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Diversity of plant assemblages in managed temperate forests: a case study in Normandy (France)

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Abstract

We investigate the patterns of variation of plant community diversity along a silvicultural cycle in a managed beech forest. A statistical model of the silvicultural cycle is constructed in order to identify: (i) the relationships between species and environmental factors, and (ii) species assemblages occurring along the successional gradient. We measure six diversity indices accounting for the structural (species richness (SR), Shannon index, evenness index), the functional (factorial diversity, FD) and the compositional dimension (similarity index within and between records) of biodiversity. We compare their patterns of variation along the succession in order to understand the different information provided by each index.

The model reveals that species assemblages occurring in regeneration stands have the highest SR along the cycle. Species coexistence in these assemblages appears to be based on non-equilibrium mechanisms. On the other hand, mature stands with closed canopy seem to host the more organised communities reflecting true coexistence based on equilibrium mechanisms.

We discuss the indicative values of the different diversity measures and their interest for the development of sustainable forest management. We advocate that conservation priorities should thus be defined in reference to the processes controlling biodiversity and to the taxonomic groups responding to these processes.

Keywords: Forest management; Beech forest; Succession; Biodiversity indicators; Canonical correspondence analysis; SFTS procedure; Species coexistence; Statistical modelling

1. Introduction

The assessment of biodiversity in managed forest has become an important issue for studying ecosystems and their conservation. Ecosystem studies have focused for the last decade on the relationships between biodiversity and ecosystem functioning (Schulze and Mooney, 1994). This question is also central in forest science (Bengtsson et al., 2000). Conservation issues mostly focus on the ecological impact of management practices as their aim is to provide practical background for sustainable management. The use of biodiversity indicators for assessing these impacts appears relevant for the definition of sustainability (Lindenmayer et al., 2000).

Biodiversity has often been considered as a structural community attribute (Samuels and Drake, 1997) which was mostly approached by the mean of species richness (SR) and derived informational indices such as Shannon index or evenness (Duelli, 1997). These indices of structural diversity are scale dependent (Palmer, 1994) and consider all species as equivalent

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(Kolasa and Rollo, 1991). The information brought by these structural indicators of biodiversity (how many species in a given ecosystem?) has been shown to depend on the type of data, the level of observation, and the spatial resolution. The intrinsic variability of these measures does not plead in favour of their robustness to assess the ecological mechanisms behind biodiversity (Huston, 1994).

As all species are not equivalent in an ecosystem (Tilman et al., 1997), it is important to take in account the functional and compositional dimension of biodiversity (Noss, 1990) for conservation purposes. This functional dimension is based on life traits and strategies of species such as regeneration, growth, dispersal (Lavorel et al., 1997). The compositional dimension is derived from species behaviour and ecological attributes of species at a given observation level (Scheiner, 1992). Both dimensions, considering species in regard to their autecology, their morphology and physiological performances provide information on the underlying mechanisms of species assemblages (Alard and Poudevigne, 2000; Kolasa and Rollo, 1991).

In this paper, we investigate the patterns of variation of biodiversity along a silvicultural cycle in a managed beech forest. With a space for time substitution (SFTS) procedure, a statistical model of the silvicultural cycle was built up using multivariate analysis and clustering methods. This approach allows us to identify: (i) relationships between species and environmental factors along the cycle, and (ii) the species assemblages representing the community types occurring along the main gradient. For each species assemblage, we measure six diversity indices accounting for the structural (*SR*, Shannon index, Evenness index), the functional (Factorial Diversity, *FD*) and the compositional dimension (Similarity index (*SI*) within and between records) of biodiversity.

The central hypothesis of this paper is that a given *SR* may result from different mechanisms of species coexistence (Nakashizuka, 2001). For conservation purposes, indicators based on this information are useless as they do not help to identify the mechanisms of species coexistence. With the help of a functional or compositional index of biodiversity, we aim at identifying the mechanisms explaining biodiversity, i.e. species coexistence. In order to understand the information provided by each diversity index, we compare their patterns of variation along the gradient. Our sampling procedure was designed so that the environmental variations recorded would not be due to sites variability. Thus, we assume that our sampling design is only based on a successional gradient and is likely to yield communities controlled by contrasted mechanisms of species coexistence (Tilman, 1994). Our understanding of the mechanisms controlling biodiversity in temperate forests is essential to propose ecologically sustainable forest management not only based on "how many species are there in an ecosystem" but also on "how do species coexist in one ecosystem" (Lindenmayer et al., 2000).

2. Materials and methods

2.1. Study sites

Study stands are located in the State Forest of Eawy, Normandy, in northern France. The annual averages of rainfall and temperature are, respectively, 800 mm and 10 °C (Brêthes, 1984). The forest is managed by the French Forestry Service and timber harvesting is its most important output. Like most French forests, stands are conducted as even-aged forest. In our case, this results in 90% of beechwood of equal age and even canopy. Nowadays, the revolution of the silvicultural cycle of this forest occurs on a 170-year basis. Though the young stands are still artificial plantations, some very recent young stands (less than 10 years) result from natural regeneration. In practice, the even-aged forest management consists of four phases: cleaning, refining, amelioration and regeneration. Cleaning is the phase where the forester eliminates the damage sources (defective and diseased trees) during the first 15 or 20 years. Refining occurs between the next 20 years and consists of spotting the better trees and favouring their development. The amelioration phase is the longest one, during which the forester intervenes by thinning the canopy. It is a selective and harvesting operation. The thinning periodicity is of 5 years between 40 and 70 years old, of 10 years between 80 and 130, and of 15 years after. During the regeneration phase between 140 and 170 years, the forester selects the trees which will bear fruits and give birth to the next generation. To facilitate the regeneration process, the forester prepares the soil by mechanically scraping the superficial layers and by using herbicides to limit the competition by herbaceous plants (Lanier, 1994).

Table 1
Description of the 20 selected stands

Stands	Age of stands (years)	Last year cut	Silvicultural phase
C1	25	1998	Cleaning
Rf2	25	1997	First thinning
Rf3	27	1996	First thinning
Rf4	32	1996	First thinning
A5	58	1997	Amelioration
A6	58	1997	Amelioration
A7	62	1998	Amelioration
A8	114	1992	Amelioration
A9	120	1995	Amelioration
A10	124	1995	Amelioration
A11	133	1995	Amelioration
A12	133	1994	Amelioration
A13	144	1993	Amelioration
A14	146	1997	Amelioration
A15	176	1991	Amelioration
A16	174	1996	Amelioration
Rg17	179	1998	Regeneration since 1995
Rg18	179	1998	Regeneration since 1995
Rg19	194	1997	Regeneration since 1990
Rg20	194	1997	Regeneration since 1990

Twenty stands were selected (Table 1) to reconstitute a potential silvicultural cycle from young plantations (24 years old) to regeneration stands. On account of the recent emergence of natural regeneration, all the stands were chosen from artificial regeneration (plantations). According to phytosociological classification, mature stands of amelioration phase belong to the *Endymio-Fagetum typicum* (Bardat, 1989; Durin et al., 1967). Mean species number occurring in this sub-association is 17 (Bardat, 1989). Our sampling procedure was designed so that the environmental variations recorded would be due only to successional changes and not to site variability. All the stands were characterised by the same parental material (loess, thickness > 80 cm) and the same topographic position (plateau). All the soils were LUVISOL according to the "*référentiel pédologique*" (AFES, 1998) equivalent to LUVISOL in World Reference Base (FAO, 1998).

