Floristic and ecological differences between recent and ancient forests growing on non-acidic soils

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ABSTRACT

The aim of this work was to investigate differences in soil chemistry and understory composition between recent forests (sites afforested in the last 170 years) and ancient forests growing on non-acidic soils. The study was carried out on hardwood forests at moderate elevation (400–600 m asl) in the Jura Mountains (N.E. France) on four main pedological substrates with different characteristics. The floristic composition of 127 stands from recent forests ($n = 65$) or ancient forests ($n = 62$) was surveyed. Some functional traits and the Ellenberg indicator values of the surveyed species were recorded. In addition, the topsoil from 30 stands was analysed. The composition of the flora was analysed by Detrended Correspondence Analysis and the species which were typical of one class of forest age were identified using a chi-square (χ^2) test. The difference between forest classes for plant traits, their indicator values, or soil chemistry was tested using the generalized linear model and Bonferroni t-tests (or Kruskall–Wallis tests). The floristic composition of the ancient forests was significantly different from that of the recent forests and was characterized by a high occurrence of shrub species in recent forests. These differences were associated with higher specific leaf area, low-range seeds dispersal, and some life forms like geophytes. There was no clear difference in soil chemistry between the two classes of forests, except for $\delta^{15}N$ values. The weakness of the difference in the soil between ancient and recent forests suggested that changes in soil chemistry caused by a former agricultural land use were not responsible for the differences in understory composition recorded. The differences in functional traits between the two forest classes supported this conclusion. We finally concluded that (i) past land use modifies the vegetation composition of current forests, even on neutral soils and that (ii) in our context, biological filters were probably responsible for these changes.

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1. Introduction

In many industrialised countries, forest surface cover has varied considerably over time (Pongratz et al., 2008). A general trend was a negative relationship between the human population and the forest cover, at least before the 20th century (Mather et al., 1999; Pongratz et al., 2008). Indeed, before the intensification of farming practices in the 20th century, any increase in human population led to an increase in food production followed by an increase in cropland cover (Bellemare et al., 2002). During the 18th and the 19th centuries, the increase in population in Western Europe (Mather et al., 1999), North America (Bellemare et al., 2002) and Australia (Meers et al., 2008) led to extensive clear cutting for farming purposes, even in regions that were not propitious for cropping. With the improvement in farming practices in the 20th century, traditional farming progressively turned into intensive agriculture and there was a dramatic increase in yields (Boulaine, 1995a, 1995b). As a consequence, many of the croplands established on former forest soils were abandoned and the land returned to forest (Mather et al., 1999). Hence, there are now two types of forest in these regions: "ancient forests" which correspond to land with continuous forest land use from time immemorial, and "recent forests" on land that was temporarily used as pastures, crop fields or farm gardens (Koerner et al., 1997; Webb, 1998). The comparison between ancient forests and recent forests began a few decades ago (e.g. Froment and Tanghe, 1967; Peterken and Game, 1984; Dzwonko and Gawronsky, 1994; Wülf, 1997; Foster et al., 1998; Hermy et al.,

1999). It is now well established that the former land use has a significant effect on the composition of the vegetation and the soil of current forests (e.g. Fuller et al., 1998; Verheyen et al., 1999) and that some species are typical of ancient forests and others are more frequent in recent forests (e.g. Verheyen et al., 2003b). However, to our knowledge, most studies cited in the literature were carried on relatively acidic soils (Honnay et al., 1999; Koerner, 1999; Verheyen et al., 1999; Bellemare et al., 2002; De Keersmaeker et al., 2004; Falkengren-Grerup et al., 2006; Fraterrigo et al., 2006; von Oheimb et al., 2008) and the results cannot be directly extrapolated to basic soils or even to neutral soils. Therefore, our first objective was to study the effect of the past land use on soil properties and on vegetation composition of forests growing on non-acidic soils.

Commonly, two hypotheses are proposed to explain the difference in vegetation composition between ancient forests and recent forests. The first hypothesis concerns the changes in ecological characteristics that occurred during periods of agricultural land use. Former crop fields have persistent effects on soil properties even after some decades (e.g. Falkengren-Grerup et al., 2006), centuries (e.g. Koerner et al., 1997; Verheyen et al., 1999) or even over a millennium (Dupouey et al., 2002; Dambrine et al., 2007; Plue et al., 2008). The main effects are higher pH values in the topsoil (Froment and Tanghe, 1967; Honnay et al., 1999; Verheyen et al., 1999), P content ($P_{AVAILABLE}$: Honnay et al., 1999; von Oheimb et al., 2008; P_{TOTAL}: Compton and Boone, 2000; von Oheimb et al., 2008), N_{TOTAL} content (Compton and Boone, 2000) or dynamic of soil N cycling and isotopic signature (Chang and Handley, 2000; Compton and Boone, 2000; Jussy et al., 2002). These differences are assumed to be a "memory" effect of past management strategies (e.g. crops, pasture, garden) and which could create new ecological conditions (i.e. a niche effect) enabling colonisation by new species. The second hypothesis concerns the biological traits of the species such as seed production, seed dispersal and inter-specific competition. Some authors have shown that ancient woodland species have low colonisation ability (Pigott, 1982; Hermy et al., 1999; Hermy and Verheyen, 2007). Under this hypothesis, floristic differences between recent and ancient forests would be the result of the ability of each species to colonise and/or compete since agriculture was abandoned. Our second objective was to test these two hypotheses in a non-acidic context.

