of plant colonisation from woodlots into hedgerows.

Some forest carabid beetles are restricted to the network of uncultivated landscape elements during their whole life cycle. These stenotypic species are able to live in agricultural landscapes at considerable distances from forests, as long as a dense network of hedgerows remains (Burel, 1989). These species can survive in woody networks as fragmented populations. Local populations are located in small woods and large intersections of hedgerows. Linear features providing a minimal tree cover can be used as dispersal corridors linking populations (Petit and Burel, 1993). A survey of individual movements was performed using radiotracking techniques on the forest carabid *Abax parallelepipedus*. Charrier et al. (1997) compared the movements in four types of landscape elements used by the species: a woodlot; a lane formed by two parallel hedgerows; a hedgerow with continuous tree cover; a hedgerow with sparse trees. The elements also differed by their adjacent land uses, either meadows or crops. The results showed walking pattern was similar in the four elements (random walk) but intensity of movements differed significantly. Fig. 2 shows movement trajectories for individuals traced in the woodlot and in the densely vegetated hedgerow. The nature of the adjacent land use, determining the sharpness of the transition between the uncultivated element and the agricultural matrix had an effect on the behaviour of the beetle. Half of the carabids left linear features to enter meadows, while only one entered young maize (*Zea mays*) crops with much bare soil. The edge between the hedgerow and the meadow appears more permeable for the beetle, whereas a sharp contrast in environmental conditions creates a barrier effect (Burel et al., 2000). The two latter case studies show that corridor quality and connection is of primary importance for determining its functional efficiency in dispersal processes. Nevertheless, direct or indirect influences of farming activities on corridor quality are not explicitly addressed neither at the site nor at the landscape scale.

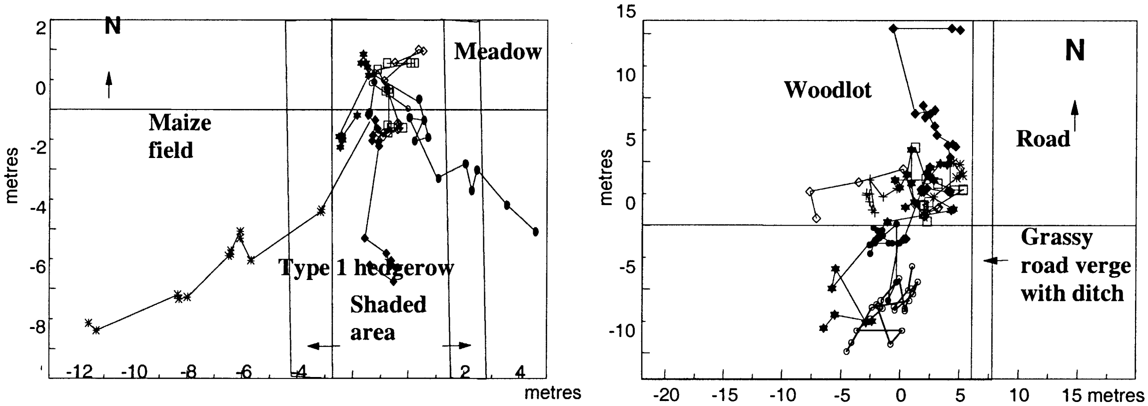

Fig. 2. Movement trajectories for *Abax parallelepipedus* individuals traced in the woodlot (left, $n = 8$ individuals) and in the densely vegetated hedgerow (right, $n = 7$ individuals). One spot = one individual (Burel et al., 2000).

5. Field boundaries in the landscape mosaic

In the late 1980s, the community of landscape ecologists experienced a shift from the patch-matrix-corridor model to a mosaic representation of landscapes (Wiens et al., 1993). This approach has been facilitated, and surely stimulated, by works on the concept of heterogeneity in ecology (Roff, 1974; Turner, 1989) and the development of numerous tools to quantify it (Turner and Gardner, 1991). The neutral matrix was questioned as a concept and landscape ecologists started to develop coloured mosaic mapping. This was in connection with a growing awareness, in the ecologists' community, of the facts that: (i) farmers exist and exhibit a valuable human, cultural biodiversity (Bunce and Howard, 1990; Baudry, 1993; Baudry et al., 2000); (ii) farmers are mainly mosaic species and organise their farm territory according to constraints and rules, and are thus collectively responsible for emerging land use patterns at the landscape scale (Thenail, 1996); (iii) farmers also manage field margins in a wide range of ways (Asteraki et al., 1994; Bannister and Watt, 1994; Baudry et al., 1998).

How do field margins experience this diversity of land uses, farming systems and farmers? The following sections present the methodology which we developed to tackle this issue and some of the results we obtained from our studies on hedgerow network landscapes in Brittany, western France.

6. Integrating former results through interdisciplinary multiple scale studies

In 1993, we started a research project on the management and ecology of bocage landscapes. The interdisciplinary research group included ecologists and agronomists (Baudry et al., 2000). The investigations were conducted in parallel, though on the same landscapes and the same landscape units (fields and fields boundaries). This enabled, from the beginning, the construction of an analytical framework linking farming activities, landscape structure and plant species composition. Initially, contrasted landscapes near each other were chosen, as landscape ecology theory predicted that they would be different in terms of species composition.