2.2. Data sampling procedure

2.2.1. Vegetation

For each stand, five vegetation records were located on the four cardinal points and on the centre of the sampling pattern (Fig. 1). Each vegetation record was performed within a 400 m^2 square plots subdivided into four equivalent parts of 100 m^2. For every part of a 400 m^2 square plot, a floristic inventory was performed for four strata: (i) herbs stratum (species $<$ 0.5 m height), (ii) small shrubs stratum (between 0.5 and 2 m height), (iii) shrubs stratum (2–8 m), and (iv) trees stratum (>8 m). The abundance-dominance of all vascular plant species was estimated with the phytosociological 7° scale: *i*—species represented by only one individual; +—species with a very small cover; 1—species with a cover $< 5\%$; 2—cover between 5 and 25%; 3—25–50%; 4—50–75%; 5—75–100%; and the percent cover of each stratum was estimated. For every 400 m^2 sample plot, a synthetic inventory was made by listing all species met in the four 100 m^2 part and attributing to them an average abundance-dominance coefficient. Nomenclature of species follows Lambinon et al. (1992). Twenty stands were chosen for the sampling, representing an overall 100 vegetation records performed in May and June 1999.

2.2.2. Environmental variables

Nineteen environmental variables were recorded for each sample. These variables were chosen for their indicative value of the main ecological factors: light and soil conditions. Three cover variables account for light conditions (% cover of trees stratum, % cover of shrubs stratum and % cover of small shrubs stratum). Concerning soil conditions, we focused on: (i) morphological characteristics of upper horizons containing organic matter (humus form), (ii) acidity of organo-mineral horizon (A horizon), and (iii) hydromorphic characteristics.

(i) Humus form is defined as the sequence of organic horizons (O horizons) and organo-mineral horizon (A horizon), the arrangement of which depends essentially on biological activity (AFES, 1998). Humus forms provide indicative value of nutrient availability for plants (Duchaufour, 1989). In each 400 m^2 sample plots, a description of humus form was made near the plot centre. Macroscopic morphological characteristics (AFES, 1998) were: depth of OL, OF and OH horizons; depth, structure and texture of the A horizon. The colour characteristics of

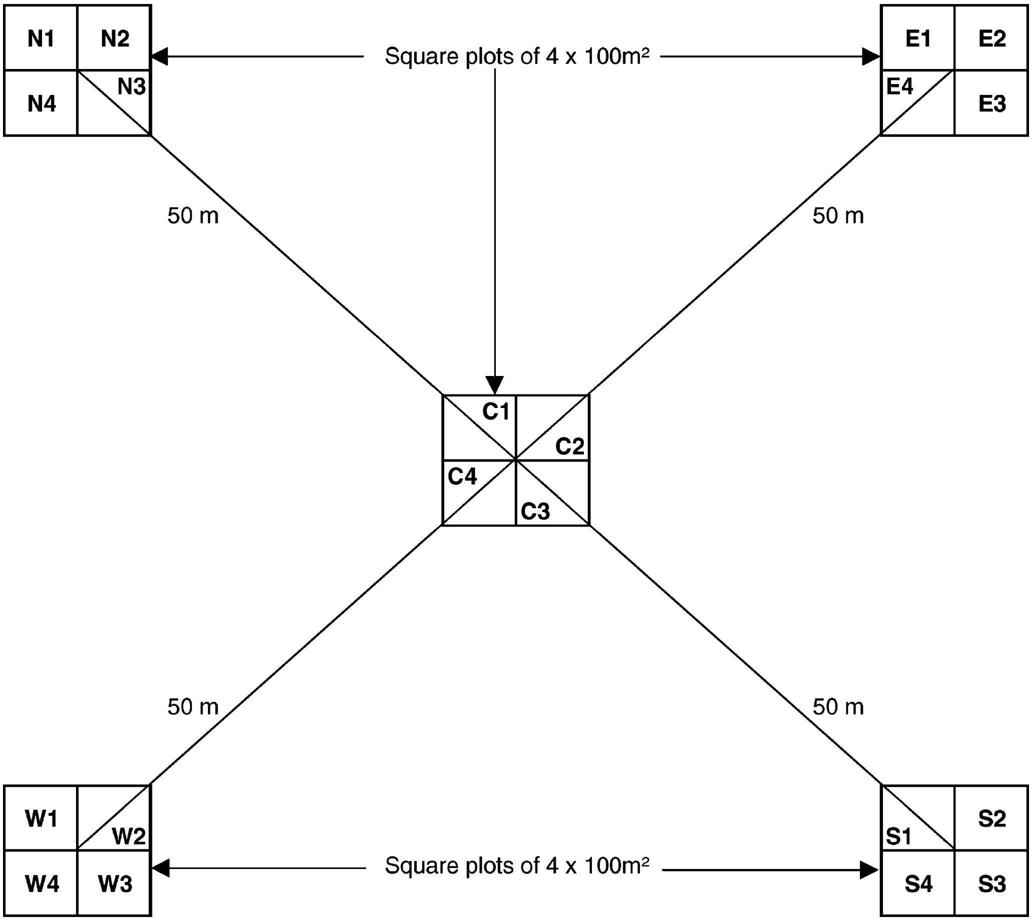


Fig. 1. Sampling design used for vegetation and soil characteristics sampling.

A horizon were measured at 3, 6 and 9 cm below the O horizons with the Munsell® Soil Colour Chart. According to Ponge and Ferdy (1997), the value index of superficial soil horizon increases when the horizon becomes lighter because of a decrease in the content of dark humified organic matter. According to them, the chroma index increases when the colour becomes brighter.

(ii) The A horizon pH KCl and pH H_2O were estimated in the laboratory (1:2.5 soil/liquid mixture). The pH H_2O was not used for multivariate analysis, but determined only in order to compute the ΔpH ($\Delta pH = pH\,H_2O - pH\,KCl$). For one type of soil, ΔpH is positively correlated with exchangeable acidity (Baize, 1988).

(iii) A boring was also made with a hand drill to estimate the hydromorphy depth and its intensity. In all 400 m^2 plots, 16 soil variables were measured during June 1999.