2. Materials and methods

2.1. Study region and sampling design

In France, half of existing forests were used for farming purposes in the 19th century (Rousseau, 1990; Cinotti, 1996; Mather et al., 1999). This was particularly true in heathland regions and mountainous regions (Mather et al., 1999). Such French regions are thus propitious areas to compare ancient and recent forests. The Jura Mountains (north-eastern France) was chosen for the present study. The study was carried out in the *Petite Montagne*, which is a natural sub-region of the French Jura Mountains, located 20 km south-east of Lons-le-Saunier (46°40′N, 05°33′E), and covering 417 km^2 (approximately 46% of forests) over a limestone substratum. The elevation is moderate, ranging from 400 to 600 m asl. The topography consists of chains of small mountains running N-S interspersed with plateaus and valleys. Annual rainfall is about 1400 mm and the average annual temperature is 9 °C. The sample sites are on brown soils (WRB classification: cambisols and calcisols; FAO/IUSS, 2006) showing varying degrees of leaching with most pH-H$_2$O values ranging from 5.0 to 7.5 (average = 6.7).

Ancient forests (AF) were defined – based on available land registers – as having been permanently covered by forest during the study period, whereas recent forests (RF) were used for

agriculture for several decades in the 19th century. The oldest historical maps available were "Napoleonian land registers" (1800 and onward). These land registers and some land registers from 1830 to the present were used to classify existing forests either as ancient forests or recent forests (Sciama and Hollard, unpublished data). The Napoleonian land registers (scale = 1/2500) were manually intersected with modern land registers. The main past land uses of RF in the *Petite Montagne* were croplands (51%) and, to a lesser extent, mowed meadows (23%) and pastures (26%). 86% of the studied RF were isolated from the surrounding AF. Current management of the stands was identical for the two forest classes (AF and RF), i.e. coppice-with-standards.

The forests were also classified into four geomorphological groups based on the soil substrate. The four substrates were representative of the sub-region and constituted a gradient of soil acidity ranging from slightly acidic soils to basic soils: (i) cherty loams (CL; decarbonated loams containing small fragments of siliceous material; mean topsoil (0–8 cm) pH 5.6), (ii) colluviums of sink (CS; decarbonated loams with a relatively deep soil profile, mostly in dolinas; pH 6.2), (iii) decarbonated clay loams (DC; pH 6.5) and (iv) marls (M; marls with clays and carbonates; pH 7.1). All stands had a mull type of humus.

Our survey comprised 127 plots split into the two forest history classes and four substrates (Table 1). To obtain a reliable comparison between AF and RF, the initial soil and the environmental characteristics of the stands should be the same for the two classes. However, the choice of the land owner to abandon a crop field, or to maintain it, could be influenced by these factors. For instance, the soil texture could be the determining variable in the decision of the farmer, as observed in Belgium where the heaviest soils were abandoned first (Honnay et al., 1999). In the same way, the slope and distance from the field to a road were found to be two of the main variables that determined abandonment of fields in the eastern USA (Flinn et al., 2005). However, in some regions, the distribution between AF and RF was not the result of ecological choices but the consequence of ownership patterns (Motzkin et al., 1996). A study in the Vosges Mountains (a region close to the Jura Mountains) showed that the location of the fields in this region of north-eastern France was mainly practical such as closeness to the farm homestead (Koerner, 1999). The ecological characteristics of the stands in our sampling area were systematically recorded and no significant differences were observed between the ecological characteristics of RF and AF stands (Table 2). Moreover, there was no significant difference of clay content or bulk density between the soils of RF and those of AF (Moares-Domínguez et al., 2001). For these reasons, we assumed that there was no initial difference in the soil or in the situation between RF and AF stands.

2.2. Vegetation and soil sampling

In each stand, a sample plot of 400 m^2 was established in a homogeneous part of the stand. In a latter study, we validated the relevance of this sampling surface by determining the surface the minimal sampling area for a vegetation survey in our study context. The minimal sampling area was estimated as 250 m^2 for a vegetation survey (Sciama, 1999). Floristic surveys were carried out from June to August 1998 and concerned all vascular plants. The Latin names of species follow the *Flora europaea* (Tutin et al., 1966–1980).

Topsoil was sampled in a total of 30 stands on cherty loams and marls (the *a priori* most contrasted substrates according to soil pH): 17 ancient forests (CL: $n = 12$; M: $n = 5$) and 13 recent forests (CL: $n = 8$; M: $n = 5$). All recent forests were former croplands. The soil sampling was carried out in the same sampling plot as for the floristic survey. In each sampling plot, five soil samples were taken in the 0–8 cm soil layer based on a systematic sampling design and

Table 1
Sampling scheme: number of plots sampled in each class of forest age and substrate.

Forest class	Cherty loams	Colluviums of sink	Decarbonated clays	Marls	Total
Recent forests	16	12	22	15	65
Ancient forests	14	10	28	10	62
Total	30	22	50	25	127

then were mixed into one bulk sample. All soil samples were collected in the same week in June.

2.3. Analysis of the vegetation dataset

2.3.1. Composition and indexes

Three aspects of diversity were studied: (i) species richness at the plot level was the total number of species found in the 400 m² plot; (ii) intra-group floristic homogeneity was estimated with the probabilistic measure of Raup and Crick (1979) to assess the floristic homogeneity within each forest class (i.e. AF or RF). These indexes were calculated over all possible pairs of plots belonging to the same forest class, substrate or both; (iii) for each forest class, a list was drawn up of all the species encountered (i.e. seen at least in one sample plot of the class concerned). The number of species encountered per forest class is hereafter referred to as "regional species pools".