Both the ecological and agronomic approaches are multiple scale: in plant ecology, field boundaries are embedded in a mosaic of fields and landscapes, whereas in agronomy boundaries are part of a land use/farming system. Our results made possible the construction of an analytical framework starting from farming systems diversity, as opposed to landscape diversity. The framework was also used to study the vegetation diversity of stream banks in the same landscapes.

6.1. The study sites

The study area is located in northern Brittany, south of Mont-Saint-Michel Bay, France (48°36′N,

Fig. 3. Illustrations of some typical hedgerows of the region.

1°32′W). The climate is temperate oceanic with average precipitation around 600 mm/annum. The delimitation of the units was based on landscape structure drawn from aerial photographs and field examination. The grain size of the field mosaic, the density of hedgerow network, and the relative abundance of grassland versus crops were all taken into account in selecting three hedgerow bocage landscape types. As the three landscapes are within 5–10 km from each other, they have a common plant species pool. Their area varies from 500 to 700 ha. In site A, the hedgerow network has the highest density, site B is intermediate, and site C is a more open landscape with a low density of hedgerows. Hedgerows are rows of oak (*Quercus robur*) or chestnut (*Castanea sativa*), in general, planted on an earthen bank 0.5–0.8 m high. The shrub layer, dominated by hazel (*Corylus avellana*), hawthorn (*Crataegus monogyna*), blackthorn (*Prunus spinosa*), broom (*Cytisus scoparius*), spindle (*Euonymus europaeus*), or gorse (*Ulex europaeus*), is rarely continuous. Most hedgerows also have gaps in the tree layer due to felling with no replacement. Trees are pruned for firewood every 9–12 years. Fig. 3 represents views of typical hedgerows of the region.

6.2. Data collection

The different investigations in agronomy and ecology on the sites started at the same time. To ensure standardisation, common basic landscape elements for analysis were defined. A field was defined as a unit of land use (one user, one set of agricultural practices) and a boundary as the segment of boundary networks (comprising any uncultivated linear feature: woody hedgerow, grassy bank and grassy strip) between two fields (Baudry and Thenail, 1999). According to our approach, relating ecological processes within a boundary to an adjacent field needs to strictly associate it with an agricultural unit of management. If a boundary is situated along a field corresponding to two different units of management (e.g. two different farmers) it is split into two different boundaries, even if its structure appears homogeneous along these two units of management. As the boundary is situated between two fields, and as the structure of the base of the boundary is in many cases an earthen bank, a structure with two sides, we assumed a boundary has two sides, each of them related to the adjacent field. So, within a boundary, two field

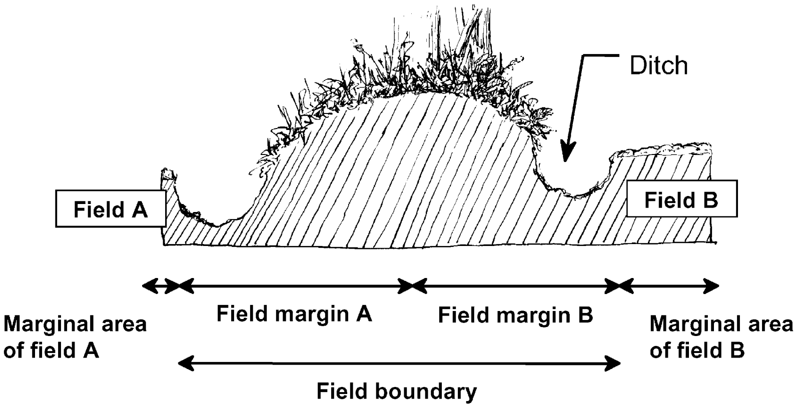

Fig. 4. Spatial delimitation of a boundary and its margins (Baudry et al., 1998).

margins were distinguished for vegetation sampling (Fig. 4).

Vegetation relevés were carried out in a sub-network of each site. The analysis of farming activities was as follows: (1) field mapping of the different land cover and crops; (2) interviews with farmers about their production systems and crop succession. The goal was to interview all the farmers having at least a field in the study sites. Sixty-nine farmers were interviewed, they farm about 80% of the land of the sites and other farmers did not accept the interview or were not found; (3) a monthly survey of management practices on the field margins of the sub-networks to record the presence of management (mowing, spraying, fire, grazing, etc.). Land cover in adjacent fields were also noted.

Herb layer vegetation was sampled in 25 m long quadrats (one quadrat per margin), placed in the middle of the field margin or stream bank to avoid intersection effects. We chose to focus on herbaceous and woody plants of the herb layer since they regenerated naturally (most of tree or shrub species of the upper layers were planted or favoured), more diverse, and consequently more likely to reflect changes in environmental factors. Plant species abundance was scored according to Tansley's scale, from 1 (few) to 5 (very abundant) (Tansley and Chip, 1926). Relevés were made on both the sides of field boundaries in 1993 or 1994, to relate vegetation data to adjacent land use. Structural characteristics of the margins (height of the vegetation, tree cover, shrub cover, canopy width, bank height, bank-ditch width, ditch depth, ditch width) were also recorded and management options of the herb layer were assessed every month during both the years. Four hundred and fifty five margins were sampled (137 in site A, 186 in site B, and 132 in site C).