2.3. Data analysis

Data analysis was performed to provide: (i) a statistical model of species–environment relationships, and (ii) indices accounting for several dimensions of biodiversity (Fig. 2). The 100 vegetation records (400 m^2) and soil records were analysed by canonical correspondence analysis (CCA) (Ter Braak, 1987; Ter Braak and Prentice, 1988) with ADE software (Thioulouse et al., 1997) in order to model the

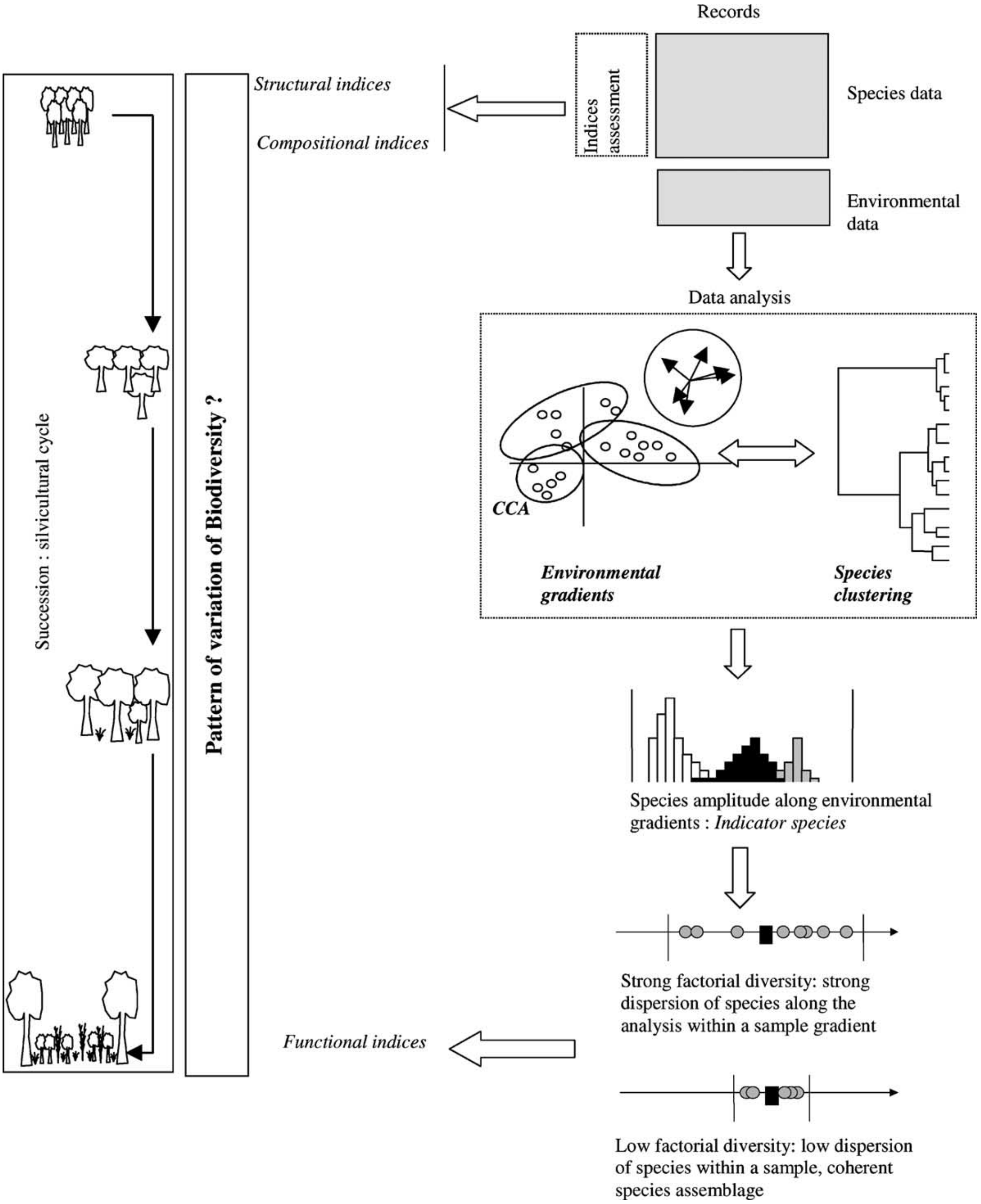


Fig. 2. Data analysis procedure.

vegetation dynamics and to identify relationships between species and environmental factors. The ordination diagram for CCA includes the species and sites scores as well as the vectors representing environmental variables which explain the major ordination axes (Alard and Poudevigne, 2000; Palmer, 1990a). Prior to the analysis, species inventoried in less than 3% of records were removed from the data set. The vegetation data table (100 records × 78 species) and the environmental data table (100 records × 19 environmental variables) were analysed together with a CCA. A Monte Carlo test (1000 permutations) was performed to validate the coupling of these two sets of data.

Hierarchical clustering (Roux, 1991) was performed on species and records CCA scores along the first two axes (Roche, 1994; Roux, 1985) using Ward's method (Ward, 1963) to identify the main types of species assemblages. The coordinates of the centre of the stars on species and records ordination diagram are equals to the mean of species or records coordinates composing the cluster. The species clustering was interpreted with autecological data from Grime et al. (1988) and Rameau et al. (1989).

For the different types of species assemblages, six different measures of diversity were investigated.

(1) α diversity which refers to the *SR* (number of species) within a given habitat or quadrat (Palmer, 1990b).

(2) Shannon diversity index (H'), a measure which informs on the structural composition of the communities (Pielou, 1975):

$$H' = \sum p_i \log_2 p_i$$

where p_i is the relative frequency of species in a record.

(3) Evenness index (J'), a structural composition index which reflects the dominance of species (Smith and Wilson, 1996):

$$J' = \frac{H'}{H'_{\max}} \quad (H'_{\max} = \log_2 \alpha)$$

(4) *FD*, is the conditional variance of records on the first factors of CCA (Chessel et al., 1982; Thioulouse and Chessel, 1992):

$$\mathrm{FD} = \sum_{j=1}^{t} p_{j/i}[C_k(j) - L_k^{(c)}(i)]^2$$

where $p_{j/i}$ is the conditional relative frequency of sample i for species j, $L_k^{(c)}(i)$ the ordination of samples on gradient by averaging, $C_k(j)$ the ordination of species on gradient by weighted averaging.

It is a within-sample diversity based on the dispersion of species in a record along a CCA factor. This measure can be considered as representing an important aspect of the ecological diversity of the record (Czaran, 1991). This index gives information on the coherence or the non-coherence of species assemblages with reference to the gradient of the *CCA* axis (Thioulouse and Chessel, 1992). *FD* can be considered as an indirect evaluation of species interactions. In combination with other indices, this measure can provide a mean to discern among the main mechanisms of species coexistence (heterogeneity, non-equilibrium, niche partitioning; Alard and Poudevigne, 2000; Balent, 1991) which is the dominant mechanism at hand.

(5) *SI*, pairwise similarity among all records of 400 m^2 plots was computed and the mean similarities for each were determined using the Jaccard index (Jaccard, 1901):

$$\text{Jaccard index} = \frac{c}{(a+b) - c}$$

where c is the number of species shared, a and b the total number of species occurring in records A and B.

This measure incorporates mean distance and dispersion of distance within the community considered (Scheiner, 1992). It accounts for which species are common to all the records (Alard and Poudevigne, 2000).

(6) Within records heterogeneity (WRH), pairwise similarity among the four records (100 m^2) of a 400 m^2 plot were computed and the mean similarities were determined using Jaccard values. This measure reflects the composition heterogeneity of a 400 m^2 plot.

3. Results

3.1. Species–environment relationships

The total inertia of the CCA is 1.593. Eigenvalues of the first four axes are respectively 0.55, 0.37, 0.16 and

0.12. Relative inertia corresponding are, respectively, 35, 23, 10 and 8%. Because of the small eigenvalues and the presumably little additional information that can be drawn from the third and fourth axes, we will concentrate on the first two axes (Fig. 3). Monte Carlo test gave a p-value < 0.001 validating the coupling of the two set of data.

