PRESENT FOREST BIODIVERSITY PATTERNS IN FRANCE RELATED TO FORMER ROMAN AGRICULTURE

E. Dambrine,[1,6] J.-L. Dupouey,[1] L. Laüt,[2] L. Humbert,[1] M. Thinon,[3] T. Beaufils,[4] and H. Richard[5]

[1]*INRA, 54280 Champenoux, France*
[2]*40, avenue d'Italie, 75013 Paris, France*
[3]*Institut Méditerannéen d'Ecologie et de Paléo-écologie, CNRS, Case 461, Faculté St-Jérôme, 13397 Marseille Cedex 20, France*
[4]*5, rue Chevigney, 25170 Emagny, France*
[5]*CNRS, Laboratoire de Chrono-écologie, 16 route de Gray, 25030 Besançon, France*

Abstract. Combined archaeological and ecological investigations in a large ancient oak forest in Central France have revealed a dense network of ancient human settlements dating from the Roman period. We demonstrate a strong correlation between present-day forest plant diversity patterns and the location of Roman farm buildings. Plant species richness strongly increases toward the center of the settlements, and the frequency of neutrophilous and nitrogen-demanding species is higher. This pattern is paralleled by an increase in soil pH, available P, and $\delta^{15}N$, indicating the long-term impact of former agricultural practices on forest biogeochemical cycles. These extensive observations in a forested region on acid soils complement and confirm previous results from a single Roman settlement on limestone. Ancient Roman agricultural systems are increasingly being identified in contemporary French forests; the broad extent and long-lasting effects of previous cultivation shown in this study require that land-use history be considered as a primary control over biodiversity variations in many forest landscapes, even after millennia of abandonment.

Key words: archaeology; Central France; land-use history; plant diversity; Roman agriculture; soil nutrient status; temperate forest.

INTRODUCTION

In Western Europe and the eastern United States, recent forests comprise between 50% and 80% of the present forest area, having developed on lands used for agricultural purposes in the 19th and early 20th centuries (Mather et al. 1998, Bellemare et al. 2002). These recent forests can be distinguished from ancient forests, which we define as lands that remained forested since the time of the most ancient available maps. This period varies from country to country according to the availability and age of written historical sources. Comparison of recent and ancient forests shows that former agricultural use is a major factor influencing biodiversity patterns in present forests: recent forests are richer in nitrogen-demanding, ruderal plants (Koerner et al. 1997, Foster 2002). Formerly cultivated soils often show specific properties compared to ancient forest soils (Compton et al. 1998, Koerner et al. 1999, Jussy et al. 2002), and these characteristics also contribute to differences in biodiversity. Moreover, some plant species appear confined to ancient forests; this is mainly due to their poor dispersal abilities (Peterken and Game 1984, Hermy 1994, Hermy et al. 1999). In view of the considerable length of time required for their recoloni-

zation of abandoned agricultural lands (Vellend 2003), these species have been given a higher conservation value. Hence, historical information is being increasingly used in the management of biodiversity and development of conservation policies.

The length of time these agricultural legacies persist is a major scientific question (Peterken and Game 1984, Peterken 1996), both for the analysis of present biodiversity patterns and for predicting the long-term impacts of current human activities on future ecosystems. Legacies are clearly visible in recent forests dating from the beginning of the 20th century (Dzwonko and Loster 1992, Foster 1992, Singleton et al. 2001). They have also been observed in western European forests dating from the 19th or 18th century (Peterken and Game 1984, Koerner et al. 1997, Wulf 1997). Where sufficiently ancient maps or texts are available, significant differences between recent and ancient forests can still be observed after 400 years (Peterken and Game 1984).

In order to examine the question of how long the consequences of agriculture can last, we searched for the oldest abandoned agricultural systems we could find in present-day forests. Forest area in Western Europe is often considered to have continuously shrunk from the first detectable Neolithic deforestations until the beginning of the 19th century, but recent surveys in large forests in France that were previously considered to be ancient have shown that many areas cultivated during Roman times were returned to forest after the third or fourth century AD, following the crisis of the Roman
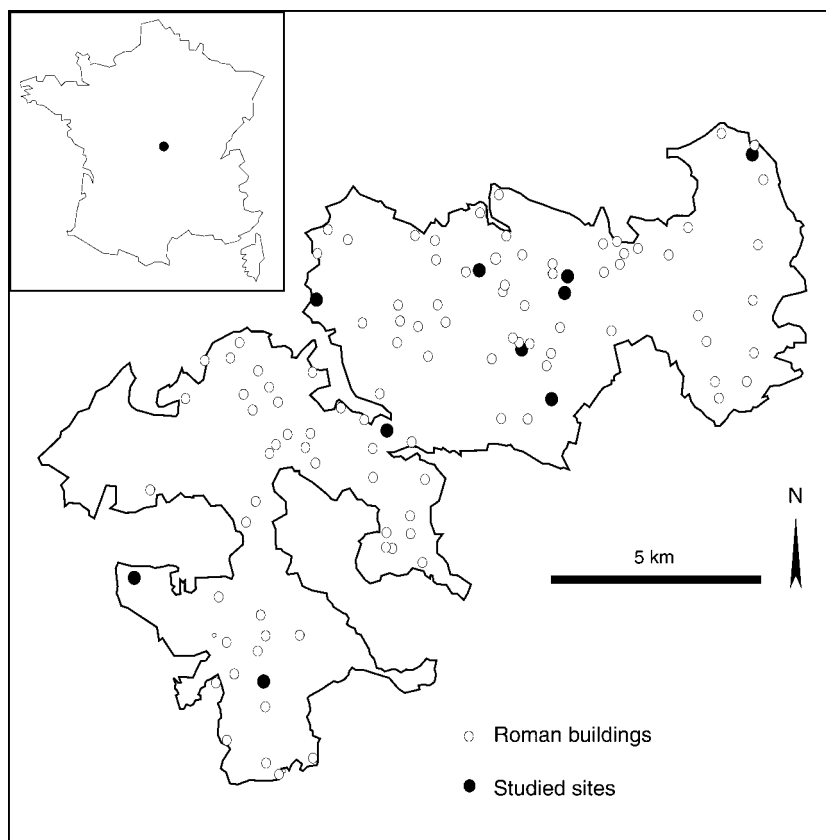
Fig. 1. Map of Tronçais forest, Central France, indicating the location of Roman buildings, after Bertrand (1996) and Laüt (2001). Sites in this study are represented by black dots.