6.3. Data management and analysis

Basic landscape features were mapped using Arc-Info as a geographical information system (GIS), and data stored in a database. Sixty per cent of the fields were in farms for which we had information from interviews. For those fields, it is possible to link land cover/use to hedgerow and farm characteristics, connecting vegetation, landscapes and farming systems.

For farming systems and hedgerow structure, we established typologies using multivariate analysis, correspondence analysis followed by cluster analysis (Legendre and Legendre, 1998). Canonical correspondence analysis (CCA) was used to relate plant species composition to environmental variables (ter Braak, 1986). Each variable was tested with Monte Carlo permutation test before inclusion into the model, and the forward selection was stopped once we reached the first non-significant variable at $P = 0.05$. Variation partitioning on two sets of variables was performed by the partial CCA approach of Borcard et al. (1992) and Økland and Eilersten (1994). The fraction of variation explained by one set of variables was obtained by CCA after forward selection of variables from this set, in order to eliminate variables which did

Table 1
Types of farming systems

Type	Characteristics
MC	Meat cattle farms
CC	Cash crop farms
ADC	Farms after dairy production cessation
MSD	Medium production (50–200 000 l quota per annum) specialised dairy farms
SDD	Small production (20–50 000 l quota per annum) diversified dairy farms
LSD	Large production (>200 000 l quota per annum) specialised dairy farms
LDD	Large production (>200 000 l quota per annum) diversified dairy farms

not contribute significantly to the variation. At each step, variables were tested with the Monte Carlo test and only variables significant at $P = 0.05$ level were included in the regression model (Le Cœur et al., 1997).

6.3.1. Farm typology

Dairy production is the dominant type of farming system in the region. Dairy farms can be classified according to milk quotas and diversity of production (cereals and meat). We made four groups of dairy farms. Some farms do not produce milk and are specialised in meat production or cash crops (cereals). Table 1 gives a description of those six farm types.

6.3.2. Hedgerow typology

The typology was built with correspondence analysis followed by a cluster analysis on the first three factors (Legendre and Legendre, 1998). The following variables were used to describe hedgerow structure: maximum tree height, dominant tree height, canopy width, width of the non-cultivated zone, tree cover and shrub cover. Six clusters were retained, the main characteristics of which are given in Table 2.

Table 2
Types of hedgerow structure

Type	Characteristics
STRU1	Tree height: 12–14 m, canopy width: 9 m
STRU2	Tree height: 10 m, gaps, canopy width: 7 m
STRU3	Tree height: 6 m, gaps
STRU4	Mainly shrubs, gaps
STRU5	Shrubs: 1.5 m, gaps
STRU6	Brambles and/or isolated trees

6.4. The hypotheses and the spatial hierarchy of factors driving plant diversity

The hypotheses tested were structured according to an hierarchical approach, from the local structure of the boundary, up to the landscape context. Our hypotheses relating vegetation to structural factors (boundary and landscape structure) are presented, and show that these factors are the results of farming activities. We translate the effects of farming activities in terms of ecological variables of importance for plants. Results on the importance of variables at each scale are presented and, finally, a hierarchy of the importance of the different sets of variables is proposed.

6.4.1. Relating vegetation to boundary structure

The first hypothesis concerned the relationships between field boundary structure and the composition of the plant assemblages of the field margin herb layer. We hypothesised that the composition of plant assemblages can be influenced by field boundary structure, because this diversity of structures provides a diversity of primary ecological factors (Tilman, 1988) that are relevant to basic plant requirements. For example, grassy banks or strips constitute open environments, favouring light-requiring species. In contrast, hedgerows with dense shrub and tree cover create a shaded forest atmosphere, low evapotranspiration and so potentially suitable conditions for the so-called forest species. Not only differences in the cover of woody species, but also differences in structures of the base of the hedgerow can account for variations in plant composition. Hedgerows planted on earthen banks adjacent to ditches provide a water gradient from base to top of the bank, and potentially recruit, at the scale of the margin, species with different preferences regarding soil moisture. This view emerged from working within a conceptual framework of the continuum model approach of vegetation science (Austin and Smith, 1989) rather than a community one.

As shown by Baudry et al. (2000), differences in boundary structures are related to the diversity of farming systems. Fig. 5 exemplifies the relationships between farm types and hedgerow structure, where the same type of farm existed on both the sides. Cash crop farms mainly have hedgerows with few trees and shrubs. In contrast, diversified productive dairy farms have dense hedgerows. Diversified dairy farms with low production exhibit an intermediate pattern. Baudry et al. (1998) analysed field margin (herb layer) structure in 15 farms. They showed that these margins differed widely from farm to farm. The structures varied from dense cover of grasses to dead leaves and mosses or bramble (*Rubus fruticosus*). Thus the structures providing shade or permitting light are dependent upon farm types.