Cover of shrub stratum (Fig. 4) accounts for most of the variation in axis 1. This axis separates records belonging to young stands from those belonging to old

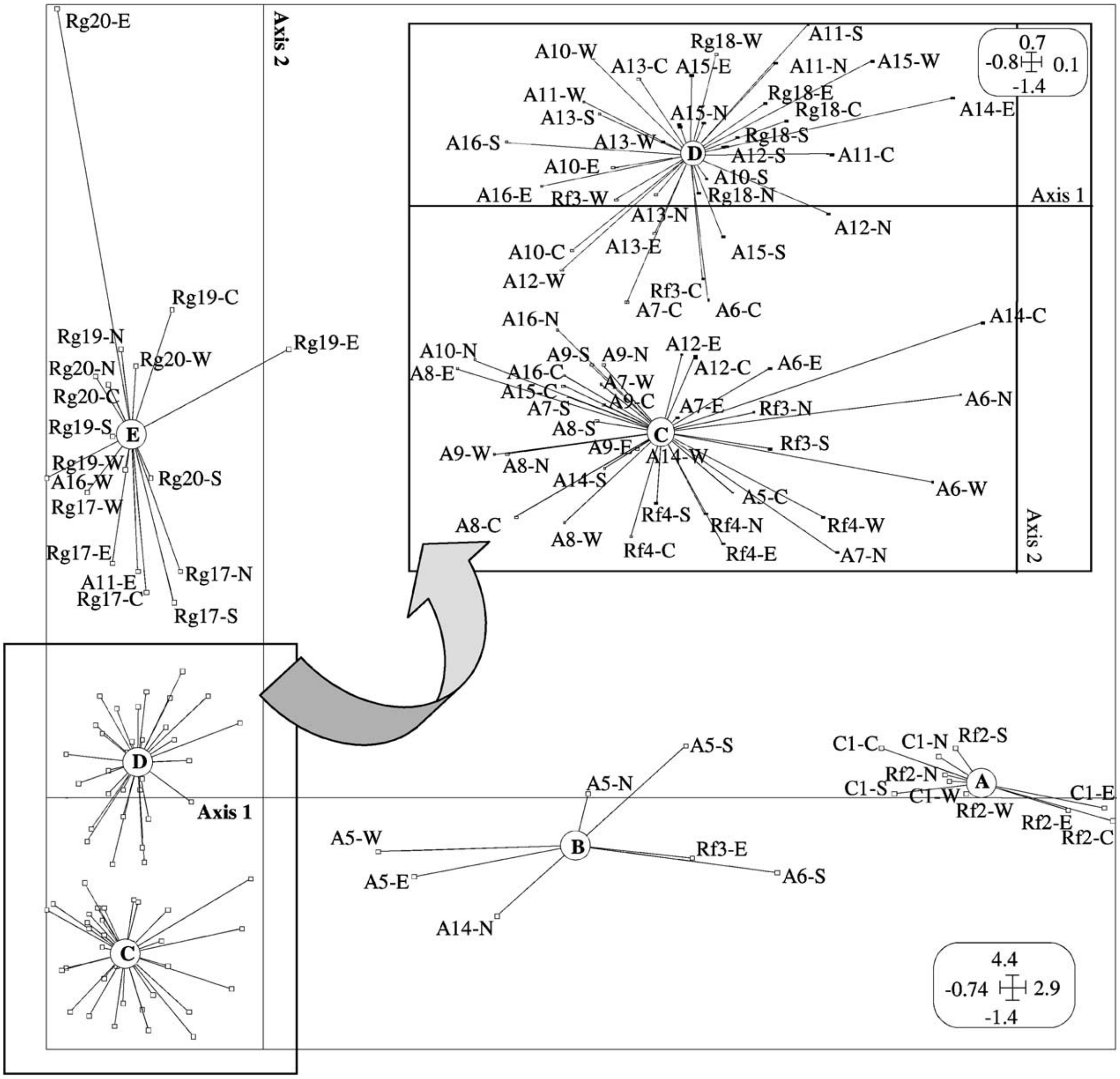


Fig. 3. CCA ordination diagram of 400 m^2 vegetation records and 100 records × 78 species. A–E represent the five groups resulting from the clusters analysis performed on CCA records scores (see Fig. 5 for dendrogramm). Concerning records appellations see Table 1. The extensions (-N, -S, -E, -W, -C) make reference to the records position within the sample design (Fig. 1), respectively, North, South, East, West, Centre. In order to make easier the diagram reading, the part concerning the groups C and D has been enlarged.

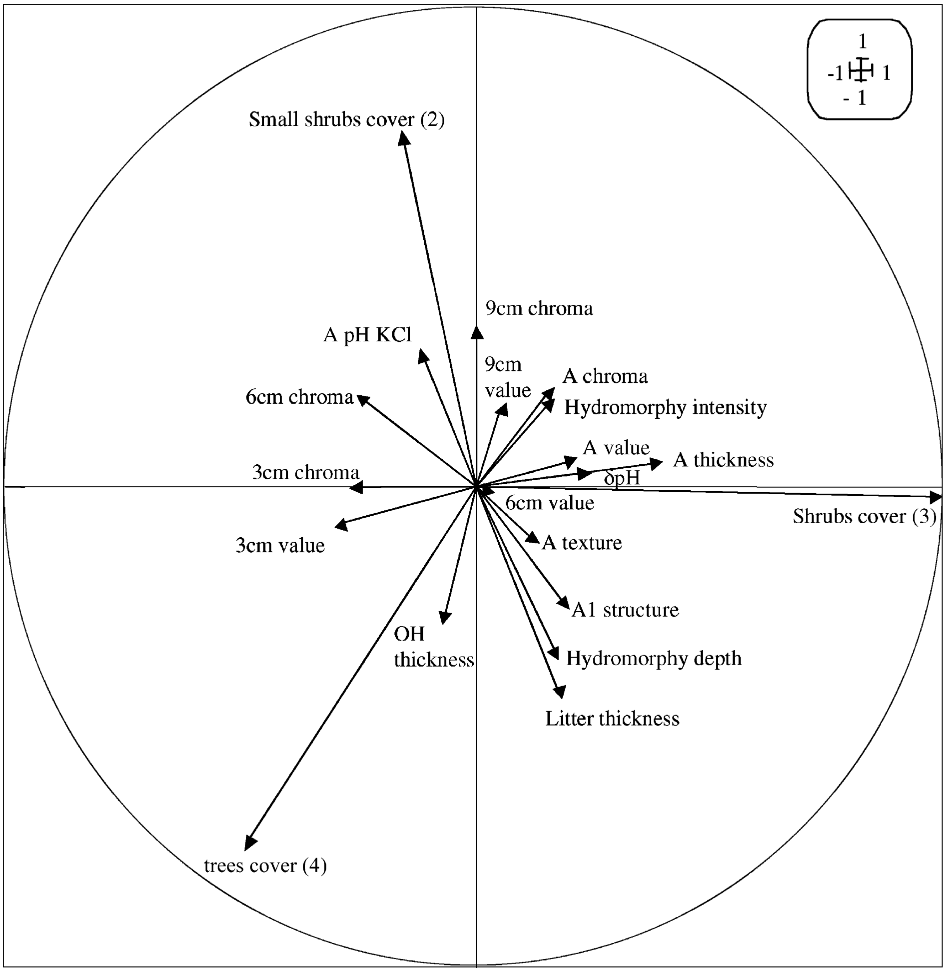


Fig. 4. Correlation circle of explicative variables (100 records × 19 variables) resulting from performed CCA.

stands. It suggests, from its positive to negative part, a gradient of stand maturation. Cover of trees stratum accounts for variation in axis 2 which separates records performed in regeneration stands to records performed in stands belonging to the amelioration phase. It can be interpreted, from its negative to its positive part, as an opening canopy gradient. Clusters analysis (Fig. 5) performed on CCA record scores identifies five groups of records ranging from young plantations (groups A and B) to old stands (groups C–E), and from stands with a closed canopy (C) to regeneration stands (E) (see Table 2). As concerns the associated characteristics of the humus form, axis 1 opposes: (i) young stands with a thick A horizon and a low Munsell value at 3 cm (indicating a strong content of dark humified organic matter) to (ii) old stands with a thin A layer and a high Munsell value at 3 cm. Axis 2 opposes: (i) closed stands with a thick litter and OH layer development, and (ii) regeneration stands with a thinner litter and OH layer and a strong superficial hydromorphy.

