Landscape Ecology (2006) 21:631–639
DOI 10.1007/s10980-005-5321-1

Report

Are similar landscapes the result of similar histories?

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Received 1 September 2004; accepted in revised form 17 November 2005

Key words: Agricultural landscape, Landscape ecology, Landscape history, Landscape metrics, Multivariate analysis, Seine floodplain

Abstract

This landscape study was based on the sampling of 20 replicated landscape sites (1 km^2 each) that were located within the floodplain of the river Seine. For each site, 13 landscape variables were measured at three dates (1963–1985–2000). The aim of this study was to investigate the overall landscape variability through its different dimensions (space vs. time) and to assess the relative importance of each dimension. We used a new statistical method, i.e., partial triadic analysis (PTA), which allowed us to assess both (1) the spatial variability of the floodplain landscape and its dynamics in time and (2) the dynamic trajectories of the landscape variables for each site. The results showed, at the floodplain scale, the same landscape pattern has emerged since 1963, although a major trend was observed which consisted in a decrease in meadows resulting from an increase in arable crops. At the site scale, landscape sites, even if they were all influenced by this general trend during the 40-year period, showed contrasting trajectories. These results suggest that similar sites in 2000 do not necessarily share common histories and that contrasting sites in 2000 may have originated from similar patterns in 1963. The issue of biodiversity surrogates is then discussed, suggesting that new landscape metrics should be developed, emphasising spatial variability and (or) temporal dynamics.

Introduction

Landscape variables describing the mosaic and structure of landscapes may be used as surrogates for biological diversity (Moser et al. 2002). Landscapes are described by metric indices referring to the number, size and juxtaposition of landscape elements. These elements are important for explaining the overall landscape patterns and their variability (Hulshoff 1995; Riiters et al. 1995; Hargis et al. 1998). Because landscapes are dynamic, such metrics can also be used for monitoring landscape changes (Dunn et al. 1991).

There are basically two kinds of approaches for dealing with the relationships between landscape metrics and biodiversity: 'between-sites' studies aim at comparing at a given date the current contrasted landscapes and their relative biodiversity (Wilson et al. 2002; Burel et al. 2003; Jeanneret et al. 2003; Shriver et al. 2004) whereas 'within-sites' studies aim at monitoring these relationships over a time period in one of very few focal sites (Berlin et al.

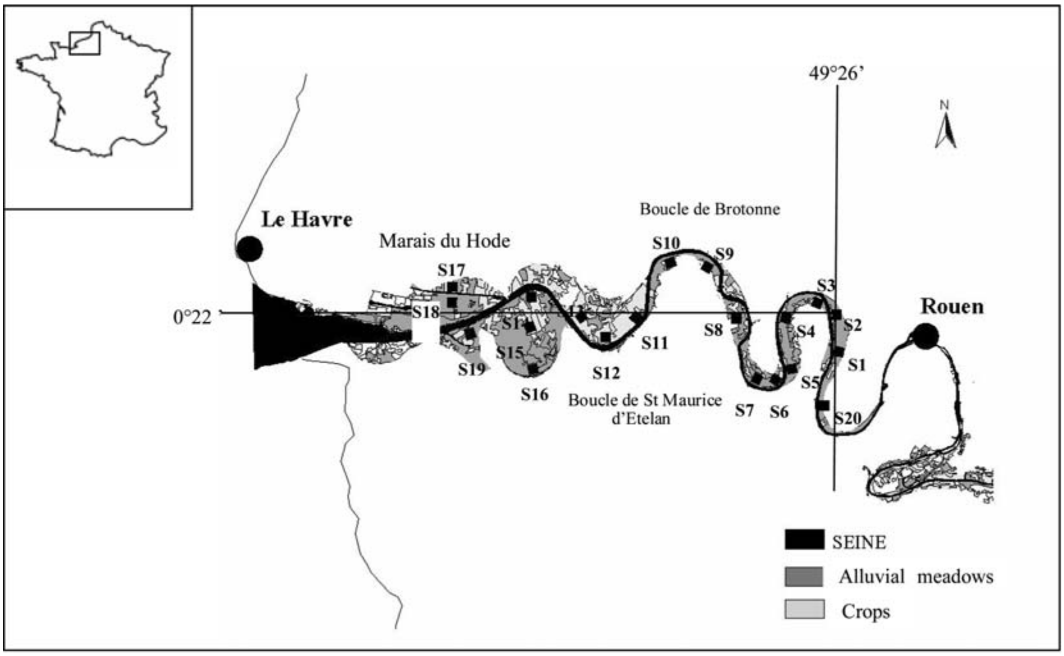

Figure 1. Lower Seine valley between Rouen and Le Havre and the location of the 20 studied sites.