The results of vegetation analyses were consistent with our hypothesis concerning the relationship between plant species composition and boundary structure. Variables describing the characteristics of tree and shrub layers of vegetation (dominant height, maximum height, canopy width, tree cover and shrub cover) explained a larger fraction of variance than those related to the bottom of the margin (bank height, bank-ditch width, ditch depth, ditch width and uncultivated zone width). The margins with the highest tree and shrub cover included species requiring conditions of forest environments (e.g. *Brachypodium sylvaticum*, *Polygonatum multiflorum* and *Hedera helix*). Hygrophilous or meso-hygrophilous species (e.g. *Pulicaria dysenterica*, *Lotus uliginosus* and *Angelica sylvestris*) were significantly more frequent in the margins showing the widest and deepest banks.

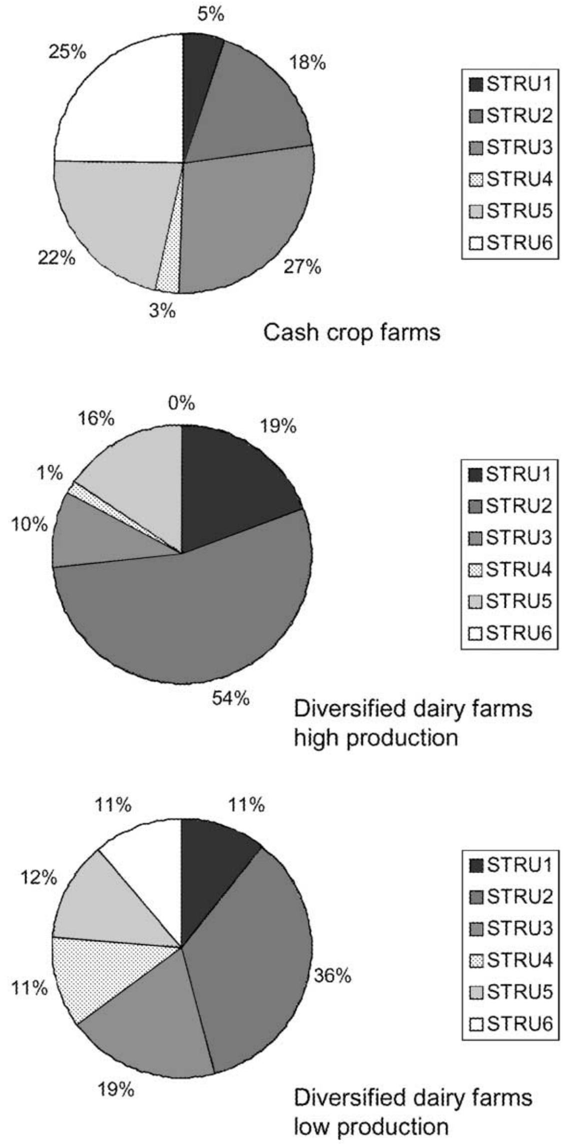

Fig. 5. Examples of the distribution of types of hedgerow structures in three farming systems (STRU1—tree height: 12–14 m, canopy width: 9 m; STRU2—tree height: 10 m, gaps, canopy width: 7 m; STRU3—tree height: 6 m, gaps; STRU4—mainly shrubs, gaps; STRU5—shrubs: 1.5 m, gaps; STRU6—brambles and/or isolated trees).

6.4.2. Relating vegetation to boundary management

The second step of the hypothesis scheme concerned the relations between field margin management and plant diversity. Farmers use a range of management practices with respect to their field margins. Wood harvesting, fire management of the herb layer, mowing, bank trampling or grazing are likely to influence the composition of plant assemblages. The way in which grazing, e.g. interferes with competition has been well-documented in prairie or grassland environments (Kydd, 1964; Puerto et al., 1990). Openings in the herb layer, created by trampling or herbicide application, create gaps for colonisation and transitory establishment of species with the

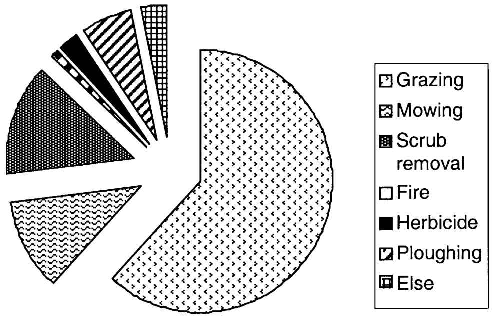

Fig. 6. Diversity of field margin management observed monthly on 600 margins over a 4 year period.

ability to use resources rapidly and with efficient dispersal mechanisms (Grime, 1979). In our landscapes, they were mainly annual species, usually found in arable areas.

Fig. 6 shows that margin management regimes are diverse. Grazing is the most frequent because it occurs whenever a field is grazed; other types of practices happen only once a year. These practices represent different disturbances, even if they are all associated with vegetation removal. Grazing is a recurrent disturbance, during the period the field is laid as grassland, while fire destroys all aerial parts of plants, as do broad-spectrum herbicides. Mowing may leave the biomass on the margin, recycling nutrients. Ploughing is the most disturbing, as it facilitates colonisation by incoming seeds or stolons, as do fire and herbicides.