Table 2
Average age of the five groups of records identified by the clusters analysis

Clusters	A	B	C	D	E
Mean age (years)	25	66	96	139	185
S.E.	0	37	47	42	15

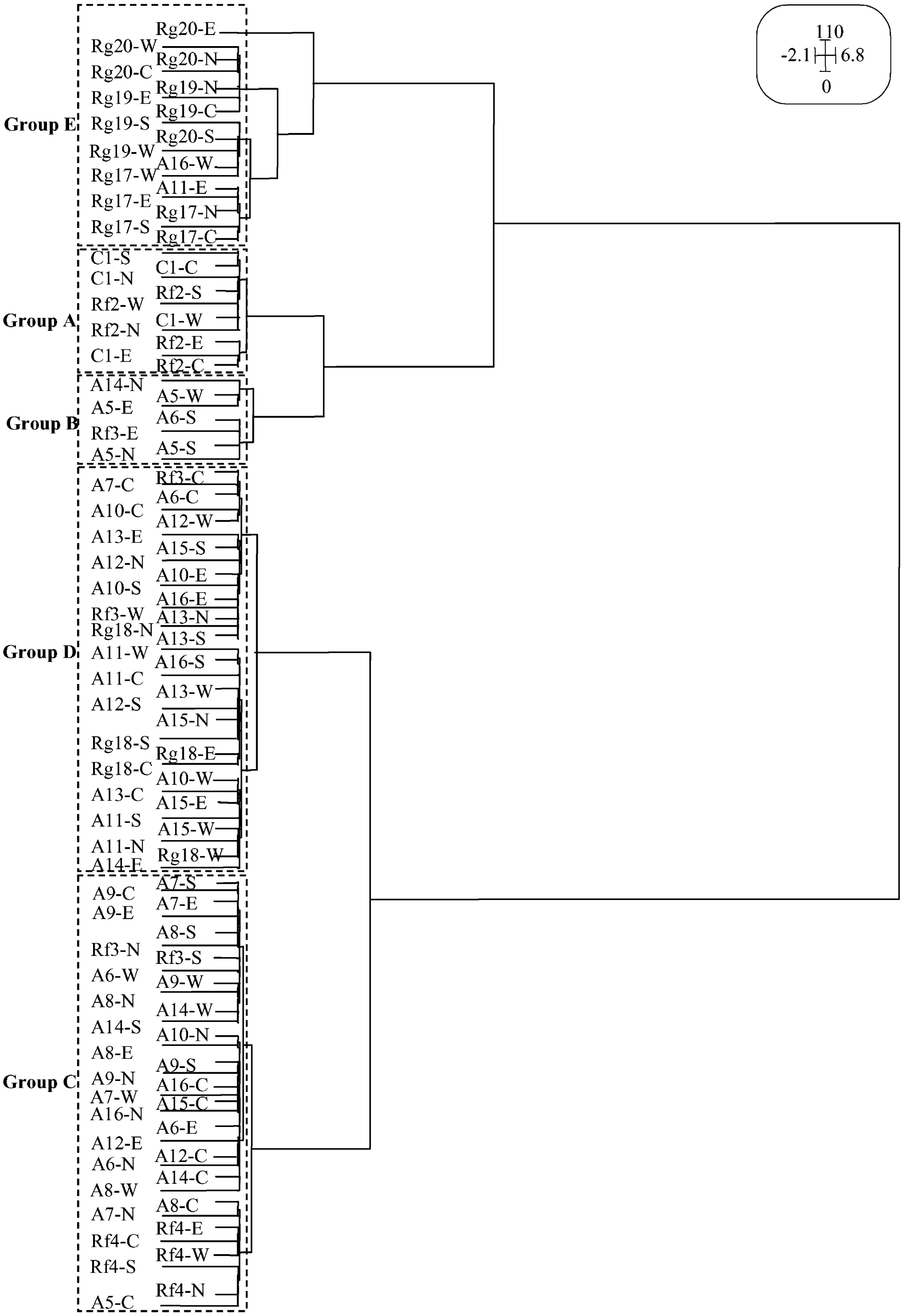


Fig. 5. Dendrogram resulting from the clusters analysis performed on the CCA records scores of the first two axes.

Clustering of species scores of the CCA identifies five groups of species (Fig. 6, Table 3):

Group a is mainly composed of individuals of *Fagus sylvatica* belonging to the shrub stratum.

Group b is mainly composed of herbaceous species like *Melica uniflora*, *Conopodium majus*, *Carex sylvatica*, *Oxalis acetosella* and a group of ferns *Dryopteris carthusiana*, *Dryopteris dilatata*, *Athyrium filix-femina*, *Blechnum spicant*. These species are shade obligatory or shade tolerant and grow on acidic mull humus form.

Group c is characterised by the juxtaposition of two kinds of species: the first one is represented by species such as *Carex pilulifera*, *Luzula pilosa*, *Hypericum pulchrum*. These are shade tolerant and have affinity for moder humus. The second type of species is composed of *Pteridium aquilinum*, *Digitalis*