2000; Garbutt and Sparks 2002). Because historical biological data are seldom available, the trade-off between exploring spatial variability and exploring temporal dynamics often focuses on spatial dimensions integrating local and regional effects (Wiens 1989; Duelli 1997; Brosofske et al. 1999; Lindenmayer 2000). As a consequence, attempts to explore all these sources of variability (space vs. time) in a given landscape are very rare, although several studies have emphasised the importance of both spatial and temporal processes for the control of biodiversity (Cousins and Eriksson 2001; Dupouey et al. 2002; Poudevigne and Baudry 2003; Lindborg and Eriksson 2004).

In this paper, we used replicated landscape sites in a floodplain landscape in order to investigate the respective weight of temporal compared with spatial variability in the overall variability of the current landscape. We aimed at answering two questions: is the present landscape variability in the floodplain a recent or an old feature? Do landscape sites with similar values for landscape metrics also share common drivers and dynamics?

Our purpose in this paper is to assess the overall landscape variability through its different dimensions (time vs. space). This is a crucial initial step that aims at giving the general framework in which biological processes occur. From this study based on landscape attributes, we then discuss the role of spatial compared with temporal sources of landscape variability for the definition of potential biodiversity surrogates.

The study was carried out in the lower Seine floodplain landscape, which has encountered major changes in the last century. These changes have progressively disconnected the river Seine from its floodplain in the lower reaches (Poudevigne et al. 1997). As a consequence, landscape dynamics are mainly influenced by agriculture, which has become the main factor of landscape organisation in this valley (Ernoult et al. 2003). Biodiversity issues are becoming important in this area as such a wetland represents a major wildlife habitat for north-western France.

Materials and methods

Study site

This survey was conducted on the lower Seine valley floodplain (Figure 1) which extends from Rouen to the Le Havre estuary (France). Twenty landscape sites (each corresponding to a 1 km × 1 km square) representative of the floodplain landscape were positioned along the river Seine at an altitude of less than 5 m above sea level. The climate is temperate oceanic (annual average temperature: 9.8 °C), mainly influenced by Atlantic depressions. The landscape is dominated by agricultural activities and consists of a habitat mosaic of wet grasslands, crops, orchards etc. (Ernoult et al. 2003). These habitats are established on recent gleysoils or fluvisoils alluvia (FAO et al. 1998).

Like many European rivers, the Seine was almost entirely channelled at the beginning of the 20th century to enhance the agricultural use of the rich alluvial soils, to secure river navigation and to prevent flooding (Meybeck et al. 1998). The embankments, which prevent the river from flooding, have disturbed the hydrological functioning of the floodplain, which until the 19th century, was subjected to regular overflowing by the Seine. Its hydrology is now related to groundwater fluctuations (Fustec and Lefeuvre 2000). This hydrological management has considerably reduced the wetlands area. Until the beginning of the 20th century, the floodplain was mainly composed of wet grasslands surrounded by a well-developed hedge network constituting a typical 'bocage' landscape. With agricultural intensification and the setting up of the drainage network, this flooded land dried up and landscape patterns became modified, with a switch to arable farming, an increasing field size and a decrease in the hedge network (Poudevigne et al. 1997).

Landscape mosaic

Each site was a 1 km^2 (Figure 1). The landscape study was conducted on the 20 sites at three dates, chosen according to changes in agricultural practices: 1963 (before the setting up of the Common Agricultural Policy: CAP); 1985 (after the setting up of the CAP) and 2000 (the present landscape).

Plots in each site were delineated and interpreted from black and white aerial photographs (National Geographical Institute (IGN); 1/20,000) for the years 1963 and 1985 and coloured aerial photographs (IGN; 1/25,000) for 2000 to obtain information on the landscape mosaic and structure. Data were collected in a GIS (Arc View 3.2; ESRI) to produce a classification according to the land cover. Ten classes were identified: arable crops, orchards, grasslands, poplar plantations, forests, buildings, tree cultivations, copses, industry and open water. Additional data concerning the hedgerow network completed the data set.