2.3.2. Plant traits and indicator values

Some of the plant functional traits which discriminate typical species of the two forest classes (e.g. Verheyen et al., 2003a; Fraterrigo et al., 2006; Van der Veken et al., 2007) were recorded from the following references: life form (Raunkiaer, 1934; Rameau et al., 1989), strategy (sensu Grime, 1977), specific leaf area (m² g⁻¹; LEDA trait base presented by Knevel et al., 2003: http://www.leda-traitbase.org), seed mass (mg seed⁻¹; data from LEDA), seed production per plant (seed plant⁻¹ year⁻¹; data from LEDA), seed dispersal type (types grouped into three classes: zoochory; anemochory; others (i.e. ballistochory, myrmecochory, etc.); data from Rameau et al., 1989), seed longevity index (sensu Bekker et al., 1998; data from LEDA), maximum height (cm; Rameau et al.,

1989), flowering phenology (mean date of flowering; months numbered from 1 to 12; Rameau et al., 1989). In our context, the seed mass and the seed production were redundant ($r^2 = 0.50$ on log transformed values) and consequently the seed production variable was not retained in the dataset.

Ellenberg indicator values of plant species (Ellenberg et al., 1991) were recorded for light (L), humidity (F), nitrogen availability (N) and soil reaction (R). These indicator values vary from 1 to 9 (but up to 12 for F). The value '1' corresponds to the lowest levels of the factor. Mean Ellenberg values for a plot were calculated over all species present in the plot.

Specific leaf area, plant height, flowering phenology and indicator values for light and humidity were used to characterize the flora of RF and AF. Life form, seed mass, seed dispersal type, seed longevity index and indicator values for nitrogen availability and soil reaction were used to determine if the eventual differences of vegetation between RF and AF were the result of some functional traits or the consequence of some soil changes.

2.4. Analysis of the soil samples

Each soil sample was analysed for pH (in a 1:2.5 soil/water suspension; ISO-10390), total carbon content (ISO-10694), total nitrogen content (ISO-11261), Cationic Exchange Capacity (Metson's method; "French Norm" NF-X31-130), exchangeable K, Na and Mg (NF-X31-108), available phosphorus content (extracted by H_2SO_4 0.004 M and NaOH 0.1 M; Duchaufour and Bonneau, 1959) and water content (gravimetric method; ISO-11465). The isotopic $^{15}N/^{14}N$ ratio of total N was measured by mass spectrometry on a soil aliquot. Results were expressed as $\delta^{15}N$, in ‰ deviations from the international standard atmospheric N_2 (Högberg, 1997).

All soil variables were used to determine if the eventual differences of vegetation between RF and AF were the result of some soil changes, excepted C_{TOT} and N_{TOT} which were used to test the effect of past land use on soil organic matter content (Compton and Boone, 2000).

2.5. Statistical data analysis

We calculated the frequency of occurrence for all species in each forest class or substrate. Then, we identified the species that were typical of one forest class using a chi-square (χ^2) test. When the frequencies were too low ($n \leq 5$), we used the Fisher's exact test rather than the χ^2-test. The frequency of the strategies (sensu Grime, 1977) was studied according to the approach of Hermy et al. (1999) and tests were performed in the same way as for the identification of typical species (χ^2-test or Fisher's exact test).

We analysed plant communities using a Detrended Correspondence Analysis (DCA), with the VEGAN package (Oksanen et al., 2006) developed for the R software (Ihaka and Gentleman, 1996).

The effects of forest history class and/or substrate were tested with the generalized linear model using one or two factors and their interaction (SAS software; SAS, 2004). Differences between forest classes or substrates taken by pairs were compared using Bonferroni t-tests (or Kruskall–Wallis tests). The variables analysed were plant traits, indicator values of plants, soil chemistry and coordinates of forest stands in the DCA.

Table 2
Ecological characteristics of sampled sites for each class of forest age.

Characteristic	Recent forests (%)	Ancient forests (%)
Topography		
Plateau	55	52
Slope	28	34
Depression	17	14
Slope		
Low (slope value <10%)	72	60
Moderate (slope value = 10–35%)	28	35
Steep (slope value >35%)	0	5
Class of soil texture		
Clayey soil	49	44
Loamy soil	51	56
Soil thickness		
Shallow soil (thickness <35 cm)	57	55
Moderately deep soil (thickness = 35–55 cm)	31	23
Thick soil (thickness >55 cm)	12	22
Effervescence to HCl	29	26
Soil stoniness		
Nil to low	57	58
High	43	42

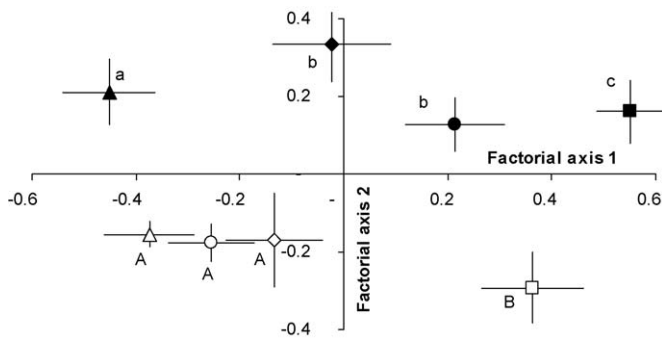Values are % of forest class population.

Fig. 1. Mean positions of recent forests and ancient forests in a Detrended Correspondence Analysis (closed symbol: ancient forest; open symbol: recent forest; triangle: marls; diamond: cherty loams; circle: decarbonated clays; square: colluvions of sink; values on axes: mean values ± one standard error of the coordinates calculated by the DCA with a 127 sampling plots × 168 species matrix; closed symbols followed by different lower case letters differ significantly at the 5% probability level for their coordinate on axis 1; open symbols followed by different upper case letters differ significantly at the 5% probability level for coordinate on their axis 1).