Table 3
Correspondence between species abbreviations and species names

Species abbreviations[a]	Species names
Fs4	*F. sylvatica* (4)
Qr4	*Q. robur* (4)
Cs3	*Cytisus scoparius* (3)
Fs3	*F. sylvatica* (3)
Cs2	*C. scoparius* (2)
Fs2	*F. sylvatica* (2)
Ia2	*Ilex aquifolium* (2)
Qr2	*Q. robur* (2)
R frut2	*R. fruticosus* (2)
Ap	*Acer pseudoplatanus*
A stol	*Agrostis stolonifera*
A nem	*Anemone nemorosa*
A fm	*A. filix-femina*
Ba	*Betula alba*
B spi	*B. spicant*
C epi	*C. epigejos*
Call sp	*Callitriche* sp.
Car o	*Carex ovalis*
Car pal	*Carex pallescens*
Car pil	*C. pilulifera*
Car rem	*Carex remota*
Car syl	*C. sylvatica*
Cb	*Carpinus betulus*
Cl	*Circaea lutetiana*
C maj	*C. majus*
C mon	*Crataegus monogyna*
Cs	*C. scoparius*
D glom	*Dactylis glomerata*
D cesp	*D. cespitosa*
D flex	*D. flexuosa*
D pur	*D. purpurea*
D cart	*D. carthusiana*
D dil	*D. dilatata*
D fm	*Dryopteris filix-mas*
Epilo ang	*Epilobium* sp.
E amyg	*Euphorbia amygdaloides*
Fs	*F. sylvatica*
F gig	*Festuca gigantea*
G tet	*G. tetrahit*
G apa	*Galium aparine*
G saxa	*Galium saxatile*
H hel	*Hedera helix*
H sp	*Hieracium* sp.
H lan	*H. lanatus*
H mol	*H. mollis*
H n-s	*Hyacinthoides non-scripta*
H pul	*H. pulchrum*
Ia	*I. aquifolium*
J con	*J. conglomeratus*
J eff	*Juncus effusus*
L gal	*Lamiastrum galeobdolon*
L peri	*Lonicera periclymenum*
L uligi	*L. uliginosus*
L multi	*Luzula multiflora*
L pil	*L. pilosa*
L nem	*Lysimachia nemorum*
M uni	*M. uniflora*
M eff	*Milium effusum*
M tri	*Moehringia trinervia*
O acet	*O. acetosella*
P nem	*Poa nemoralis*
P triv	*Poa trivialis*
P mult	*Polygonatum multiflorum*
P hydr	*Polygonum hydropiper*
Pa	*Prunus avium*
P aqui	*P. aquilinum*
Qp	*Quercus petraea*
Qr	*Q. robur*
R frut	*R. fruticosus*
S c	*Salix capraea*
S eru	*Senecio erucifolius*
S a	*Sorbus aucuparia*
S sylv	*Stachys sylvatica*
S gram	*Stellaria graminea*
S holo	*Stellaria holostea*
S media	*Stellaria media*
T scor	*T. scorodonia*
V riv	*Viola riviniana*

[a] Numbers following species abbreviations inform on which stratum belong the species: 4—trees stratum; 3—shrubs stratum; 2—small shrubs stratum.

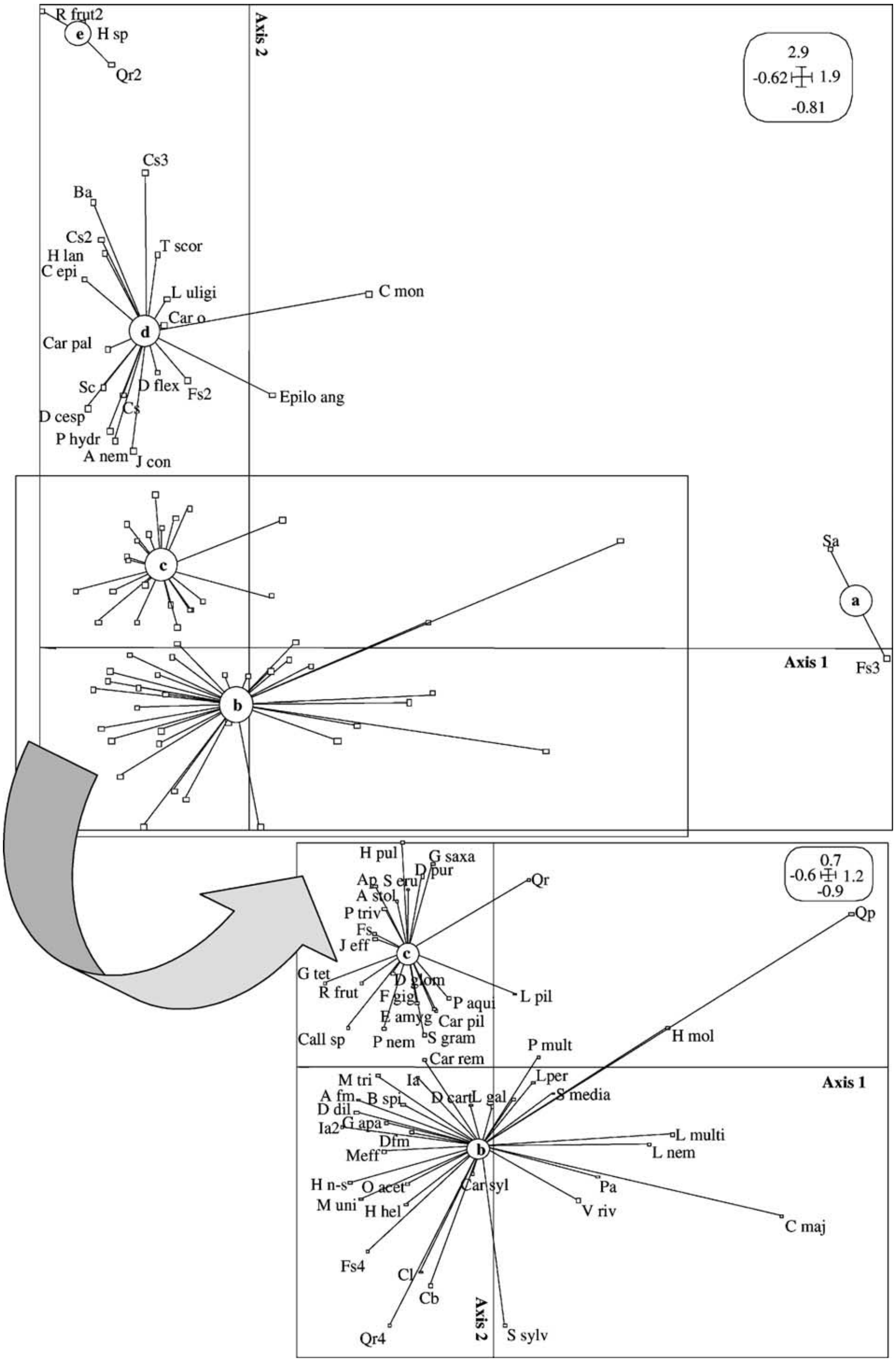
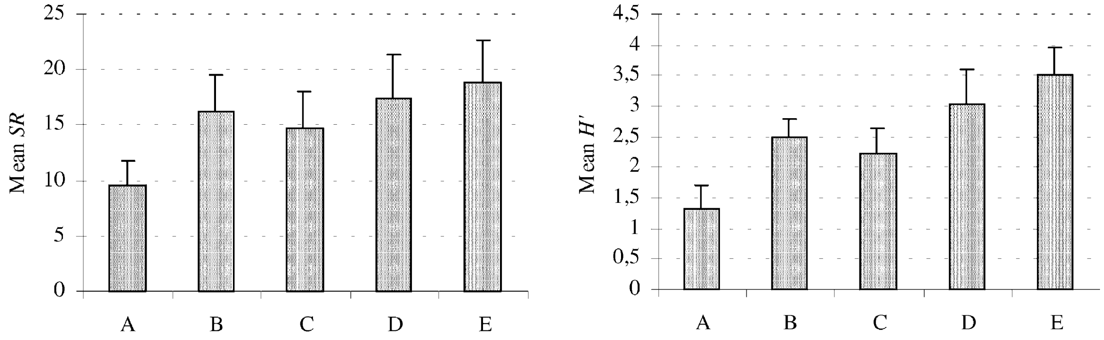
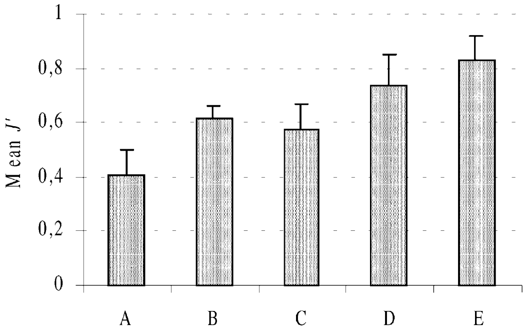


Fig. 6. CCA ordination diagram of species (100 records × 78 species). Groups a–e are the five groups resulting from the clusters analysis performed on the CCA species scores. In order to make easier the diagram reading, the part concerning groups b and c has been enlarged. See Table 3 for the correspondence between species abbreviations and species name.