Landscape structure metrics

The analysis was conducted on the vector coverage using the software package FRAGSTATS for Arc view (McGarigal and Marks 1995). The indices used in the analyses were: the number of patches (NP), mean shape index (MSI), patch size coefficient of variation (PSCV), Shannon's evenness (SHEI) and juxtaposition index (IJI). These indices were selected from a complete list of indices described in (McGarigal and Marks 1995) after a correlation analysis was conducted on the complete list. An additional index was used: the connectivity index (CON) which was calculated for quantifying the network quality (Burel and Baudry 1990). Metrics data were calculated for each site and for each date (1963–1985–2000).

Data analysis

All data were processed by multivariate analysis with ADE-4 software (Thioulouse et al. 1997).

A Partial Triadic Analysis (PTA) (Thioulouse and Chessel 1987) was computed for the study of the spatio-temporal structure of floodplain landscapes. Several examples of application can be found in ecology (Aliaume et al. 1993; Blanc et al. 1998; Rossi 2003). The aim of this method is to analyse a three-way table (i.e., a data cube; in this study of landscape variables * sites * date) presented as a sequence of two-way tables. The general aim of this method is to determine the proportion of variability in the landscape variables that depends on space or on time. For our study, PTA offered the possibility to study these tridimensional data in two ways (Figure 2): (A) it assessed the spatial variability of the floodplain's landscape variables and its dynamics in time (data are considered as a series of tables for each date, i.e., table-date: rows = sites * columns = landscape variables) and (B) it studied the dynamic trajectories of the landscape variables per site (data were considered as a series of tables for each site, i.e., table-site: row = dates * columns = landscape variables). These two outputs are two steps which were performed independently.

The principle of each step is to define, firstly, the common structure of the tables, which is called the Compromise (analysed by a PCA), then to study the structure variability through each table (Blanc 2000). Such analysis, which focuses symmetrically on (1) the dynamics of overall spatial variability of the floodplain and (2) the variability of spatial dynamics of each site, is particularly relevant for answering the initial questions, i.e., the floodplain trajectory compared with the site trajectories. It allowed us to weight, within the overall variability, the potential contribution of space compared to time.

Results

Dynamics of landscape spatial variability at the floodplain scale

The first procedure of the PTA was conducted on the three tables for each date (rows = sites × columns = landscape variables). The two major gradients were determined by the interpretation of the first two axes of the compromise (Figure 3a and b). Axis 1 (35.97% of the total inertia) opposed the variables 'Crops' and 'MSI' to 'number of patches', 'connectivity' and 'hedges'. These variables characterise on the one hand the arable landscape with large rectangular fields and on the other hand 'bocage' landscape with many small fields and with a connected hedgerow network. Axis 2 (17.45% of the total inertia) opposed 'crops' and 'buildings' to 'meadows' and 'MSI' and therefore contrasted a homogeneous landscape dominated by crops to a homogeneous landscape dominated by meadows. The projection of landscape variables of the separate analysis for each date on the compromise plan showed that each date is close to the compromise structure (Figure 3c). Indeed, for a given variable, the projection for each date is close to other dates. It is only the variable's weight (represented by the size of the arrow) which changes according to the date. Only the variable SHEI (Shannon evenness) had a clearly different impact on the classification according to the date studied. The landscape heterogeneity at the floodplain scale has therefore been determined by the same gradients since 1963.

The projection on the compromise plan of the 20 sites in the separate analysis for each date (Figure 3d) also showed that for each site, the three dates were close to each other. This indicates that the two major gradients which have