Empire (Dupouey et al., *in press*). Few archaeological investigations have taken place in forests compared to open cultivated areas because aerial identification of ancient settlements is not possible under forest cover, and artifacts are not brought back to the soil surface by plowing. This previously led to the questionable impression that ancient forests had never been cultivated before the historical period. Nevertheless, a preliminary search through archaeological databases yielded more than 2000 mentions of Roman occupation, including all kinds of activities, located throughout French forests (Maussion 2003). In addition, systematic inspection of the ground surface in French forests has recently brought to light large agricultural cadastres dating from Roman times (Mangin et al. 2000, Laffite et al. 2002). We were able to use these surveys to study the consequences of 2000-yr-old agricultural practices on today's landscape. In a large forest in Central France, we tested the hypothesis that the location and intensity of Roman land use influences present-day spatial patterns of plant diversity and soil properties.

STUDY AREA

The Tronçais forest covers 10 600 ha of a homogeneous sandy plateau in Central France (Fig. 1; Plate 1).

It is located 50 km west of Moulins in the Berry region. It is the most well-known source of high-quality oak wood in France, often used in casks for vintage wine aging. The soils are mostly sandy acidic inceptisols developed from sandstone or alluvial sand deposits, with various degrees of hydromorphy (Bonfils 1970). The forest is mainly composed of pure even-aged high-forest stands of *Quercus petraea*. All available historical documents point to a long and continuous forest history. The first available map (Fleury, dated from 1665, scale 1:7300) indicates forest boundaries very similar to the present ones. By the 17th century, this forest, as with most forests in France, was being heavily exploited for wood products and grazing. At that time, the king's advisers, Doquère (in 1645) and Hurault (in 1670), described Tronçais as a forest of more than 10 000 ha, among which 600 only were exploitable and the rest was composed of young stands, wetlands, and open areas spotted with old trees that were annually burned to improve grass growth for grazing. During the 18th century, the forest was being progressively transformed into a high forest, though at the beginning of the 19th century, the major part was still managed as coppice with standards for coal production and clog making.

In this ancient forest, 108 Roman settlements were recently found (Fig. 1) by surface surveys of stones, tiles, and ceramics (Bertrand 1996, Laüt 2001). Standard archaeological references have determined that these remnants date from the first to the fourth centuries AD. More recent artifacts, from the early Middle Ages, have also occasionally been found. Some buildings appear as 0.1–1 m high elevations made of stones covering between 10 and 100 m². But many were only detected from the surface collection of ceramic remains, notably in mole hills. A few large sites contain several buildings. The largest site covers an area of 9000 m².

Methods

We made a spatial analysis of the human settlements at the landscape level. The 108 buildings were located on a 1:2500 soil type map and on a 50-m digital elevation model using a geographical information system. The average proportions of all soil types and topographic conditions encountered in 100-m radius buffer zones centered on each settlement were compared with proportions observed in equivalent buffers distributed at random throughout the forest.

Plant community composition and soil properties were assessed in 186 plots along gradients of increasing distance (0–500 m) from the center of 10 Roman sites. The sites were chosen to cover a range of settlement sizes because size could have influenced the intensity of land use. We selected three large sites containing several buildings and seven small sites. All stands were even-aged high forest dominated by *Quercus petraea* with *Carpinus betulus* in the understory. They were all dense mature stands, between 92 and 197 years old, except for one stand which was 37 years old. In each plot (10 × 10 m), the complete list of phanerogams and terricolous mosses was drawn up and the soil was described and sampled. Soil humus, color, texture, and stoniness were described along a profile to a depth of 1 m by auguring. The upper mineral soil (0–10 cm) was sampled over a 400-cm² area and sieved (4 mm) to collect archaeological artifacts. Tile, mortar, and ceramic pieces were counted. Soil samples were air dried and analyzed for pH, total C and N (dry combustion), and acid-extractable P (Craddock et al. 1985); $\delta^{15}N$ and coarse sand content were measured after sieving (200 μm).

At four sites the buildings were excavated. Different types of occupation were suggested by the artifacts and the spatial layout of the buildings: tile making, iron smelting, religious use and farming. An assessment of past tree-species composition was made by examining charcoal separated from sets of soil samples (14 total) taken from the surface to the bedrock (~0.8 m depth) at three locations, 20 m from a settlement, and 240 m and 440 m from a second settlement, respectively. All charcoal pieces larger than 0.4 mm were identified following Thinon (1988) and Schweingruber (1990) procedures and weighed. The charcoal was not dated. At two sites, pollen grains were analyzed following

conventional methods (Moore et al. 1991). Eight soil samples were collected at 30–40 cm or 50–60 cm in the center and at the periphery of a shallow, intermittently wet depression in the close vicinity of the buildings. These sediments contained Roman artifacts but had possibly been disturbed. The pollen was poorly preserved and two samples could not be used.

The species data (186 plots × 178 species) were subject to detrended correspondence analysis (DCA), using the CANOCO package (ter Braak and Smilauer 2002). Conventional options were used: detrending was done by segments and rare species were down weighted (Jongman et al. 1995). Canonical correspondence analysis (CCA) using distance from the center of the Roman sites and soil characteristics as explanatory variables did not improve upon the results using the DCA. In order to interpret the DCA results, we calculated in a second step the Pearson correlation coefficients between each axis and measured environmental variables as well as Ellenberg et al.'s (1992) indicator values for nitrogen, acidity, and light. Species are scored on a nine-point scale, according to their ecological requirements. Low values for nitrogen (N_{Ell}), acidity (R_{Ell}), and light (L_{Ell}) indicate preferences for nitrogen-poor, acid, and shady conditions, respectively. These indicator values have been shown to correlate well with measured environmental characteristics in a broad range of conditions over Western Europe (Schaffers and Sykora 2000, Wamelink et al. 2002). For each plot, the indicator values were averaged over all observed species, giving mean plot indicator values for nitrogen, acidity, and light.