3. Results

3.1. Differences in composition of the vegetation among substrates and classes of forest age

The analysis performed on vegetation surveys revealed a significant ($P < 0.001$; test performed on the DCA coordinates on the first axis) difference in vegetation composition between substrates (Fig. 1). The Kruskall–Wallis test on all of the substrates taken in pairs showed significant differences except for cherty loams and decarbonated clays, whose coordinates could not be separated. The DCA coordinates on the second axis significantly ($P < 0.001$) discriminated plots in the two forest history classes (Fig. 1). Within each forest history class, differences among substrates were also found (Fig. 1). In both forest classes, CS and M were at the extremes of the range of substrates. In the same way, the number of species present at a rate of more than 25% only on one substrate was higher for CS ($n = 15$) and M ($n = 11$) than for CL ($n = 2$) or DC ($n = 0$). For M, DC and CL, the floristic differences were much less pronounced for RF (maximal difference on the mean coordinates on the first axis = 0.24; Fig. 1) than for AF (maximal difference = 0.66). This higher homogeneity of the vegetation of RF was also quantified with the F value (calculated with DCA coordinates on the first axis for M, DC and CL, Fig. 1): RF = 1.6 and AF = 8.2. The probabilistic measure of Raup and Crick was higher for ancient forests than for recent forests (AF = 4.67×10^{-2}; RF = 2.07×10^{-2}) which indicated a more homogeneous vegetation among RF plots than among AF plots. The "regional species pool" was similar in the two forest classes considering the number of plots in each class. Ancient forests had slightly, but not significantly, higher species richness than recent forests (33.8 sp. versus 30.8 sp. in the recent forests; Table 3). There were significantly more herbaceous and tree species in AF plots than in RF plots, whereas shrubs were more numerous in RF plots than in AF plots (Table 3). These differences were most pronounced in DC plots.

A list of the typical species in each forest history class (all substrates taken together or for each substrate separately) is presented in Table 4. There were 31 typical species of ancient forests: 25 herbaceous species, 2 shrub species and 4 tree species. The number of species typical of recent forest was of the same order of magnitude as for ancient forests ($n = 26$) but with a different distribution among herbs, shrubs and trees (11, 12 and 3 species, respectively). Indeed, the typical shrub species were

Table 3
Mean floristic richness, Ellenberg indicator values and mean soil properties among classes of forest age and substrates.

	Floristic richness	Tree richness	Shrub richness	Herb richness	Light (Ell.)	Humidity (Ell.)	Soil reaction (Ell.)	Nitrogen (Ell.)	pH (H$_2$O)	C$_{TOT}$ (g kg^{-1})	N$_{TOT}$ (g kg^{-1})	C/N	CEC (cmol$_c$ kg^{-1})	δ^{15}N (‰)	Available P (g-P$_2$O$_5$ kg^{-1})
RF	30.8 ± 1.1	6.0 ± 0.2	9.4 ± 0.4	15.0 ± 0.9	4.9 ± 0.1	4.9 ± 0.0	6.8 ± 0.0	5.3 ± 0.0	6.2 ± 0.3	49.8 ± 4.3	3.9 ± 0.3	12.8 ± 0.6	23.4 ± 1.8	1.2 ± 0.3	0.20 ± 0.04
AF	33.8 ± 1.2	7.0 ± 0.2	7.7 ± 0.4	18.7 ± 1.0	4.6 ± 0.1	5.0 ± 0.0	6.6 ± 0.0	5.3 ± 0.0	6.0 ± 0.2	49.8 ± 4.8	3.4 ± 0.4	13.8 ± 0.6	23.1 ± 2.5	0.3 ± 0.2	0.17 ± 0.02
RF-DC	30.3 ± 1.4	6.0 ± 0.4	9.9 ± 0.6	14.1 ± 1.2	5.0 ± 0.1	4.8 ± 0.0	6.9 ± 0.0	5.2 ± 0.1	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
AF-DC	36.8 ± 1.6	7.3 ± 0.3	7.5 ± 0.4	21.6 ± 1.4	4.6 ± 0.1	5.0 ± 0.0	6.7 ± 0.1	5.4 ± 0.1	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
RF-CS	29.5 ± 3.0	5.2 ± 0.6	6.7 ± 0.7	16.9 ± 2.1	4.6 ± 0.1	5.0 ± 0.1	6.8 ± 0.1	5.6 ± 0.1	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
AF-CS	34.8 ± 3.9	6.8 ± 0.9	6.2 ± 0.8	21.3 ± 2.6	4.3 ± 0.1	5.2 ± 0.1	6.5 ± 0.1	5.7 ± 0.1	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
RF-CL	29.4 ± 2.4	5.8 ± 0.5	9.0 ± 0.8	14.1 ± 1.8	5.0 ± 0.1	4.9 ± 0.0	6.7 ± 0.2	5.3 ± 0.1	5.5 ± 0.2	42.2 ± 3.5	3.7 ± 0.3	11.4 ± 0.4	21.0 ± 2.5	1.7 ± 0.3	0.26 ± 0.05
AF-CL	29.1 ± 2.0	6.1 ± 0.3	7.6 ± 0.9	15.3 ± 2.1	4.5 ± 0.1	4.9 ± 0.1	6.4 ± 0.1	5.3 ± 0.1	5.6 ± 0.2	41.3 ± 4.3	3.0 ± 0.4	14.1 ± 0.9	19.1 ± 3.0	0.2 ± 0.4	0.19 ± 0.03
RF-M	34.4 ± 2.5	7.0 ± 0.3	11.1 ± 0.5	15.9 ± 2.3	5.1 ± 0.1	4.8 ± 0.1	7.0 ± 0.1	5.2 ± 0.1	7.2 ± 0.1	62.0 ± 7.4	4.1 ± 0.5	15.1 ± 0.6	27.3 ± 2.6	0.3 ± 0.1	0.10 ± 0.01
AF-M	31.0 ± 2.8	7.8 ± 0.6	10.1 ± 1.1	13.0 ± 1.8	4.9 ± 0.1	4.8 ± 0.0	6.7 ± 0.1	5.1 ± 0.1	6.9 ± 0.2	70.2 ± 4.4	4.2 ± 1.0	12.8 ± 0.5	32.5 ± 1.5	0.4 ± 0.2	0.12 ± 0.02
Forest age effect	–	**	**	*	***	**	–	–	–	–	–	–	–	*	–
Substratum effect	–	**	***	***	**	***	***	***	***	***	–	**	***	–	**
Interaction	–	–	–	*	*	**	–	–	–	–	–	–	–	*	–