With respect to the influence of management on plant species composition, our results showed that, for sites A and C, this set of management variables shared an important fraction of variance. This was also true for adjacent land cover, so that cover and management were correlated in this case. This was is especially true for the grazing modality, which is almost always associated with grassland, although some farmers may graze their cattle in maize fields after harvest in order to benefit from fallen cobs. However, in site B, land cover and margin management appeared poorly related. Annual weed species (e.g. *Sinapis arvensis*, *Euphorbia helioscopia* and *Bilderdykia convolvulus*) were more frequently found in margins sprayed with herbicide than in other type of management. In grazed margins, we preferentially found perennial species, either hygrophilous (e.g. *Mentha aquatica* and *Juncus acutiflorus*) or mesophilous (e.g. *Lolium perenne* and *Poa pratensis*).

6.4.3. Relating vegetation to adjacent land cover/land use

In the third step, we hypothesised a relationship between the plant assemblages of the herb layer and the adjacent land cover and/or land use. Fig. 7 illustrates the differences in land use between farm types for maize and permanent grassland. When maize area increases, that of permanent grassland diminishes. Cash crop farms have mainly cereals and oilseed rape. Thus farm type provides a surrogate for land use.

Naturally, field farming practices differ according to the nature of the field. Margins adjacent to cropped fields are more likely to receive fertiliser or pesticide misplacement or mechanical disturbance by machinery than those along permanent grasslands. Woodlots, sunken roads or verges generally constitute a more stable environment. Finally, adjacent fields can act as a source of plant propagules for field margin colonisation. For example, a disturbed field margin, adjacent to a cropped field is more susceptible to colonisation by weed species than is a disturbed margin adjacent to a grassland, because the marginal area of a cropped field is a better source of propagules of these species than a grassland (McAdam et al., 1994).

Results of the CCA of vegetation data showed a significant relationship between adjacent land cover and plant species composition in adjacent boundaries. Perennial, either hygrophilous (e.g. *Apium nodiflorum*, *M. aquatica* and *J. acutiflorus*) or mesophilous (e.g. *Potentilla erecta* and *Dryopteris filix mas*) species characterise margins adjacent to permanent or long-term grasslands. The margins adjacent to woodlots show a floristic composition close to that of margins adjacent to grassland, but the so-called forest species (e.g. *Hypericum pulchrum*, *Polypodium vulgare* and *Blechnum spicant*) are more frequently found here. Annual weed species (e.g. *Fumaria vulgaris*, *Senecio vulgaris* and *Lapsana communis*), that are found in cropped areas, are significantly more frequent in margins adjacent to crops than in any other margin location. As margins adjacent to crops are also the more frequently sprayed with herbicide, the combination of disturbances and availability of propagules is probably responsible for the colonisation of margins adjacent to crops by weed species.

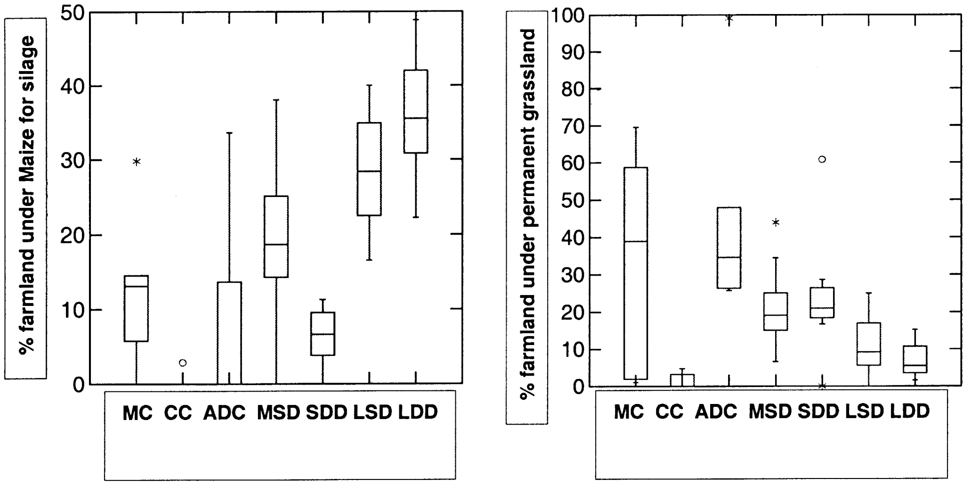

Fig. 7. Areas of crop types in the different farming systems (MC: meat cattle farms; CC: cash crops farms; ADC: farms after dairy production cessation; MSD: medium production (50–200 000 l quota per annum) specialised dairy farms; SDD: small production (20–50 000 l quota per annum) diversified dairy farms; LSD: large production (>200 000 l quota per annum) specialised dairy farms; LDD: large production (>200 000 l quota per annum)). Boxplots indicate interquartile ranges around median with whiskers indicating maximum and minimum values and outliers shown as ∗ or ○.

6.4.4. Relating vegetation to farm type

This type of analysis was only performed for stream banks, as farm type was one of the variables used in the sampling scheme. These farm type variables could be tested because Thenail (1996) documented them. Therefore, our ecological sample was stratified according to her results. A balanced ecological sample was built based on farming activities that are not visible in the field, using the results of former agronomic studies. This methodological aspect is an important point that emphasises, once again, the necessity of integrated studies joining agronomic and ecological investigation to a common framework.