The impact of Roman occupation on soil and vegetation characteristics was tested using the following covariance model:

$$X_{ij} = \alpha + \text{Site}_i + \beta \times \log(\text{Dist}_{ij}) + \varepsilon_{ij}$$

where X_{ij} is the value of the observed variable X at plot j in site i; α is the intercept; Site_i is the effect of site j; Dist_{ij} is the distance of plot j from the center of site i; and ε_{ij} is the error term. Only the five sites displaying more than 14 plots were used. Because of a nonlinear response, distance (Dist_{ij}) was log-transformed. Due to the unbalanced design, models were fitted using the GLM procedure of SAS. Effects were considered fixed and tested in a type III analysis (SAS Institute 1999). Normality of the residuals was checked by visual inspection.

In order to remove between-site variability when plotting the relationship between environmental variables and distance from the center of the site, variables were standardized for each site by subtracting the average value over all the plots located far from the center. For this purpose, the total sample was divided into two balanced groups according to the distance from the center of the sites: the inner (<100 m, 85 plots) and outer (100–500 m, 101 plots) zones. These two zones were also used to identify the plant species preferring or avoiding the
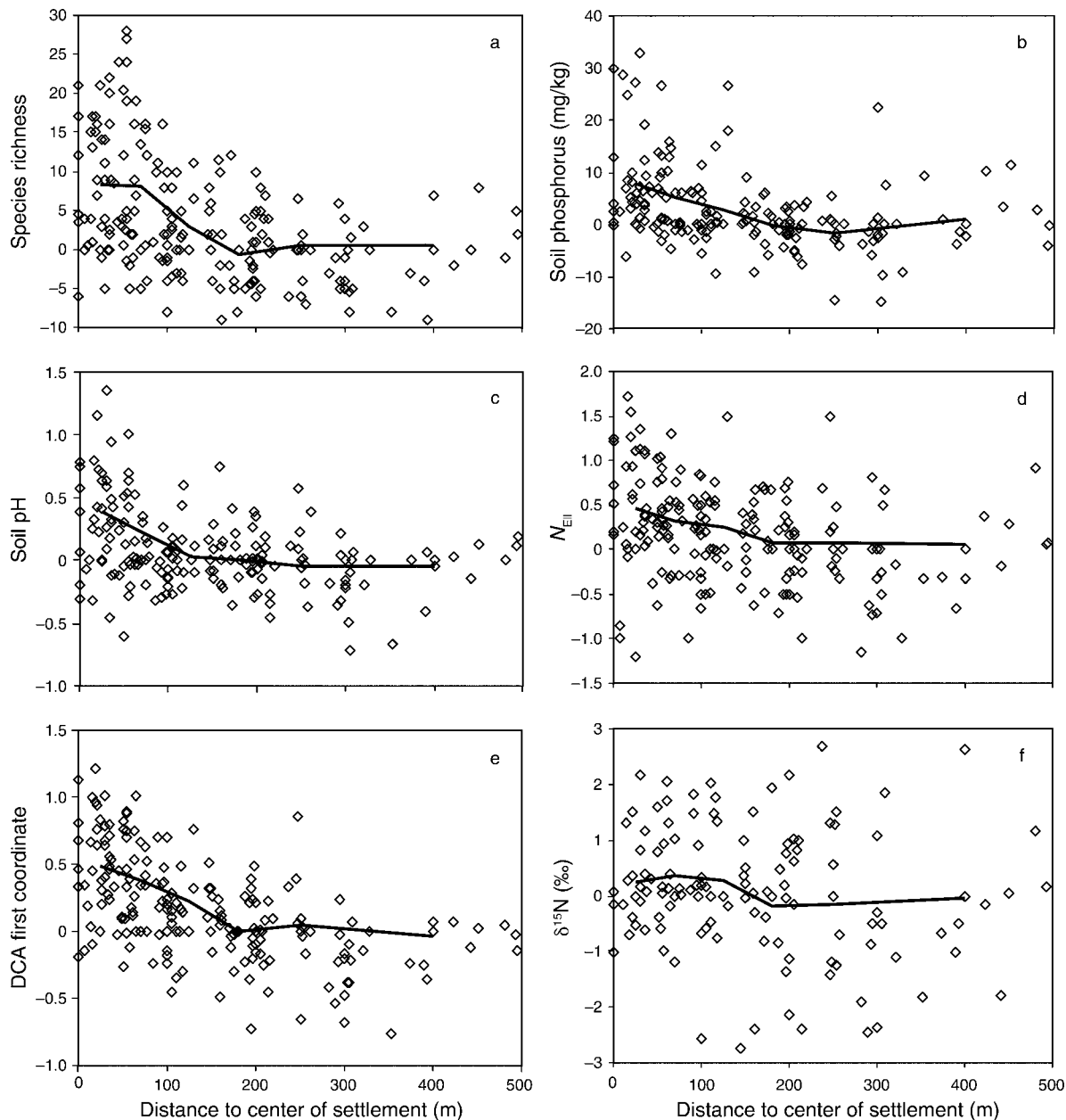
FIG. 2. Vegetation and soil characteristics as a function of distance to the center of the 10 settlements: (a) species richness, (b) soil phosphorus content, (c) soil pH, (d) Ellenberg's indicator value for nitrogen, (e) scores on the first axis of a detrended correspondence analysis (DCA), and (f) $\delta^{15}N$. For all panels, the y-axis represents departure from the mean calculated at a given site for all plots in the outer zone (100–500 m). Solid lines join average values over sets of 30 plots.

settlements. The difference in frequency of occurrence of each species between the inner and outer zones was tested according to a Fisher's exact two-tailed test.