Class of forest age: RF – recent forest, AF – ancient forest; Substrates: DC – decarbonated clays, CS – colluvions of sink, CL – cherty loams, M – marls; mean values, standard errors and probability levels (***: $P < 0.001$; **: $P < 0.01$; *: $P < 0.05$) from a test using the generalized linear model; Ell.: Ellenberg indicator value; n.d.: not determined.

Table 4
List of species typical of ancient forests and recent forests.

Vegetation layer	Typical species	AS	CL	CS	DC	M	Life form	Strategy	SLA	Seed mass	Seed disp.	Seed long.
(a) Ancient forests												
Herbaceous species	*Ajuga reptans*	**		**	*		Hc	CSR	36.1	1.40	O	0.48
	Anemone nemorosa	***	*	*	**	(*)	G	S/SR	30.0	3.00	O	0.02
	Carex sylvatica	***	(*)	**	(*)		Hc	S	n.a.	12.90	O	0.71
	Convallaria majalis	**	**			*	G	S/SC	n.a.	18.00	Z	0.13
	Euphorbia amygdaloides	**			***		Ch	n.a.	24.0	3.30	O	0.33
	Euphorbia dulcis	(*)					Hc	n.a.	33.3	n.a.	O	n.a.
	Festuca heterophylla	(*)					Hc	n.a.	n.a.	1.44	A	0.00
	Fragaria vesca				(*)		Hc	CSR	21.2	0.30	Z	0.31
	Galeopsis tetrahit			*			Th	R/CR	33.8	4.10	Z	0.45
	Galium odoratum	***		(*)	***	(*)	G	CS/CSR	79.9	5.35	Z	0.11
	Lamiastrum galeobdolon	(*)	(*)				Hc	S/SC	n.a.	2.00	O	0.10
	Lathyrus vernus	**	*		**		G	n.a.	32.2	15.00	Z	0.11
	Lilium martagon	*		(*)	*		G	S/SC	n.a.	7.32	A	0.00
	Luzula pilosa	***	*	**	**		Hc	S	n.a.	1.03	O	0.53
	Melica uniflora				*		Hc	S/SC	n.a.	2.90	O	0.00
	Milium effusum	*			*		Hc	S/CSR	n.a.	1.10	Z	0.53
	Ornithogalum pyrenaicum				*		G	n.a.	n.a.	7.67	n.a.	0.72
	Oxalis acetosella				(*)		Hc	S/CSR	60.8	1.41	O	0.19
	Phyllitis scolopendrium				(*)		Hc	n.a.	n.a.	n.a.	O	n.a.
	Phyteuma spicatum	***		(*)	***		Hc	n.a.	n.a.	0.15	O	0.00
	Poa nemoralis				(*)		Hc	S/CSR	n.a.	0.20	A	0.39
	Primula elatior	*			(*)		Hc	n.a.	n.a.	0.85	A	0.00
	Solidago virgaurea		(*)				Hc	S	19.6	0.49	O	0.12
	Vicia sepium	*		*	***		Hc	C/CSR	39.0	18.70	O	0.03
	Viola reichenbachiana	**			*		Hc	S	29.1	1.21	O	0.33
Shrubs	*Buxus sempervirens*		*			(*)	Ph	n.a.	n.a.	14.30	O	0.00
	Viburnum opulus			(*)			Ph	SC	17.9	35.00	Z	0.00
Trees	*Acer pseudoplatanus*	***		**	***	(*)	Ph	C/SC	22.5	n.a.	A	0.00
	Populus tremula	*					Ph	SC	14.6	0.11	A	0.00
	Prunus avium	**			**		Ph	SC	n.a.	187.00	Z	0.00
	Quercus petraea	**	(*)		*		Ph	SC	n.a.	2342.20	O	0.00
(b) Recent forests												
Herbaceous species	*Dactylis glomerata*				(*)		Hc	C/CSR	21.8	0.90	A	0.15
	Epipactis helleborine	*			*		G	S	28.4	n.a.	n.a.	0.00
	Geum urbanum				*	*	Hc	S/CSR	40.4	1.90	A	0.05
	Glechoma hederacea		(*)				Hc	CSR	35.8	0.69	A	0.20
	Helleborus foetidus	**	(*)		(*)		Ch	SC/CSR	n.a.	11.34	O	0.00
	Neottia nidus avis				(*)		G	n.a.	n.a.	n.a.	A	n.a.
	Pulmonaria montana		*				Hc	n.a.	n.a.	n.a.	O	n.a.
	Stachys officinalis			(*)			Hc	S	n.a.	11.40	A	0.29
	Tamus communis	**	(*)	*	*		G	C/CR	n.a.	17.90	Z	0.00
	Taraxacum officinale		*				Hc	R/CSR	n.a.	0.70	A	0.26
	Veronica chamaedrys		(*)				Hc	CSR	28.7	0.21	O	0.32
Shrubs	*Cornus sanguinea*	***	**		(*)		Ph	C/SC	n.a.	66.70	A	0.01
	Crataegus laevigata			*			Ph	n.a.	20.2	143.40	Z	0.07
	Crataegus monogyna	***	(*)	(*)	**		Ph	SC	13.7	140.00	Z	0.00
	Daphne laureola	(*)			(*)		Ph	SC	9.3	n.a.	Z	0.00
	Euonymus europaeus	***	*	***	(*)		Ph	SC	9.0	44.40	Z	0.00
	Ligustrum vulgare	*	*		*		Ph	SC	14.1	21.80	Z	0.04
	Lonicera periclymenum				*		Ph	SC	n.a.	n.a.	Z	0.04
	Lonicera xylosteum	*			**	(*)	Ph	n.a.	n.a.	4.00	Z	0.00
	Prunus spinosa	***	*		**		Ph	SC	16.8	225.80	Z	0.00
	Ribes uva-crispa				*		Ph	SC	29.3	3.33	Z	0.00
	Rubus caesius				(*)		Ch	SC	n.a.	3.60	Z	0.00
	Viburnum lantana	*			*	*	Ph	n.a.	n.a.	44.00	Z	0.00
Trees	*Picea abies*		(*)				Ph	n.a.	n.a.	7.00	A	0.08
	Quercus robur	(*)					Ph	SC	14.0	3378.00	O	0.00
	Salix capraea				(*)		Ph	n.a.	n.a.	n.a.	A	0.02