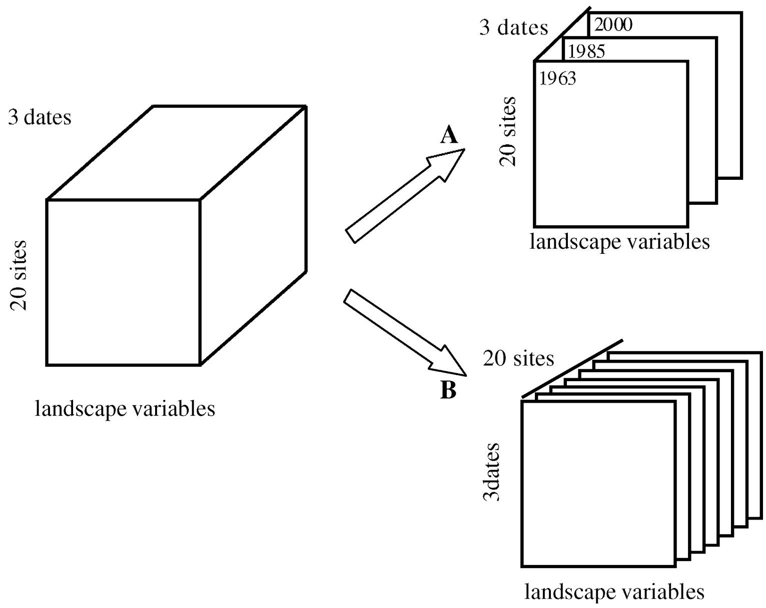

Figure 2. Tridimensional table of data (dates–sites–landscape variables). Way 'A' – Identification of a spatial structure common to the 3 dates called 'first compromise' and study of this temporal permanence. Way 'B' – Identification of a temporal structure common to the 20 sites called 'second compromise' and study of this spatial permanence.