(a) Species richness (*SR*) (b) Shannon index (*H'*)



(c) Evenness index (*J'*)

Fig. 7. Mean values of structural diversity indices (*SR* (a), Shannon index (b) and evenness index (c)) for each groups resulting from the clusters analysis of CCA records scores.

purpurea, *Galeopsis tetrahit* which are non-shade-tolerant species.

Group d is mainly composed of species like *Teucrium scorodonia*, *Holcus lanatus*, *Deschampsia flexuosa*: non-shade-tolerant species. Among these species, a group of species such as *Calamagrostis epigejos*, *Deschampsia cespitosa*, *Juncus conglomeratus*, *Lotus uliginosus* which are hydrophilic species can be distinguished.

Group e is mainly composed of species belonging to the small shrubs stratum such as *Quercus robur* and *Rubus fruticosus*.

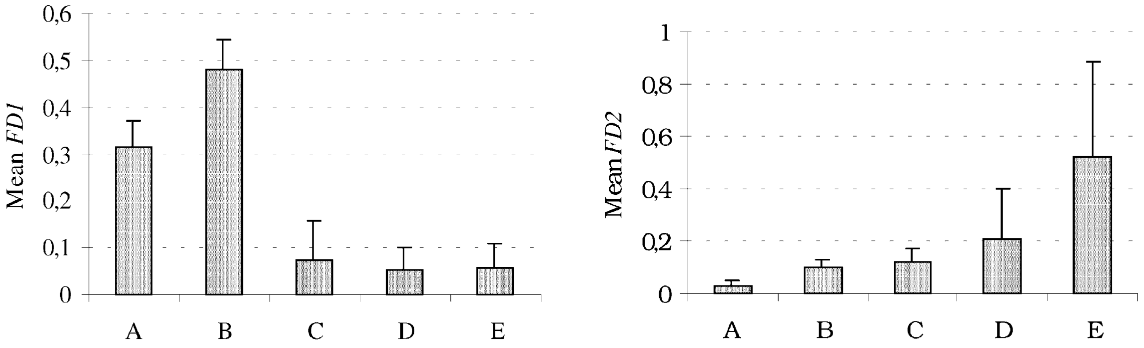
3.2. Diversity indices

We represented the six diversity indices for the five groups of records obtained by the clusters analysis of CCA scores (Excel software) (Figs. 7 and 8). *SR*, Shannon index (*H'*) and Evenness index (*J'*) showed the same patterns of variation. The highest mean values were obtained by group E (regeneration stands), while the lowest were obtained by group A (young plantations). Along axis 1, *FD1* (*FD* along axis 1) clearly opposes young stands (groups A and B) with high value from the old stands and the regeneration stands (groups C–E). Along the axis 2, the mean values of *FD2* (*FD* along axis 2) show a more regular pattern of variation from young stands (groups A and B) to regeneration stands. The *WRH* and *SI* did not show significant variations between the different groups. Nevertheless, young stands (A and B) have the lowest values of *WRH*, and young (A) and regeneration stands (E) have the lowest values of *SI*.

4. Discussion

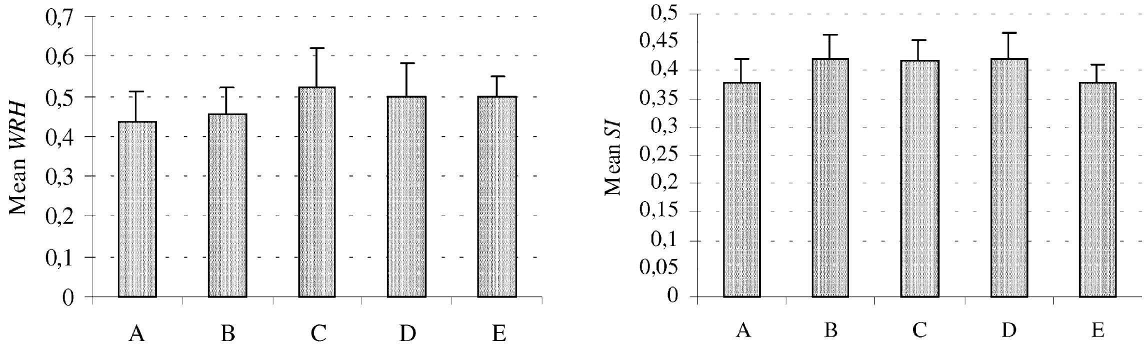
4.1. Validation of the statistical model

SFTS procedure coupled with multivariate analysis and clustering methods allowed us to construct a



(a) Factorial diversity (*FD1*) along axis 1

(b) Factorial Diversity (*FD2*) along axis 2



(c) Within records heterogeneity (*WRH*)

(d) Similarity index (*SI*)

Fig. 8. Mean values of functional diversity indices (FD along axis 1 (a) and axis 2 (b)) and compositional indices (WRH (c) and SI (d)) for each groups resulting from the clusters analysis of CCA records scores.

statistical model of the silvicultural cycle. One of the main criticisms of such a procedure is the divergence which can exist between system trajectory predicted by the model and trajectory observed with a long-term study (McCune, 1992). Nevertheless, our model of species turn-over supports the general model of vegetation development of forest secondary succession formulated by Bormann and Likens (1979). Furthermore, soil characteristics recorded along the modelled gradient reflects the formation of moder humus forms from young plantations to mature stands and mull humus form from mature stands with closed canopy to regeneration stands. This alternation of phases of organic matter accumulation and incorporation have already been shown along a silvigenetic cycle of a natural beech forest in France (Ponge and Delhaye, 1995). Nevertheless, our results based on a morphological description of humus forms cannot allow us to conclude that ecological processes associated to these patterns are the equivalent.

Stand characteristics (stand maturation and canopy thinning) are the most important factors influencing the composition of species assemblages. Soil characteristics do never account for the maximum of explained variance in the CCA. We can thus assume that autogenic factors (stand characteristics) mostly influence plant community composition while allogenic factors (soil characteristics) have secondary influence on species occurrence. It must be emphasised that the successional gradient is not considered as a linear statistic gradient between stages but an ecological cycling process. Therefore, this successional gradient is associated with both axes, based on different botanical and ecological variables. We can therefore assume that: (1) these two axes may reveal different mechanisms of species coexistence, and (2) the statistical model accurately reflects species assemblage changes along a silvicultural cycle, regarding variations in humus forms, and species turn-over along the cycle.