Typical species of ancient forests and recent forest were determined according to a χ^2-tests comparing the frequency of each species in each forest class with its frequency in the whole set of plots (***: $P < 0.001$; **: $P < 0.01$; *: $P < 0.05$; (*): $P < 0.1$); AS – all substrates; CL – cherty loams; CS – colluviums of sink; DC – decarbonated clays; M – marls; life form (Raunkiaer, 1934): Ch – chamaephytes; G – geophytes; Hc – hemycryptophytes; Ph – phanerophytes; Th – therophytes; strategy (Grime, 1977): C – competition, S – stress, R – ruderal. SLA – specific leaf area ($m^2\ g^{-1}$; from LEDA trait database http://www.leda-traitbase.org; see Knevel et al., 2003). Seed mass (mg seed^{-1} from LEDA trait database). Seed dispersion (Rameau et al., 1989): A – anemochory; Z – zoochory; O – others (barochory; myrmecochory; …). When two dispersion modes were mentioned, only the most efficient was retained (A > Z > O). Seed longevity (index proposed by Bekker et al., 1998: values range from 0 (strictly transient) to 1 (strictly persistent); from LEDA trait database). 'n.a.' – not available.

mostly present in RF whereas typical herbaceous species were more present in AF. Typical RF (or AF) species were more numerous on DC than in plots on CS, CL and, overall, M (Table 4).

3.2. Functional traits and soil properties

AF species were characterized by the dominance of hemicryptophyte species (53% of AF species; Table 4) and by a high proportion of geophyte species (19%). The list of RF species was dominated by phanerophyte and chamaephyte species (total = 62%). However, these differences were, at least partly, related to the relative proportion of the forest layers. Indeed, when taking into account only the herbaceous layer, there was no difference of life form between AF species and RF species. In AF, there were significantly ($P = 0.001$) more species with an S strategy than in RF. Conversely, SC species were significantly more numerous in RF than in AF.

AF species had significantly higher SLA ($P = 0.042$; AF = 32.9 ± 4.6 m^2 g^{-1}; RF = 21.7 ± 2.9 m^2 g^{-1}) and seed longevity ($P = 0.005$; AF = 0.20 ± 0.04, RF = 0.06 ± 0.02) than RF species. There were also significant differences between AF and RF species in seed mass ($P = 0.034$; AF = 6.2 ± 1.6 mg, RF = 41.2 ± 14.7 mg) when the trees were not taken into account. All these results were still significant ($P < 0.050$) when the species that were only slightly associated (only 0.05–0.10 P scores for chi-square (χ^2) tests) with a forest class (AF or RF) were not included. The high mean value of seed mass of RF species was linked with a high proportion of species producing berries or drupes dispersed by birds (Table 4: e.g. *Crataegus laevigata*; *Crataegus monogyna*; *Lonicera periclimenum*; *Lonicera xylosteum*; *Prunus spinosa*). Forty-eight percent of AF species had a long-range strategy of seed dispersal (19% of anemochory; 29% of zoochory). This value was much higher (84%) for RF species (36% of anemochory; 48% of zoochory).

The mean height of RF species was higher than that of AF species ($P = 0.016$). But this difference was more the consequence of the high frequency of shrubs in the RF list (AF: 25/31 species in the herbaceous layer; RF: 11/26; Table 4) than of a difference in plant height for each vegetation layer. Indeed, there was no longer a significant difference when plant height was assessed layer by layer. The mean date of flowering (months numbered from 1 to 12) of AF species (4.7 ± 0.2) was not significantly different from that of RF species (4.4 ± 0.2).