The results of vegetation analyses showed a significant relationship between the plant composition of the herb layer of stream banks and the variable "farm type". Diversified dairy farms with large production preferentially include on their stream banks annual nitrophilous weed species (e.g. *Matricaria perforata*, *Solanum nigrum*, *Stachys palustris* and *Bromus sterilis*). Stream banks adjacent to fields utilised by cash crop farms show similar pattern of floristic composition, including especially *Anagallis arvensis*, *Avena fatua* and seedlings of the nitrophilous shrub *Sambucus nigra*. At the opposite extreme, perennial species intolerant to nitrogen enrichment (e.g. *Pimpinella major*, *Trifolium pratense* and *Centaurea nigra*) characterise the flora of stream banks found in farms after dairy production has ceased.

6.4.5. Relating vegetation to landscape type

We hypothesised that landscapes differing in the spatial arrangement of their elements, and especially the density of their hedgerow networks, are likely to include different plant species assemblages in their field margins. The three study sites differed in the type of hedgerows, their density, as well as by the types of farms. Fig. 8 gives the density of the different types of hedgerows in the three sites. For all types, site C has the least density of hedgerows. Site A has the highest density for the three most dense types of vegetation, and site B, for the least dense. Overall, sites A and B differ more by the type of hedgerows than by the total density. These results mean that in site A, windbreak and shade effects are greater than in site B.

Differences in farm types, hedgerow density and differences in recent landscape dynamics certainly affect plant species composition. The three sites have different proportions of the different farm types (Fig. 9). Site A is dominated by dairy farms of

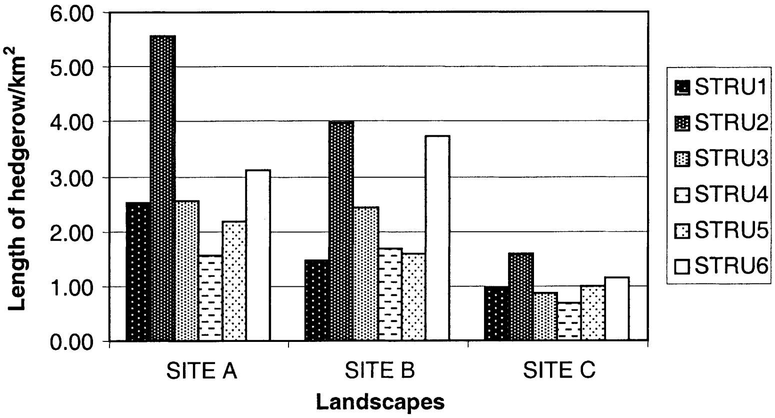

Fig. 8. Density of the different types of hedgerows in the three sites (STRU1—tree height: 12–14 m, canopy width: 9 m; STRU2—tree height: 10 m, gaps, canopy width: 7 m; STRU3—tree height: 6 m, gaps; STRU4—mainly shrubs, gaps; STRU5—shrubs: 1.5 m, gaps; STRU6—brambles and/or isolated trees).

medium size, site B is very diverse, and site C has highly productive farms either in milk or cash crops. These differences explain the present landscape structures and land uses mediated by different techniques of production and levels of inputs.

Within a context of landscape dynamics from fine grain to coarse grain (Morant et al., 1995), present day landscapes of different grain sizes represent different stages in the dynamics. They are presently different because their history, in terms of agricultural activities is different. Once established, perennial plant species, especially the clonal ones, can persist despite less favourable conditions (Peterken and Game, 1981). In this respect, the species we record today can be seen as evidences of past ecological conditions. Harper's (1977) inspired and famous claim should more often be kept in mind: "Vegetation is interpreted as a stage on the way to something. It might be more healthy and scientifically more sound to look more often backwards and search for the explanation of the present in the past, to explain systems in relation to their history rather than their goal."

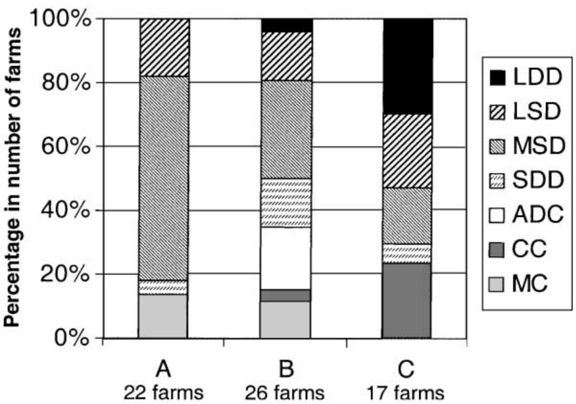

Fig. 9. Area of the different farm types in the three sites.

Differences in grain size and density of hedgerow networks can be responsible for mesoclimatic differences at the landscape scale, as documented in early agronomic studies of hedgerow network landscapes (Cabom, 1957; Damagnez, 1976; Guyot and Seguin, 1976; Olesen, 1976). Finally, limited empirical evidence (Baudry, 1985) showed that municipalities differing in their landscape characteristics harboured significantly different floras in their hedgerows.