RESULTS AND DISCUSSION

Reconstruction of land cover and land use at the Roman sites

Total soil charcoal mass was highest (421 kg/ha) at the location closest to the center of a settlement (20 m).

At the second settlement, charcoal mass was 227 kg/ha at 240 m and 143 kg/ha at 440 m. The decrease with distance tends to support the notion that this is anthropogenic charcoal which formed with the clearance of the forest for agriculture. Samples at all soil levels to bedrock revealed a large dominance of *Quercus* (between 78% and 100% of charcoal mass). Heathland species (*Fabaceae* and *Ericaceae*) were virtually absent. Cereal pollen was found in five out of the six pollen samples analyzed, varying between 2.7% and 11.1% of the total,
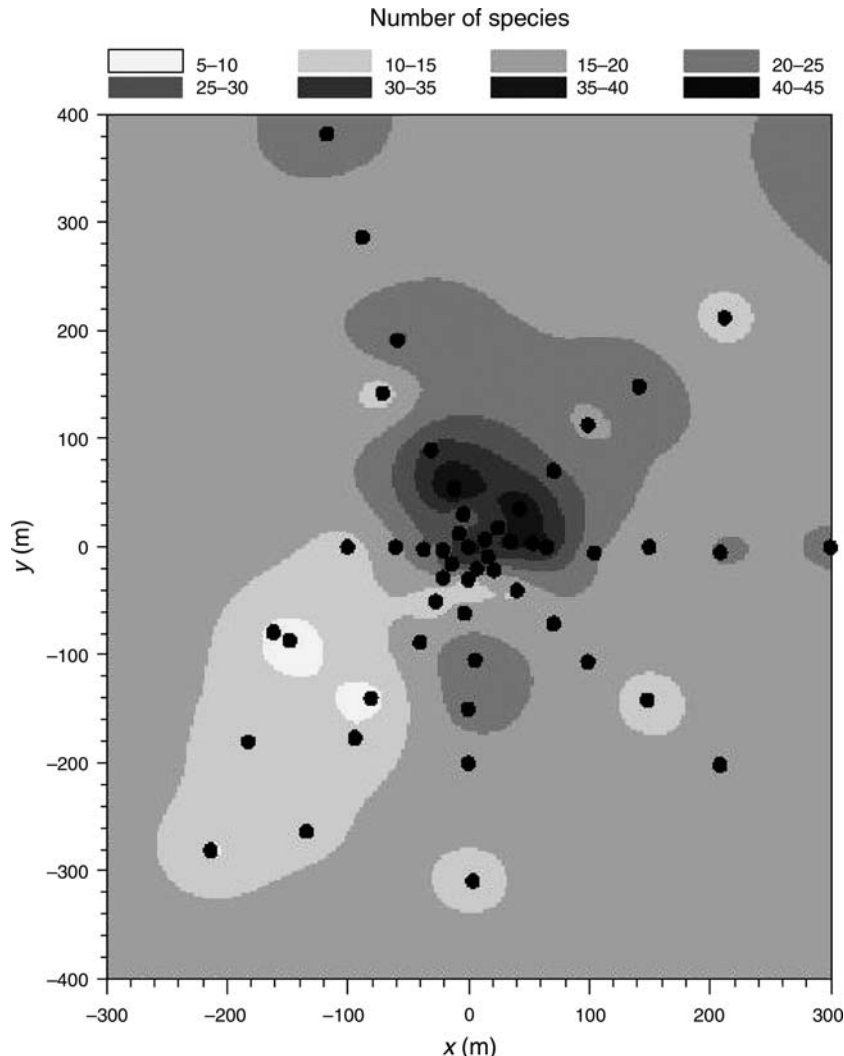
Fig. 3. Kriged map of species richness (number of species) around the large "La Pelloterie" Roman settlement. Dots show sampling plots. Note that there is a small area with species richness of 40–45, but it is covered in this map by a sampling plot.

indicating former cultivation. The high percentage of arboreal pollen (between 71% and 91%) suggests a forested landscape.

The pollen assemblages described here, and plant and animal macroremains found in the nearby cities of Argenton sur Creuse (*Argentomagus*), Levroux, and Bourges, as well as written sources, provide some indication of ancient farming practices. Common wheat (*Triticum aestivum* L.) was the most common cereal, accompanied by emmer (*Triticum dicoccum* Schuebl.) and barley (*Hordeum vulgare* L.). Legumes (*Vicia faba* L., *Lens culinaris* Medik.) and fruit trees were also commonly cultivated (Batardy et al. 2001). At Troncais, dominance of forest taxa in pollen assemblages and oak in charcoal suggests agriculture in small clearings. Furthermore, animal bones indicate animal husbandry; cattle, together with pigs, horses, and poultry were raised (Laüt 2001).

Latin authors repeatedly mention the need for regular fertilization after plowing, using ashes or animal manure (Columella 1961: chapters II and V). This fertilization involved a transfer of mineral elements from remote areas, probably forests, to the cultivated areas surrounding the farms, through cattle grazing and fuel wood collection. Domestic garbage, including some broken ceramics, was redistributed with manure and ashes. Indeed, we observed that the density of ceramic pieces in the soil was generally greater near to settlements.