According to mean Ellenberg indicator values, the floristic composition of AF was significantly more shade tolerant than that of RF (Table 3). This was also the case within each substrate type. Although the differences were not significant between the two forest classes for the mean indicator values for soil reaction (R), we observed a few more acidophilous species in ancient forests. There was no significant difference in the N indicator value between the two forest classes.

Soil δ^{15}N differed significantly between RF and AF, but there was almost no significant difference between forest classes for any other soil variable we studied (Table 3). Only a few interactions between the forest classes and the pedological substrate were observed (Table 3). For instance, even not significantly different, the content of available P tended to be higher in RF soils than in AF soils for the CL class (Table 4). On the other hand, soils on M had very similar values of available P.

4. Discussion

Our results confirmed previous studies indicating significant differences in floristic communities between recent and ancient forests (e.g. Wülf, 1997; Hermy et al., 1999). The most obvious difference concerned the vertical structure of the vegetation. Indeed, there were more species in the shrub layer in recent forests whereas there were more herbs in ancient forests than in recent forests. The shrub richness in recent forests was probably the consequence of former colonisation of abandoned fields. Some of the shrubs in our study area should thus be considered as relicts from previous stages in vegetation succession (Glenn-Lewin et al., 1992; Verheyen and Hermy, 2001b).

The analysis of the vegetation composition showed that some species were typical of one forest class. Considering the difference of vertical structure between ancient forests and recent forests, it was not surprising that the majority of the species typical of recent forests were shrubs. In the same way, most of the species typical of ancient forests in the present study context were herbaceous species. Some of the later species, such as *Anemone nemorosa*, *Carex sylvatica*, *Euphorbia amygdaloides*, *Milium effusum* or *Luzula pilosa*, were already classified as species of ancient forests in other European regions (Dzwonko and Gawronsky, 1994: Carpathian Mountains; Hermy, 1994: Flanders; Peterken and Game, 1984: Lincolnshire). It is noticeable that, in addition to these well known species of ancient forests, some of the species we identified as belonging to ancient forests have rarely been cited before (e.g. *Lilium martagon*).

The vegetation in recent forests was significantly more heliophilous than in ancient forests (Hermy et al., 1999; Wülf, 2003). These differences were not biased by current stand management because, in the *Petite Montagne* region, there is no difference in the management of recent forests and ancient forests (Sciama, 1999). The differences in plant light requirements may be due to the persistence of ruderal species, or species used by man, in RF which significantly affects the mean value of the indicator for light. In the same way, AF species have higher Specific Leaf Area than RF species. A higher leaf surface area with the same biomass is an adaptation to shade conditions, like in mature forests, and confirmed the hypothesis that AF species should be considered as particularly adapted to forest conditions. Furthermore, as previously shown by Wülf (2003), there were more competitive species in recent forest than in ancient forest (see tests on strategy types). Finally, in the present study context, some clear differences were observed in the composition of vegetation of ancient forests (with species particularly adapted to forest conditions) and recent forests (with ruderal species or species from the vegetation succession). It is thus important to understand the processes of discrimination between these kinds of species. As stated in Section 1, there are commonly two hypotheses which could explain such differences between ancient forests and recent forests: (i) changes in ecological conditions (mainly soil properties) and (ii) biological filters during afforestation of abandoned croplands (like abilities of species for dispersal, recruitment or competition). In the *Petite Montagne* area, the effect of land-use history on soil was weak. The present work did not provide evidence of any significant difference (like Bellemare et al., 2002) in, for instance, soil acidity between recent and ancient forests as previously reported by other authors (e.g. Wilson et al., 1997; Compton et al., 1998). Indeed, there was no significant difference in R Ellenberg indicator values and soil pH between the two forest classes, even if a very slight trend was observed. Other soil variables showed no obvious difference between ancient and recent forests, except δ^{15}N. Overall, we suppose that the relative fertility and the high acid neutralising capacity of the soils of our study could mask the effect of land use on soils, especially for the marls class which has the highest pH values. It should be noted that most studies that showed a strong effect of land use on soil characteristics were conducted on soils with relatively low fertility and acid neutralising capacity (Koerner et al., 1997; Wilson et al., 1997; Compton et al., 1998). In the case of the soil δ^{15}N, a discrepancy between recent and ancient forests is quite a common result (Handley and Raven, 1992; Koerner et al., 1997; Chang and Handley, 2000; Jussy et al., 2002; Compton et al.,

2007). Higher soil δ^{15}N for cropped soils, or recent forest soils, may be the result of repeated isotopic fractionation (Compton et al., 2007) combined with high nitrification rates (Jussy et al., 2002; Compton and Boone, 2000) and nitrate leaching (Handley and Raven, 1992). However, in our context, the soil δ^{15}N variable was more the exception than the rule as there was no strong difference in soil properties between recent and ancient forests. Therefore, we concluded that the first hypothesis explaining floristic differences (i.e. a change in soil characteristics) was not validated in our study context (i.e. neutral soils). This conclusion is further supported by experimental approaches showing that ancient forest species are able to grow on enriched soils (Hipps et al., 2005) or when transplanted to soils of recent forests (Petersen and Philipp, 2001; Graae et al., 2004).