4.2. Pattern of diversity along the silvicultural cycle

4.2.1. Variation of diversity indices

The construction of models identifying diversity changes along successional and site quality gradients is an important issue in forest management in order to understand to what extent management practices influence diversity patterns (Roberts and Gilliam, 1995). To be a useful tool for management, these models must account for the three dimensions of biodiversity (composition, structure and organisation), i.e. they must underline which species coexist in a community, how they coexist and what are the mechanisms of their coexistence (Alard and Poudevigne, 2000). In our study, we assess biodiversity with structural, compositional and functional diversity indices in order to: (i) model its patterns of variation along a silvicultural cycle, and (ii) understand the underlying mechanisms of species coexistence.

Patterns of variations of *SR*, H' and J' seem to support the general model formulated by Franklin (1982): diversity increases to a peak before canopy closure, declines to its lowest values under closed canopy and increases again when canopies of young and mature stands reopen. Following these indices, regeneration stands (group E) exhibit the highest levels of biodiversity. When considering priorities for conservation in temperate forest, one can see that this structural information is not sufficient for management decisions.

Values of *SI* found in this study are globally higher than those of other temperate broad-leaf forests (Scheiner and Rey-Benayas, 1994). We explain these high values by the sampling method used: selection of stands developed on the same soil, with the same management and situated in one forest may reduce factors of variability in plant communities. Moreover, the absence of significant variation of SI indicates that a majority of species do not show a strong association with a particular successional stage. Halpern and Spies (1995) have done the same report in a natural forest of United States. This means that changes in our species assemblages are likely to be structural (the number of species) or functional (the species interactions) rather than compositional (species turn-over) along the succession. This is probably also a consequence of forest intensive management.

The information brought by *FD* measures depends on the ecological interpretation of the two axes of the CCA. Axis 1 reflects stand maturation and a high *FD1* can be interpreted as the coexistence of early-successional species with late-successional species. This non-coherence should reflect non-equilibrium conditions, i.e. change from young to mature stand or heterogeneity conditions (mosaic of different successional stages within one plot). At the opposite, low *FD1* should reflect more stable or homogeneous assemblages.

Axis 2 accounts also for successional changes, i.e. canopy opening reflecting light availability. High *FD2* should also indicate non-equilibrium mechanisms or heterogeneity (canopy gaps) to allow the coexistence of shade-tolerant species with non-shade-tolerant species.

The non-significant variations of WRH between the different groups of records and our sampling design allows us to consider only non-equilibrium and equilibrium mechanisms to explain for species coexistence within the five species assemblages.

4.2.2. Species diversity and coexistence within the different stands

Stands structure have often been described as the major factor determining forest vegetation (Koop, 1989). Others factors, biotic or abiotic, can also explain variations in structural diversity. Strong dominance of one or few species (Yorks and Dabydeen, 1999), soil characteristics such as nutrient availability (Gilliam and Turrill, 1993); litter thickness (Okland, 1988) or ground surface disturbance caused by logging operation (Deconchat and Balent, 2001) can influence species occurrence.

Regarding *FD* on axis 1, groups A and B appear to be unstable assemblages occurring in young stands with the ecologically incoherent coexistence of early-successional with late-successional species. The difference between them is the higher structural diversity in group B. Low structural diversity in young plantations can be explained by the strong cover of *Holcus mollis* which limits the recruitment of shade-tolerant species. Vegetative spread from rhizome fragments

(Grime et al., 1988) and scraping before plantation may favour the invasion of this species in such a shade environment. Persistent shade during stand maturation makes it regress. Recruitment of true shade-tolerant species could then occur and explain higher structural diversity in group B.

After young plantations, mature stands with closed canopy appear to have the lowest structural diversity. We assume that development of moder humus form under closed canopy is a determining factor. Firstly, moder is associated with a low nitrogen and phosphorus availability (Duchaufour, 1997). This is harmful to mull species such as *M. uniflora* which have strong requirements towards these nutrients (Duchaufour, 1989). Secondarily, strong litter thickness associated with this moder humus form is considered to limit plant establishment (Facelli and Pickett, 1991; Graae and Heskjaer, 1997; Sydes and Grime, 1981). Regarding *FD* along the two axes, species assemblages of group C appear to be the most ecologically coherent. These mature stands with closed canopy can be interpreted as the most organised communities (Kolasa and Rollo, 1991) reflecting true coexistence and stable conditions. This suggests that niche partitioning and equilibrium mechanisms would be preferably found in these successional stage.

Following structural indices, groups D and E appear to have the highest diversity. This can be explained by the establishment of new species after canopy thinning. Following canopy disturbance, this trend seems to be a general pattern in temperate forest (Bormann and Likens, 1979). Non-shade-tolerant species taking place in canopy gaps coexist with shade-tolerant species persisting under shade of trees or small shrubs. This ecologically non-coherent coexistence is indicated by the high *FD* on axis 2. Then, the high *SR* of these stands should be based on non-equilibrium mechanism as heterogeneity, measured at this given scale, is not significantly different than other stands.

4.3. Implications for biodiversity management

Recent insight on the biodiversity crisis have focused on the necessity to maintain ecosystem structure and functioning (Franklin, 1993). The definition of an ecosystem of reference (Aronson et al., 1993) should thus consider both aspects. Recent researches have underlined the poor indicative value of *SR* on ecosystem functioning (Wardle et al., 1997). Indeed, different mechanisms of species coexistence can hide behind a given level of *SR* (Gigon and Leutert, 1996). Our results show that the different dimensions of biodiversity (richness vs. organisation) exhibit contrasted patterns of variation along the same silvicultural cycle.

Reaching the highest level of organisation does not imply reaching the highest SR. Priorities for conservation should thus be defined on the basis of which biodiversity dimensions to consider. Priority to system organisation (i.e. the functional dimension) means preserving an ecological process (niche partitioning) and maintaining stable mature communities. Priority to SR (structural dimension) means in our case study the maintenance of system instability or heterogeneity. Although we worked on a very simplified forest system, the information brought by SR or community organisation contrast strongly as far as the implications for management are concerned.

Increasing stand heterogeneity, shortening the rotation length and timber periodicity should thus favour structural dimension of biodiversity, while long-term maturation should increase the organisation characteristic. However, plant diversity is not the only component of biodiversity, especially in our intensively managed and thus over simplified systems. We should also focus on other taxonomic groups and the patterns of variation they exhibit along the same gradient. It is not sure, for example, that the hot-spots of plant diversity (richness or organisation) coincide with those of other groups. If bird communities generally reach the highest SR during the regeneration phase (Ferry and Frochot, 1970), Arpin et al. (1998) have shown a parallelism between vegetation, humus form and soil fauna (earthworm and nematode). Moreover, there are strong assumptions that some groups, such as lichens, fungi or mosses, exhibit the highest SR when plant assemblages reach their highest organisation (Bardat, 1989). In other words, some species would only establish in old growth forest and thus be considered as indicators of organisation or originality of these ecosystems.

The conservation of biological diversity is one of the goals of sustainable forestry (Lindenmayer et al., 2000). To reach this purpose, an understanding of how management practices affect forest biodiversity is a necessary condition (Bengtsson et al., 2000). It needs to develop appropriate standards of comparison between managed stands (Roberts and Gilliam, 1995). Development of diversity indicators based on one taxonomic group or one dimension of diversity may not be sufficient to assess the effect of management on biodiversity.

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