Species diversity related to soil properties and Roman settlements

The number of species per plot (a measure of α diversity) increased sharply from remote areas to the center of the settlements (Figs. 2a and 3), by nine species, on average. This increase was due to a rise in the
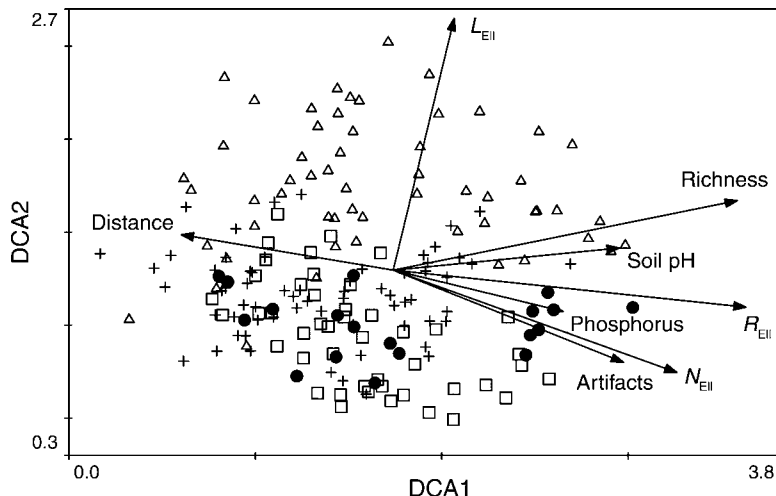
Fig. 4. Detrended correspondence analysis of the 186 plots × 178 species showing plot positions and correlations with environmental variables along the first two axes. The three sites where more than 19 plots were sampled are represented by triangles, squares, and circles. The other seven sites are grouped together as crosses. Parameters are: artifacts, the number of archaeological artifacts; distance, the distance from the main building of each site; L_{Ell}, N_{Ell}, and R_{Ell}, Ellenberg's indicator values for light, nitrogen, and pH, respectively; phosphorus, soil acid-soluble phosphorus; richness, total plant species richness (number of species of phanerogams and terricolous mosses); soil pH, soil pH in water. Only variables with correlation coefficients with an absolute value >0.4 for one or both axes are displayed.

number of vascular plants only, whereas moss species richness did not change (3.7 species per plot, on average). A total of 160 species was found within the inner zones (<100 m from the center), while only 131 species were found in the outer zones (100–500 m) even though the area sampled was larger in the latter. Thirty-nine species were significantly more frequent near the center of the settlements, according to Fisher's exact test (see Appendix). These species were typical of neutral soils, especially many shrubs such as *Crataegus monogyna*, *Euonymus europaeus*, *Rosa arvensis*, *Acer cam-*

pestre, or *Prunus spinosa*. Others were nitrogen-demanding species (*Ajuga reptans*, *Urtica dioica*, *Geranium robertianum*, *Scrophularia nodosa*, *Poa trivialis*). Only seven species were more frequently found >100 m from the center (Appendix); they were typical of acidic soils (*Molinia caerulea* and three moss species: *Dicranella heteromalla*, *Leucobryum glaucum*, and *Polytrichum formosum*) or previously known as ancient forest species (*Convallaria maialis* [Hermy et al. 1999]).

The first three axes of the detrended correspondence analysis of plant community composition explained 19%
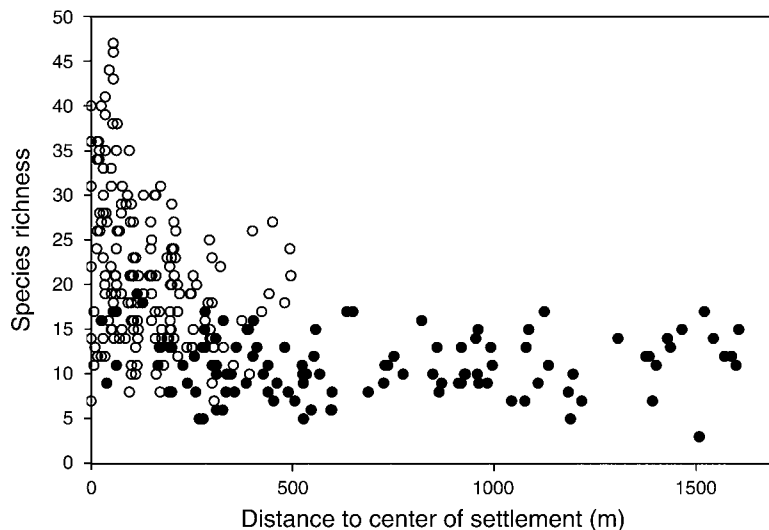

Fig. 5. Species richness (number of species) as a function of distance to the center of the settlement. Open circles show present study plots sampled around the settlements; closed circles show previous forest inventory covering the whole forest.

PLATE 1. Roman settlement excavated in the Tronçais forest, Central France. This 10 000-hectare forest with poor sandy soils is the most famous source of high-quality oak wood in France. It was assumed to be an ancient forest, never deforested, but 108 Roman settlements were recently found by surface surveys. Agriculture activities around these ancient settlements, although abandoned since the 4th century A.D., still deeply influence forest biodiversity. Photo credit: L. Laüt.

of the total variance, a high percentage in view of the total number of species analyzed (178). The first axis (eigenvalue 0.24, gradient length 2.3 SD units, 10% of explained variance) was significantly and positively correlated to species richness per plot ($r = 0.80$), soil pH ($r = 0.51$), soil phosphorus ($r = 0.40$), Ellenberg's indicator values for pH R_{Ell} ($r = 0.85$) and nitrogen availability N_{Ell} ($r = 0.67$), the abundance of archaeological artifacts ($r = 0.52$), and negatively to the distance to the center of the site ($r = -0.47$; $P < 0.001$ in all cases). There was no relationship between the position of plots along this first axis and the site to which they belonged (Fig. 4). The second axis (eigenvalue 0.14, gradient length 2.0 SD units, 6% of explained variance) contrasted plots related to high values of L_{Ell} (Ellenberg's light indicator value) with plots related to low values of L_{Ell} (correlation of 0.65 with L_{Ell}). Those plots which contained light-demanding species all belonged to

the youngest stand. Both the diversity patterns and the DCA results suggest that ancient human occupation is a major determinant of present forest plant diversity, habitat types, and soil fertility. Areas near ancient settlements have higher species richness, distinct floristic character, and more nutrient-rich soils.

The link between the occurrence of ancient human activity and vegetation patterns is further supported by an independent dataset of 151 vegetation plots (400 m²) surveyed for a previous forest inventory (Delaunay et al. 1991). This sample covered the entire range of natural ecological conditions occurring in the Tronçais forest, mostly outside the Roman settlements. In the forest as a whole, the vegetation was mostly composed of acidophilous species and no one site appeared richer in species than those closer to the Roman settlements (Fig. 5).