On the other hand, the results of the present study were in agreement with those of previous works that propose biological filters as the main hypothesis explaining the difference in vegetation between ancient and recent forests (e.g. Matlack, 1994; Brunet and von Oheimb, 1998; Verheyen et al., 2003a; Hermy and Verheyen, 2007). Indeed, our AF species included a high proportion of species with a relatively low seed dispersal range (e.g. Bellemare et al., 2002; Wülf, 2003; Meers et al., 2008). In the same way, a high proportion of AF species had a life form, like geophyte species, that is not adapted to disturbances caused by farming activities (Froment and Tanghe, 1967; Peterken and Game, 1984). At first reading, some of the results of the present study were not in line with those of the literature, for instance the mean seed mass and the mean seed longevity of the AF and RF species (Verheyen et al., 2003a). However, the colonising ability of a species does not depend on only one functional trait; all the traits have to be taken into account (Verheyen and Hermy, 2001a; Verheyen et al., 2003b). Indeed, the AF species of the *Petite Montagne* have higher seed longevity than those of RF species. Nevertheless, many of the RF species which are characterized by very low seed longevity also produce heavy fruits (i.e. berries or drupes) that are efficiently dispersed over long distances by birds (Jacquemyn et al., 2003). This trait explained their status as RF species in spite of their low seed longevity. Fraterrigo et al. (2006) also observed interactions between past land use, life-history traits and composition of the vegetation, which suggest that the functional traits responsible for the differences in the understory of ancient forests and of recent forests are context dependant. In other words, depending on the region concerned, functional traits that show a significant difference in mean value between the two forest classes may be not always the same. Under this hypothesis, the absence of significant differences between AF and RF species for traits like flowering phenology is not in contradiction with the literature because of the existence of many sources of interaction between ecological variables. This was clearly true for the effect of the pedological substrate. Although most of the ancient forest species cited in the present work are commonly found in European old woodlands, the floristic communities of each forest class depend on the substrate type as shown by the first axis in Fig. 1. Altogether, the CS vegetation was quite different from the vegetation on other substrates, especially in recent forests (Fig. 1). This result was probably the consequence of particular soil conditions (Appendix A). The substrate influenced the number of typical species (e.g. DC has more typical AF species than other substrates; Table 4) and the list of the typical species (e.g. *Buxus sempervirens* was identified as an ancient forest species only on cherty loams and marls). The nature of the interaction between the typical species and the substrate was not the same for all the species. Some species had a clear ecological preference for one or two substrates and could thus not logically be identified as a typical AF species for the other substrates. For instance, *B.*

sempervirens was absent from all CS sample plots, whatever their past land use. Some other species displayed a true interaction between the substrate and the past land use. For example, *Acer pseudoplatanus* and *E. amygdaloides* were present on all substrates at around the same frequency rate (frequency of occurrence in one class of substrate: *A. pseudoplatanus* = 18–33%; *E. amygdaloides* = 6–7%) but were typical of AF for only certain substrates (Table 4). It should be also noticed that the unbalanced study design has probably biased these substrates × species interactions. Indeed, the DC population was the highest in frequency (Table 1) which could have caused the statistical tests to be more often significant (e.g. *E. amygdaloides*). However, CS and M had a fairly similar size of population (Table 1) but displayed very different results (Table 4). The bias caused by the study design was therefore only partial and there were real interactions between substrates and species.

To conclude, our results showed that past land use had significant effects on the vegetation of current forests growing on non-acidic soils. This study confirmed results commonly found for acidic soils and hence supports the idea that they may be generalized to most soils. Moreover, our results and those cited in the literature suggest that biological processes may be the main factors explaining differences in floristic composition between recent and ancient forests (Verheyen and Hermy, 2001a; Van der Veken et al., 2007). During the period of agricultural land use, species typical of ancient forest were lost from the soil seed bank in only a few decades (Bossuyt and Hermy, 2001). Subsequently, some of these species did not re-colonise the forest habitat. We speculate that this result was mainly due to limitation of dispersal (e.g. Whitney and Foster, 1988), limitation of recruitment (Verheyen and Hermy, 2001a), or because of their limited ability to compete with ruderal species that had already colonised the recent forests (De Keersmaeker et al., 2004). Past land use may have a significant effect on soil properties (e.g. Compton and Boone, 2000), but this effect interacts with the initial soil properties and is often of low intensity (von Oheimb et al., 2008) and sometimes insignificant (e.g. Bellemare et al., 2002; the present study). The changes in soil chemistry seem to increase with the initial poverty of the soils. In any case, it seems that the potential shift in soil properties is not strong enough to directly explain the absence of certain species (Hipps et al., 2005). More generally speaking, the selection of some species as typical of ancient forests is a complex process that interacts with many parameters like forest age and area (Jacquemyn et al., 2001), landscape patchiness and connectivity (Dzwonko and Loster, 1989; Grashof-Bokdam, 1997), the type of past land use (Wülf, 2004), the plant's ecological traits, soil properties and the criteria that led to the abandonment of agriculture. Most of these variables are highly dependent on the region concerned. This dependency to the regional context suggests that the patterns of vegetation discrimination between ancient and recent forests cannot be directly extrapolated from one area to another. With the aim of improving management of forest biodiversity, the establishment of lists of typical species should not be seen as the final objective, and we should have a special focus on the interactions among these variables both at the local and the regional scale (Jacquemyn et al., 2001).

Appendix A. Ecological characteristics of colluviums of sink compared to other substrates.

Characteristic	Colluviums of sink (%)	Other substrates (%)
Topography		
Plateau	0	62
Slope	0	36
Depression	100	2
Class of soil texture		
Clayey soil	37	48
Loamy soil	63	52
Soil thickness		
Shallow soil (thickness <35 cm)	19	61
Moderately deep soil (thickness = 35–55 cm)	19	29
Thick soil (thickness >55 cm)	62	10
Effervescence to HCl	16	29
Soil stoniness		
Nil to low	94	52
High	6	48

Values are % of forest class population.

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