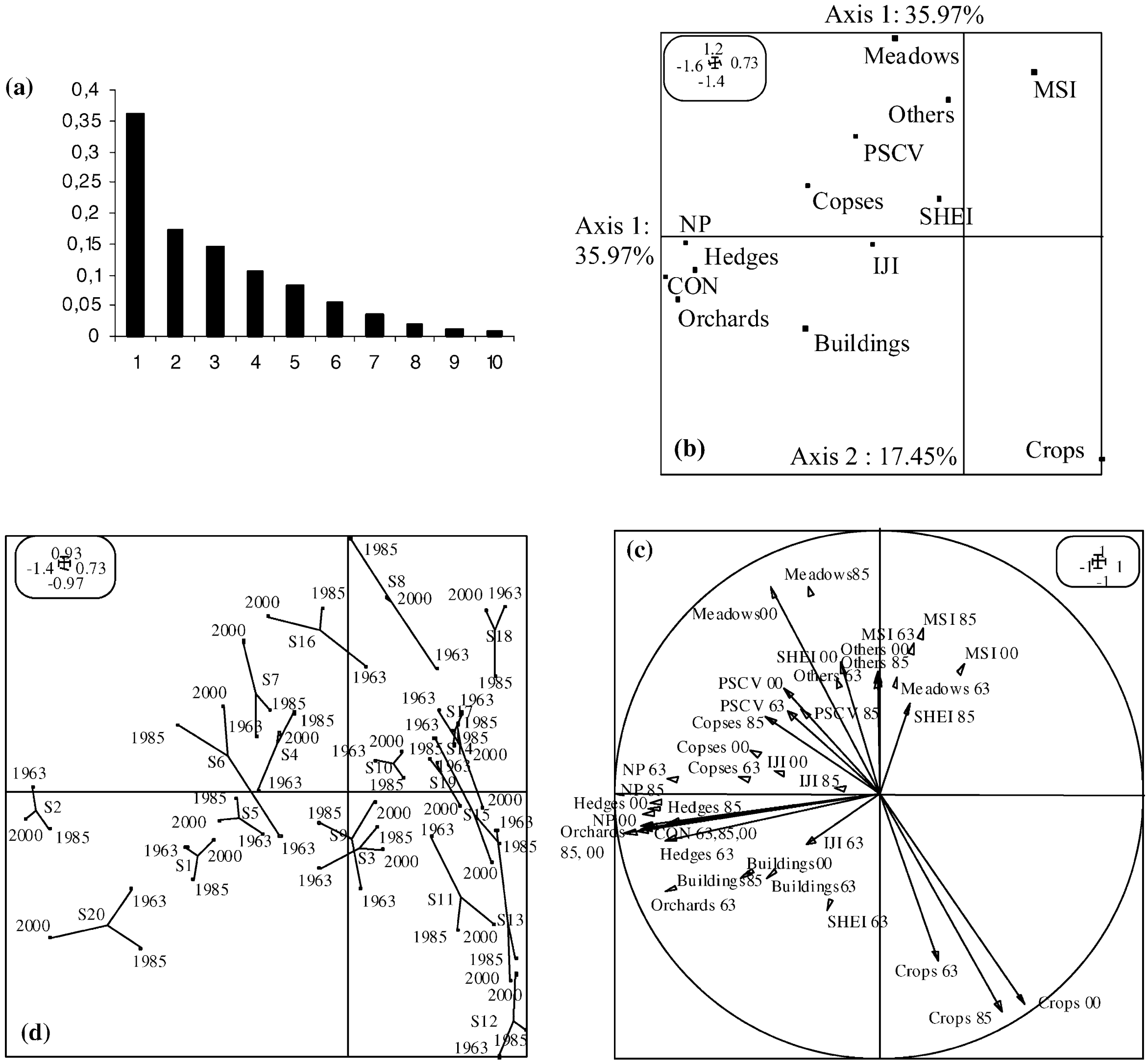

Figure 3. Dynamics of landscape spatial variability at the floodplain scale: PTA of tables-date. (a) Eigenvalue diagram. (b) Plan 1–2 of the compromise. (c) Landscape variables plotted for each date in plan 1–2 of the compromise for each analysis. (d) Sites plotted for each date in plan 1–2 of the compromise for each analysis.

been stable since 1963 have contrasted the same sites since 1963 and that the landscape classification of the floodplain has been rather stable during this time period. However, this overall stability masks a general trend, as shown in the dynamics of landscape variables (Table 1). There has been a great increase of crops between 1963 and 1985 and a stabilisation since 1985, while meadows decreased between 1963 and 1985 then stabilised. Shannon evenness increased during this period. The landscape became more heterogeneous.

Variability of the landscape dynamics at the site scale

The second procedure of the PTA was performed on the 20 tables for each site (rows = dates; columns = landscape variables). The compromise (Figure 4b) gave an average picture of the landscape variables which best explained the variations of the landscape pattern at the three dates for each site. Axis 1 (87.51% of the total inertia: Figure 4a) opposed the variables ‘meadows’, ‘hedges’, ‘connectivity’ and ‘IJI’ to ‘crops’, ‘SHEI’ and ‘PSCV’.

Table 1. Mean values of indices selected for sites structure study for the three dates.

	1963	1985	2000
Others	2.85 (10.14)	3.26 (10.68)	4.46 (69.61)
Copses	0.33 (0.86)	0.48 (0.95)	0.38 (0.94)
Crops	13.54 (16.73) a	41.08 (25.26) b	41.37 (31.19) b
Building	0.11 (0.35)	0.53 (1.50)	0.65 (1.94)
Meadows	79.43 (18.24) a	51.25 (21.31) b	50.33 (26.05) b
Orchards	3.91 (4.72)	3.37 (4.80)	2.30 (3.66)
Hedges	5263.52 (3450.70)	3751.29 (2983.62)	4136.76 (3243.81)
NP	56 (40)	59.35 (42.10)	54.2 (42.84)
MSI	1.41 (0.22)	1.39 (0.14)	1.44 (0.19)
PSCV	112.22 (74.88)	111.53 (50.76)	116.84 (55.82)
SHEI	0.42 (0.25) a	0.65 (0.23) b	0.56 (0.24) b
Con	122.95 (121.80)	88.55 (93.03)	104.25 (108.42)
IJI	57.51 (14.86)	49.15 (13.67)	49.39 (15.34)

Values presented in parenthesis represent the standard error. Different letters indicate significant differences at $p = 0.05$ (Tukey HDS test). For many indices the test cannot be realised.