Based on the digital elevation model and soil map, the spatial analysis of settlement location showed settle-

TABLE 1. Analysis of covariance of vegetation and soil characteristics as a function of site and distance to the center of the settlements.

	Vegetation			
Parameter	No. species	First axis of DCA analysis	Ellenberg's pH indicator value	Ellenberg's light indicator value
Distance F	47.4***	113.1***	99.2***	0.7[NS]
Site F	6.3***	7.0***	6.6***	19.7***
R^2	0.33	0.48	0.44	0.35
Distance from center				
<100 m	25.3	1.95	5.3	4.6
100–500 m	16.8	1.20	4.3	4.6

Notes: For each variable, the F values and associated tests of the effects of distance (log-transformed, $df = 1, 145$) and site ($df = 4, 145$) are given in the first two rows. The third row reports total R^2 of the model. In addition, the last two rows present the average values of the variable below and above 100 m from the center.

** $P < 0.01$; *** $P < 0.001$; NS, not significant ($P > 0.05$).

ments were scattered over most of the landscape but preferentially located not far from a source of water. All soil types were equally occupied, except the most hydromorphic ones, which cover 13% of the forest on average but 4% only in the 100 m radius circles around the settlements (significant difference at $P < 0.01$). Thus, ancient farmers tended to avoid these unsuitable soils. However, the average species richness on hydromorphic soils (13.8 species per plot) as compared to other soils (11.7 species per plot) was not significantly different. Thus, at the scale of the entire forest, an initial selection of better-drained soils cannot explain present patterns of species richness.

Another feature that strongly argues for human influence is that distance to the center of the site is a strong determinant of soil variations around the buildings. Soil P content, pH, and $\delta^{15}N$ increased and C/N ratio decreased significantly towards the center of the settlements (Fig. 2b, c, f; Table 1). Carbon and nitrogen contents were not related to building location. The area of influence varied among sites, from 0 to almost 4 ha. Differences in fertility prior to the founding of settlements cannot be entirely ruled out as a factor, but within each site, none of soil depth, soil type, or soil texture was significantly related to the distance from the center of the settlement. Moreover, an analysis of covariance showed that the local abundance of artifacts in the soil, in addition to the distance to the center, explained a significant proportion of the total variance of vegetation diversity ($P < 0.0001$). However, at three sites where excavations and surface surveys had demonstrated the presence of bronze smelting, tile making, and a temple—but no agriculture—no significant relationship between distance to the center of the site and plant diversity or soil characteristics was found.

The role of past soil modifications in the present distribution of biodiversity

Several mechanisms could explain this fine tuning of forest biodiversity by the intensity of ancient land-use. Given the small spatial scale and long time span involved, plant dispersal limitation is an unlikely explanation whereas soil modification is more likely. Higher soil pH near the buildings and in locations with a high artifact content is probably related to the dispersal of lime mortar found in several ruins, and possibly also to marling, which was a common practice in Gaul before and during Roman times (Columella 1961: chapters II and XVI). Soil P content is known to be elevated at formerly cultivated sites where manuring was carried out (Craddock et al. 1985). The high $^{15}N:^{14}N$ ratio can be related to both the input of ^{15}N enriched manure and an increased mineralization of soil nitrogen (Koerner et al. 1999, Jussy et al. 2002). Such effects have also been described in New England, on agricultural fields abandoned a century ago (Compton and Boone 2000), but it is surprising to see the effect in fields cultivated during Roman times.

Persistence of soil modifications over 1500 years

The maintenance of the soil and vegetation patterns for more than 1500 years is probably related to several features: tight cycling of P and N, progressive release of Ca through the dissolution of $CaCO_3$ originally introduced by human activity, and the long-lasting effect of this combined fertilization on the mineralization of soil organic matter. In Tronçais and other forest ecosystems on poor and acidic sandy soils, leaching of nutrients is quite low. As bole wood is very poor in nutrients, most of the annual uptake by trees returns to the soil surface via litter fall and is rapidly recycled. When nutrients are in short supply, this tight cycling limits the leaching or precipitation of nutrients and ensures the conservation of plant-available nutrient reserves. A tight cycling of P was suggested by Dupouey et al. (2002) in an oak forest on limestone growing on a former Roman cadastre. Soil available phosphorus was low in the undisturbed areas, and oak leaf phosphorus was deficient, while leaf and soil phosphorus levels were high close to the Roman settlements.

Data required for the determination of nutrient budgets since Roman times at our study sites are lacking, but measurements are available from a nearby

TABLE 1. Extended.

Soil						
P (mg/kg)	pH	C (%)	N (%)	C:N	Sand (%)	Soil $\delta^{15}N$ (‰)
42.1***	31.9***	2.7[NS]	0.1[NS]	23.6***	2.6[NS]	8.3**
26.8***	7.2***	38.0***	55.8***	15.9***	13.1***	2.2[NS]
0.55	0.30	0.41	0.50	0.30	0.27	0.09
26.4	5.1	2.3	0.14	16.6	43	−0.98
20.2	4.8	2.6	0.14	19.1	42	−1.43

oak stand growing in similar climatic conditions (Ulrich et al. 2002). Present annual wet deposition of N (50% as NO_3) is 7 kg·ha^{-1}·yr^{-1}. Assuming constant ammonia deposition in relation to the permanence of low intensity husbandry in this region, but low nitrate deposition because NO_x emissions were much lower before the industrial revolution (Holland et al. 1999), the mean annual N deposition, averaged over the last 1500 years, was probably between 3 and 5 kg·ha^{-1}·yr^{-1}. Loss of N via drainage is less than 1 kg·ha^{-1}·yr^{-1} as it is in most broadleaf stands in low pollution areas (Rothe et al. 2002). The average present N store in the 0–10 cm soil layer at Tronçais is 1.2 Mg/ha (Bonfils 1970). Over the last 1500 years, the cumulative N deposition would thus have been four to six times higher than the soil store. Typical differences between contemporary forest and cropland soil $\delta^{15}N$ are about 4‰ (Riga et al. 1971, Koerner et al. 1997, Moares et al. 2001), so the small variation in soil $\delta^{15}N$ observed between the center and the periphery of our sites (0.45‰) can probably be related to the dilution of the initial signal by the cumulative deposition of nitrogen. Part of this 0.45‰ difference may also result from an enhanced mineralization still active in formerly cultivated areas.