Concerning vegetation, the results of the CCA again showed a significant relationship between plant species composition of the boundaries and the type of landscape. Samples from site A were characterised by perennial, heliophilous and xerophilous species, that are preferentially found on top of earthen banks (e.g. *Fragaria vesca* and *Geum urbanum*) or perennial species preferring forest habitat (e.g. *P. multiflorum*, *Lathyrus montanus* and *Euphorbia amygdaloides*). Numerous weed species (e.g. *Cardamine hirsuta*, *Oxalis europaea* and *Veronica arvensis*) were found in plant relevés from site B. And finally, margins of site C preferentially contained either weed species (e.g. *Capsella bursa pastoris*, *A. fatua* and *M. perforata*) or shade preferring or hygrophilous species (e.g. *Achillea ptarmica*, *Lysimachia vulgaris* and *Hieracium umbellatum*).

6.4.6. Hierarchy of environmental variables

The results of separate analyses of field margin vegetation from the three study sites showed that there was a significant relationship between plant species composition of the herb layer and variables which describe farming activities at both the field margin scale and field scale. Fig. 10 displays average inertia per variable for each set of variables, in each site, with only the significant ones retained (Økland and Eilersten, 1994). At the field margin scale, there was a significant relationship between both the structure and management, and the plant species composition. At the field scale, the type of land cover and the identity of the land user (farmer using the field) significantly influenced the plant composition of the herb layer. Comparing the variances associated with the different sets of variables, to propose a hierarchy of their contribution, we found that the management of the herb layer is the variable with the lowest inertia. The nature of the adjacent land cover is, most of time, as important or more important than the structure of the margin itself in determining the composition of plant assemblages. So, generally speaking, the local structural conditions and adjacent land cover affect plants in the herb layers of field margins more, than by the disturbances related to direct management. A possible explanation is that we have considered only management during the year of vegetation survey; as management change from year to year, it would be better to take into account the accumulation of successive management practices to show their effect. If most field boundaries experience the same succession of practices, they cannot explain much of the differences in vegetation; only when the overall practices are different, can be the cause of plant assemblage diversity.

When a second CCA was carried out by pooling the data from the three landscapes we obtained the hierarchy displayed in Fig. 11. As variables are somewhat correlated, only the part of variance explained by each variable not shared with other variables is shown. Concerning variances of "margin structure", "margin management" and "adjacent land cover", the same pattern of hierarchy as in separate analyses of data from each landscape was found. However, the most important feature here was the highest amount of variance explained by the variable "landscape type". This suggests that the plant assemblages of field margins are primarily explained by overall environmental variables, acting at the landscape level. Further, information is available in Le Cœur et al. (1997).

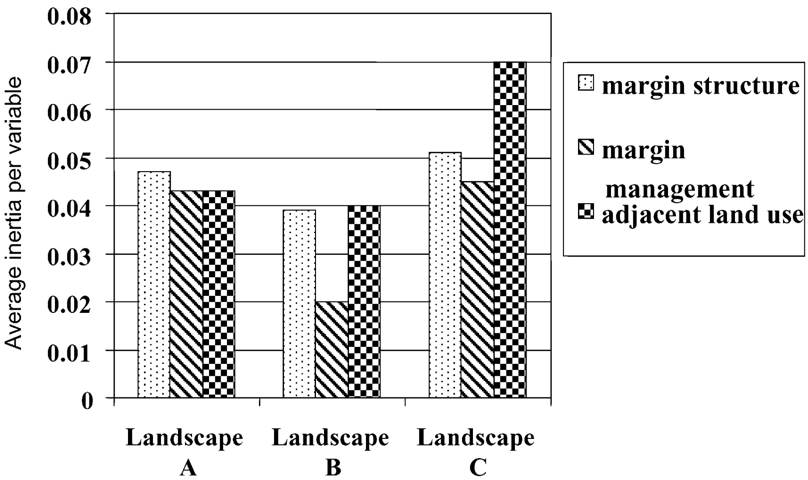

Fig. 10. Hierarchy of the different sets of variables in explaining plant species composition in field boundaries. Results of separate CCA of data from the three landscapes.

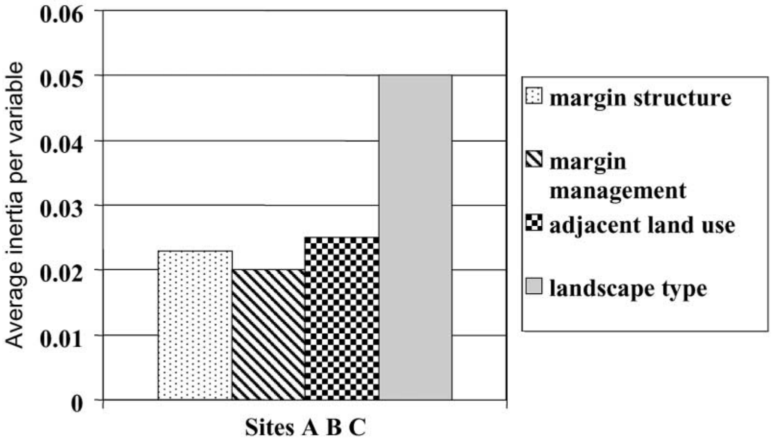

Fig. 11. Hierarchy of the different sets of variables in explaining plant species composition in field boundaries. Results of CCA combining data from the three landscapes.