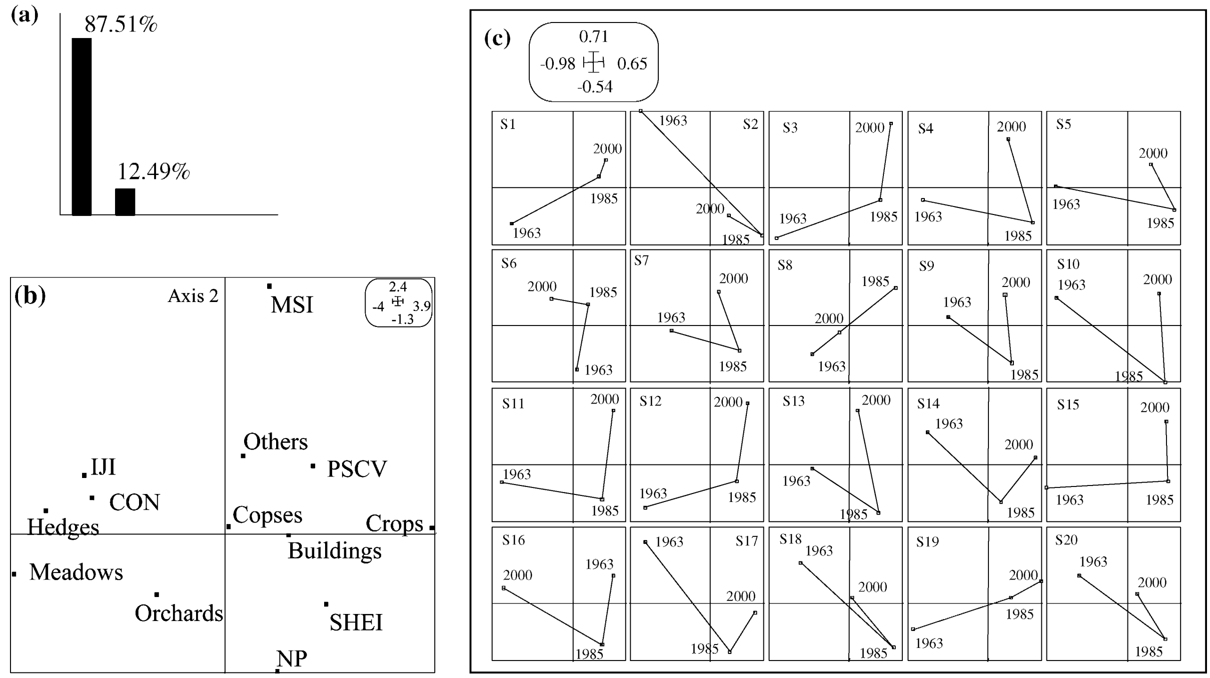

Figure 4. Variability of the landscape dynamics at the site scale: PTA of tables-site. (a) Eigenvalue diagram. (b) Plan 1–2 of the compromise. (c) The rows–dates projection of each table-site in plan 1–2 of the compromise.

It contrasted the 'bocage' landscape dominated by meadows with a more diversified landscape dominated by crops. Axis 2 (12.49% of the total inertia) opposed a landscape with many fields, where the land cover diversity was strong to landscape with irregular sized fields. The projection of each site at the three dates on plan 1–2 of the compromise (Figure 4c) allowed us to study the trajectory of each site. We observed that the majority of sites in 1963 were characterised by 'meadows', 'hedge' and 'connectivity'. Axis 1 generally contrasted the year 1963 with the other two dates. The dynamics between 1963 and 1985 resulted in a general decrease of meadows, hedges and an increase of crops and heterogeneity of land cover. The dynamics between 1985 and 2000 varied according to the sites. Each site had its own dynamics independently of other sites.

Comparison between scales

The comparison of the two procedures of the PTA allowed us to group the sites together in terms of their landscape attributes (way 1) or their trajectories–histories (way 2). Our results showed that (1) sites may have similar landscape features and exhibit different trajectories (e.g., S6–S7; S1–S20); (2) sites may have similar trajectories but different landscape features (e.g., S10–S20); and (3) sites may be consistent for both landscape features and trajectories (e.g., S11–S12–S13).

Discussion

The study of landscape patterns and changes is generally performed with two symmetrical purposes: the identification of their driving factors, which may be correlated to abiotic conditions or agricultural orientations, and the prediction of their consequences on ecological processes. As far as the first point is concerned, the general trend experienced by the landscape of the Seine floodplain, i.e., a loss of grasslands and an increase of crops, is in agreement with many studies in Europe (Ihse 1995; Fjellstad and Dramsta 1999; Burel et al. 2003). Such land use change is likely to be correlated with the recent agricultural changes (Poudevigne et al. 1997) which are driven by large-scale modern agricultural policies (Robinson and Sutherland 2002). This trend represents a major component of global change (Vitousek 1994) experienced in most of the other European countries (Meeus 1993; Bouma et al. 1998). However, the initial spatial variability of the floodplain described in 1963 is still recognisable at present. This suggests a meta-stability of the floodplain due to strong agricultural impediments (abiotic factors) which may represent a force of inertia in such a wetland (Ernoult et al. 2003). Despite this trend emerge from a grain size of a square kilometre, it is likely to occur at a larger grain with the same extent (i.e., the whole valley) as the main indices explaining the changes are known to exhibit constant response with changing scale (Wu 2004).