Similarly, any original difference in exchangeable Ca stores inherited from former cultivation would have been strongly diluted by subsequent atmospheric deposition. Hence, the slow and continuous release of Ca from lime or calcareous mortar is more likely the cause of the maintenance of a higher pH close to the center of the settlements.

The variation in N mineralization and availability, illustrated by the gradients of both vegetation composition and soil C:N between settlements and outlying areas, is most probably related to the variation in pH (Persson et al. 2000) and P levels. N mineralization would likely be mediated by soil bacterial or mycorrhizal communities; spatial patterns of microbial communities in relation to nutrient dynamics and soil and vegetation gradients remain to be explored.

CONCLUSION

Our results show that forest biodiversity is still strongly influenced by ancient cultivation almost two millennia after abandonment of human occupation. Furthermore, this impact did not disappear during a period of forest over-exploitation. These results from acid soils confirm and extend previous results for a small Roman settlement on limestone (Dupouey et al. 2002). The example of the Tronçais forest suggests that, except for the most acidic and humid areas, many present forests located within the territory of the former Roman Empire may well have been cultivated in the past. Such legacies of ancient agriculture in present forests are not restricted to temperate zones or the Roman period. Recent investigations in the tropics have shown the long-term legacy of prehistoric agriculture on tropical forest biodiversity (Heckenberger et al. 2003, Willis et al.

2004). In fact, any type of agriculture involving long-term fertility transfers and accumulation across the landscape may create long-lasting, possibly irreversible, spatial heterogeneities in biodiversity patterns because of the conservative character of forest biogeochemical cycles. Hence, understanding present patterns of biodiversity requires the investigation of land-use history on a much longer time scale than previously thought.

LITERATURE CITED

Batardy, C., O. Buchsenschutz, and F. Dumasy. 2001. Le Berry antique, milieu, hommes, espaces, atlas 2000, 21st supplement to the Revue Archéologique du Centre de la France. Revue Archéologique du Centre de la France, Tours, France.

Bellemare, J., G. Motzkin, and D. R. Foster. 2002. Legacies of the agricultural past in the forested present: an assessment of historical land-use effects on rich mesic forests. Journal of Biogeography 29:1401–1420.

Bertrand, E. 1996. Les sites antiques. La lettre du Pays de Tronçais 2:1–48.

Bonfils, P. 1970. La forêt de Tronçais—Etude pédologique. Revue Forestière Française 22:35–43.

Columella, L. J. M. 1961. On agriculture (De Re Rustica) books 1–4. Harvard University Press, Cambridge, Massachusetts, USA.

Compton, J. E., and R. D. Boone. 2000. Long-term impacts of agriculture on organic matter pools and nitrogen transformations in central New England forests. Ecology 81:2314–2330.

Compton, J. E., R. D. Boone, G. Motzkin, and D. Foster. 1998. Soil carbon and nitrogen in a pine–oak sand plain in central Massachusetts: role of vegetation and land use history. Oecologia 116:536–542.

Craddock, P. T., D. Gurney, F. Pryor, and M. J. Hughes. 1985. The application of phosphate analysis to the location and interpretation of archaeological sites. Archaeological Journal 142:361–376.

Delaunay, A., J. P. Nebout, and T. Beaufils. 1991. Bocage Bourbonnais—Forêt de Tronçais, Typologie des stations forestières. CRPF Auvergne, CEF Allier, France.

Dupouey, J. L., E. Dambrine, M. Georges-Leroy, C. Dardignac, and J. C. Rameau, editors. In press. Forêt, Archéologie et Environnement. INRA/ONF/DRAC Lorraine Fontainebleau, France.

Dupouey, J.-L., E. Dambrine, J. D. Laffite, and C. Moares. 2002. Irreversible impact of past land use on forest soils and biodiversity. Ecology 83:2978–2984.

Dzwonko, Z., and S. Loster. 1992. Species richness and seed dispersal to secondary woods in southern Poland. Journal of Biogeography 19:195–204.

Ellenberg, H., H. E. Weber, R. Düll, V. Wirth, W. Werner, and D. Paulisson. 1992. Zeigerwerte von Pflanzen in Mitteleuropa. Scripta Geobotanica 18:1–248.

Foster, D. R. 1992. Land-use history (1730–1990) and vegetation dynamics in central New England, USA. Journal of Ecology 80:753–772.

Foster, D. R. 2002. Insights from historical geography to ecology and conservation: lessons from the New England landscape. Journal of Biogeography 29:1269–1275.

Heckenberger, M. J., A. Kuikuro, U. T. Kuikuro, J. C. Russell, M. Schmidt, C. Fausto, and B. Franchetto. 2003. Amazonia 1492: pristine forest or cultural parkland? Science 301:1710–1714.

Hermy, M. 1994. Effects of former land use on plant species diversity and pattern in European deciduous woodlands. Pages 123–144 in T. J. B. Boyle and C. E. B. Boyle, editors. Biodiversity, temperate ecosystems, and global change, Springer, Berlin, Germany.

Hermy, M., O. Honnay, L. Firbank, C. Grashof-Bokdam, and J. E. Lawesson. 1999. An ecological comparison between ancient and other forest plant species of Europe, and the implication for forest conservation. Biological Conservation 91:9–22.

Holland, E. A., F. J. Dentener, H. B. Braswell, and J. M. Sulzman. 1999. Contemporary and pre-industrial global reactive nitrogen budgets. Biogeochemistry 46:7–43.