The same methodological approach was applied to stream banks. Fig. 12 shows the inertia explained by the variables we tested. However, at the stream bank scale, we found no relationship between structure and plant composition of herb layer. Our explanation for this difference between field margins and stream banks is based on two arguments. First, the diversity of structure is not as great in the case of stream banks as it is for field margins: in our landscapes, most stream banks are woody features. So, the range of values for the variables describing structure of the upper layers is narrower in the former case. Second, differences in water gradients that were important in explaining differences in margin plant assemblages are, of course, less variable in the case of stream banks. At the field scale, a significant relationship between plant assemblages and two new explanatory variables, crop succession and farming system, was found. Here again, the variable "landscape type" explained the highest amount of variance.

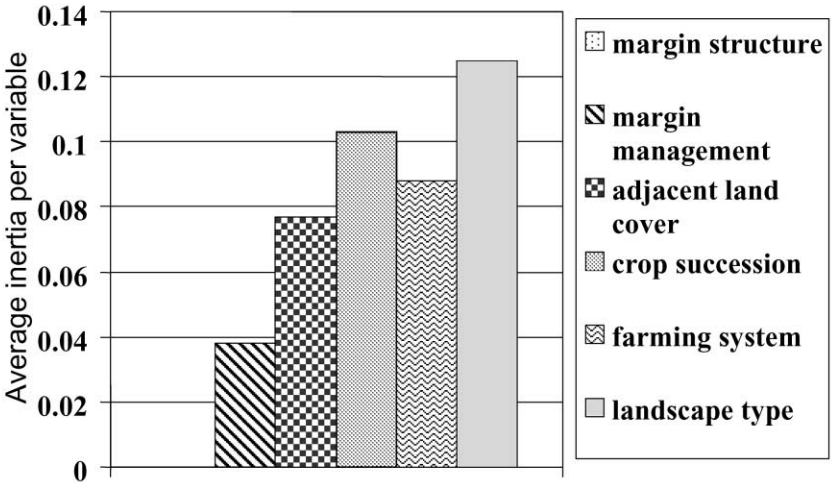

Fig. 12. Hierarchy of the different sets of variables in explaining plant species composition in field stream banks. Results of CCA combining data from the three landscapes.

7. Discussion and conclusion

From this brief account of the history of the ecology of field boundaries, two aspects may be emphasised:

1. The different steps do not imply a rejection of former approaches. Analysis of hedgerows as parts of network components does not mean that local factors (light, humidity and nutrients) are not important, or are less important than corridor effects. Our analyses, based on plant species abundance in the herb layer of field margins, showed that local structural factors were highly significant in determining plant species composition. In this respect, they are consistent with results reported by (Baudry, 1985; Hegarty et al., 1994; Marshall and Arnold, 1995; Rozé, 1976; Boatman et al., 1994), which showed relationships between flora and hedge structure.

   By looking at corridor effects, we added a new process: dispersal, which accounted for an important part in the variation of vegetation of boundaries or forests. The shift to the landscape/farming mosaic incorporates new processes, mainly in the realm of farming systems (crop succession, land use and management practices). Management practices are no longer considered as deleterious disturbances but should be integrated in a positive way within the farming system framework. The theory grows by successive incorporation.
2. The results for landscape management are also important. A single boundary approach helps to decide which are "important" boundaries or hedgerows, given their species composition. The network approach stresses the role of connectivity to maintain dispersal. Finally, the mosaic approach emphasises both the importance of landscape design and of production/management practices. The shift is from a "protection" to a management approach. It encourages us to see field boundaries not as historical remnants of wilderness, but simply as margins of modern fields. Barrett and Barrett (1997) emphasise this shift from a static protection of "ecological heritage object" to a preservation of ecosystem processes as important in conservation biology.

The mosaic approach requires testing in different conditions. It has a great potential to generate new hypotheses. The possibilities of designing sampling to test the relative weight of hedgerow structure, landscape structure, farming systems opens new avenues to understanding human activities as driving factors of biodiversity, to deciphering the scales of the variables driving changes in biodiversity, and also to design multiple scale land use policies.

The definition of good management practice at the boundary/margin scale is attractive but has, at least, two shortcomings: (1) if the same practices, how good they are, are applied everywhere, biodiversity will certainly decrease (we have shown that diversities of margin structures and managements are responsible for associated diversities of plant species compositions); (2) it does not take into account the internal diversity of land uses and their short time scale dynamics in farms. Setting objectives at the farm scale or for landscape units may be more efficient than setting standards for individual boundaries.

The incorporation of processes at a coarser scale must occur and it will be in the form of on the one hand, biogeography and the effect of regional species pool and, on the other hand, the diversity of policies regulating agriculture and of their implementation.

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