A previous study suggested the shift from a landscape organisation based on soil constraints towards an organisation based on individual farm strategies for the period 1963–2000 (Ernoult et al. 2003). This trend was observed on one site (site 2) but can probably be generalised to the major part of the valley. As a consequence, the orientation of farm systems during this period (meat compared to milk orientation) may have led either to the removal of the initial differences between landscape sites, since abiotic conditions became less important, or the divergence of landscape structures between initially similar sites, since the influence or different farming systems became more important. This could explain why, at the site scale, we observed contrasting trajectories between sites during the 40-year period, which suggest that similar landscape sites in 2000 do not necessarily share common histories and therefore the same driving factors, or that contrasting sites in 2000 may have originated from similar patterns in 1963.

As far as the ecological consequences are concerned, critical issues have been identified that may explain the overall difficulty of predicting ecological processes from landscape analysis (Li and Wu 2004). Predicting biodiversity from landscape patterns lies in the use of landscape indices as potential biodiversity surrogates. Amongst the potential pitfalls, two major problems are likely to occur our study: the inherent limitation of landscape indices and the conceptual flaws in landscape analysis (Li and Wu 2004). Concerning the first problem, (i) we avoided the use of complex metrics (fractal, contagion indices) which were removed and replaced with the simplest indices with which there were correlated and (ii) our analysis combined both landscape composition and structure which was likely to capture changes that may not be detected by several metrics alone. For example, the variable SHEI (Shannon evenness) was associated to a land use which was different for each date. This mitigates its potential role in the overall dynamics of the seine flood plain landscape as it does not affect the overall stability. As far as the second problem (conceptual flaws) is concerned, one have to be aware that landscape patterns are susceptible to explain only the spatial dimension of biodiversity, i.e., all what has to do with dispersion and island geography while the non-spatial dimension of biodiversity, i.e., all what is concerned with biotic interactions, is likely to remain hidden in such analysis (Li and Wu 2004).

We introduce in this paper another major pitfall which lies in the importance of non-equilibrium vs. equilibrium conditions between biodiversity and the landscape variables that are likely to play an active role on it. Metrics based on landscape structure and landscape history may be used as two facets of biodiversity surrogates. The first facet refers to the influence of present landscape patterns on local compared to regional biodiversity and looks for correlations between biodiversity and landscape metrics (Moser et al. 2002; Dauber et al. 2003). Such correlations are likely to be detected when landscapes are stable enough to allow equilibrium conditions to occur. However, this condition is seldom met because the time dimension is not a part of this facet. The second facet will refer to the importance of landscape changes at both levels of biodiversity. Our data suggest that behind an overall stability of landscape gradients over 40 years, local changes are important and thus may have an impact on local communities. Furthermore, such a preliminary study allows us to detect potential situations where non-equilibrium conditions may alter the correlation between biodiversity and landscape metrics. In other words, where history may have a major role in the explanation of the structure of communities, biodiversity surrogates should be defined with reference to this time dimension. Future research on biodiversity surrogates should focus on the role of past dynamics on local diversity. Two scales should be considered: (1) the regional scale because the species pool, which constrains local diversity (Zobel 1997), is likely to exhibit long-term variations under the influence of general landscape trends; (2) the local scale because communities may respond to rapid and local landscape changes, even with a time lag.

When considering landscape metrics, as possible surrogate data, key factors to consider when looking for potential surrogates are (1) the relevant spatial scale at which species may perceive their surrounding environment and its changes and (2) the time lag that may occur between landscape changes and species responses. We particularly need to validate in this geographical context the hypothesis that different taxonomic groups should exhibit contrasting behaviour in the face of landscape changes (Söderström et al. 2001; Sauberer et al. 2004). We especially intend, in our further research, to validate the trade-off between sessile organisms (e.g., plants) which are likely to respond slowly to fine-scale changes and mobile organisms (e.g., birds) which may respond rapidly to broad-scale landscape changes. This multiple landscapes analysis is probably the most appropriate way for establishing such reliable relationships between landscape pattern and ecological processes such as biodiversity (Li and Wu 2004).

Acknowledgements

This work was made possible by the financial support of the 'Conseil regional de Haute – Normandie' in the form of a research grant to A. Ernoult. The authors would like to acknowledge F. Burel and D. Delahaye for correcting the manuscript. We also acknowledge Joana Colomer for her help in data recording. The authors also wish to thank R. Britton and L. Galmiche for correcting the English.

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