Jongman, R. H. G., C. J. F. ter Braak, and O. F. R. van Tongere. 1995. Data analysis in community and landscape ecology. Cambridge University Press, Cambridge, UK.

Jussy, J. H., W. Koerner, E. Dambrine, J.-L. Dupouey, and M. Benoît. 2002. Influence of former agricultural land use on net nitrate production in forest soils. European Journal of Soil Science 53:367–374.

Koerner, W., E. Dambrine, J.-L. Dupouey, and M. Benoît. 1999. $\delta^{15}N$ of forest soil and understorey vegetation reflect the former agricultural land use. Oecologia 121:421–425.

Koerner, W., J.-L. Dupouey, E. Dambrine, and M. Benoît. 1997. Influence of past land use on the vegetation and soils of present day forest in the Vosges mountains, France. Journal of Ecology 85:351–358.

Laffite, J. D., E. Dambrine, J.-L. Dupouey, and M. Georges-Leroy. 2002. Le parcellaire gallo-romain de la forêt domaniale de Saint-Amond à Favières (Meurthe-et-Moselle): relevé et étude du parcellaire du « Grand Rinchard ». Revue Archéologique de l'Est 51:465–476.

Laüt, L. 2001. L'occupation du sol dans l'Antiquité en forêt de Tronçais. Prospection, Inventaire, Prospection thématique annuelle, Sondages, Document Final de Synthèse. Rapport à la Direction Régionale de l'Archéologie et de la Culture de la Région Centre, Paris, France.

Mangin, M., J.-L. Courtadon, P. Fluzin, and E. de Laclos. 2000. Village, forges et parcellaire aux Sources de la Seine. L'agglomération antique de Blessey-Salmaise (Côte-d'Or). Presses Universitaires Franc-Comtoises, Besançon, France.

Maussion, A. 2003. Occupation ancienne du sol et milieux forestiers actuels en France métropolitaine. Synthèse bibliographique. INRA-Nancy, Champenoux, France.

Mather, A. S., C. L. Needle, and J. Fairbairn. 1998. The human drivers of global land cover change: the case of forests. Hydrological Processes 12:1983–1994.

Moares, C., D. Sciama, E. Dambrine, J. L. Dupouey, J. C. Gégout, and C. Bréchet. 2001. Evolution des stocks de carbone et de la disponibilité de l'azote lors de la dynamique de recolonisation des prairies abandonnées du Jura. Etude et Gestion des Sols 2:119–144.

Moore, P. D., J. A. Webb, and M. E. Collinson. 1991. Pollen analysis. Second edition. Blackwell, Oxford, UK.

Persson, T., A. Rudebeck, J. H. Jussy, M. Colin-Belgrand, A. Priemé, E. Dambrine, P. S. Karlsson, and R. M. Sjöberg. 2000. Soil nitrogen turnover: mineralisation, nitrification and denitrification in European forest soils. Pages 297–331 in E. D. Schulze, editor. Carbon and nitrogen cycling in European forest ecosystems. Ecological Studies 142. Springer-Verlag, Berlin, Germany.

Peterken, G. F. 1996. Natural woodland. Ecology and conservation in northern temperate regions. Cambridge University Press, Cambridge, UK.

Peterken, G. F., and M. Game. 1984. Historical factors affecting the number and distribution of vascular plants species in Central Lincolnshire. Journal of Ecology 72:155–182.

Riga, A., H. J. van Praag, and N. Brigode. 1971. Rapport isotopique naturel de l'azote dans quelques sols forestiers et agricoles de Belgique soumis à divers traîtements culturaux. Geoderma 6:213–222.

Rothe, A., C. H. Huber, K. Kreutzer, and W. Weis. 2002. Deposition and soil leaching in stands of Norway spruce and European Beech: Results from the Höglwald research in comparison with other European case studies. Plant and Soil 240:33–45.

SAS Institute. 1999. SAS/STAT user's guide. Version 8. SAS Institute, Cary, North Carolina, USA.

Schaffers, A. P., and K. V. Sykora. 2000. Reliability of Ellenberg indicator values for moisture, nitrogen and soil reaction: a comparison with field measurements. Journal of Vegetation Science 11:225–244.

Schweingruber, F. H. 1990. Microscopic wood anatomy: structural variability of stems and twigs in recent and subfossil woods from Central Europe. Third edition. Birmensdorf, Eidgenössische Forschungsanstalt WSL, Birmensdorf, Switzerland.

Singleton, R., S. Gardescu, P. L. Marks, and M. Geber. 2001. Forest herb colonization of postagricultural forests in central New York State, USA. Journal of Ecology 89:325–338.

ter Braak, C. J. F., and P. Smilauer. 2002. CANOCO reference manual and CanoDraw for Windows user's guide, Version 4.5. Microcomputer Power, Ithaca, New York, USA.

Thinon, M. 1988. Utilisation de la microscopie episcopique interferentielle pour l'identification botanique des charbons de bois. Pages 179–188 in T. Hackens, A. V. Munaut, and C. Till, editors. Wood and archaeology, acts of the European symposium, Louvain-la-Neuve, PACT 22, Council of Europe, Strasbourg, France.

Ulrich, E., P. Coddeville, and M. Lanier. 2002. Retombées atmosphériques en France entre 1993 et 1998. ADEME, Paris, France.

Vellend, M. 2003. Habitat loss inhibits recovery of plant diversity as forests regrow. Ecology 84:1158–1164.

Wamelink, G. W. W., V. Joosten, H. F. van Dobben, and F. Berendse. 2002. Validity of Ellenberg indicator values judged from physico-chemical field measurements. Journal of Vegetation Science 13:269–278.

Willis, K. J., L. Gillson, and T. M. Brncic. 2004. How "virgin" is virgin rainforest? Science 304:402–403.

Wulf, M. 1997. Plant species as indicators of ancient woodland in northwestern Germany. Journal of Vegetation Science 8:635–642.

APPENDIX

Frequency of species according to the distance to the center of the archaeological settlements (*Ecological Archives* E088-087-A1).