Relative importance of historical and natural factors influencing vegetation of secondary forests in abandoned villages

Relativní význam historických a přírodních faktorů ovlivňujících vegetaci sekundárních lesů zaniklých vesnic v Doupovských horách

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The factors influencing plant species diversity in secondary and ancient forests can differ. Apart from environmental variability caused by natural conditions, secondary forests are influenced by historical factors (previous human activity). However, the effect of historical factors on vegetation is not fully understood. Secondary forests that have developed in abandoned villages in the Doupovské hory mountains, Czech Republic, were surveyed and compared with ancient forests in an attempt to determine the effect of historical factors and separate it from that of natural gradients. The results show that secondary forests in abandoned villages form a unique type of vegetation that differs from ancient forests mainly in the presence of species indicating a high nutrient content and and high pH of the soils. This indicates that the previous high nutrient input in the villages still influences the soils and causes the differences. Variability of village forests is influenced mainly by a gradient in the available phosphorus content of the soils, soil moisture (approximated by wetness index) and organic matter content. The pattern in the phosphorus content and pH indicate a different intensity of historical influence in the centre compared to the periphery of the villages. Vegetation variability is modified by former land-use and village structure. The effect of historical factors is relatively strong and cannot be explained by coincidental initial conditions.

K e y w o r d s : ancient forests, Doupovské hory mountains, historical land-use, secondary forests, vegetation diversity, succession

Introduction

Depopulation of rural areas in developed countries results in many landscape changes. One such change is an increase in the area of secondary forest (Farina 1998, MacDonald et al. 2000). Secondary forests differ from ancient forests (forests with a long historical continuity, for definition see Peterken 1981) in many ways. It is often stressed that there is a lower diversity of forest herb species in secondary forests. This is explained mainly in terms of the poor ability of forest herb species to colonize secondary forests and is documented for Europe as well as North America (e.g. Dzwonko & Loster 1989, Matlack 1994, Peterken & Game 1984, for a review see Flinn & Vellend 2005). From this point of view secondary forests have a low conservation value. Nevertheless, the above-mentioned studies are restricted to a specific ecological group of species and were in many cases carried out in planted secondary forests. Hence, there is a poor knowledge of the diversity of vascular plant species in secondary forests originating by natural succession. This can lead to erroneous evaluation of the importance of secondary forests in the ecology of landscapes and wrong recommendations for landscape management.

The factors influencing plant species diversity in secondary forests may be different from those in ancient forests. Apart from environmental variability caused by natural conditions, secondary forests are influenced by historical factors (previous human activity). Historical factors are generally regarded as important in secondary succession (Prach & Řehounková 2006). For example, ploughing results in a deepening of the A soil horizon and the application of fertilizers in a high content of nitrogen, potassium and phosphorus, and increase in pH (Blume & Sukopp 1976). In contrast, harvesting and grazing results in the exhaustion of nutrients (Hrabě & Halva 1993, Hill & Carey 1997). There are differences in the persistence of human-caused changes. For example nitrogen is usually quickly washed out (Fried & Broeshart 1967, Bielek 1984) while phosphorus has a low mobility in soil (Fried & Broeshart 1967). High content of phosphorus can persist for centuries in the vicinity and inside abandoned settlements (Bleck 1969, Siegl 1998). Other examples of permanent human-caused changes are various small geomorphological shapes, such as terraces, walls and ruins. Sites formerly influenced by human activities form a fine scale mosaic of patches in an abandoned landscape. Some authors (Motzkin et al. 1996, Koerner et al. 1997, Wulf 2004) have demonstrated the influence of previous land-use on vegetation. Siegl (1998) records a zonation in vegetation dependent on the distance from long time abandoned settlements.

Historical events often result in processes that are interesting "natural experiments". However, constraints are encountered when studying the effect of history on vegetation. Since the "natural experiments" are unique in time and space, they cannot be replicated and their initial conditions manipulated. This may result in some underlying factors erroneously being interpreted as historical effects. For example, pastures in certain regions are on dry sites and meadows wet sites; therefore the eventual differences in vegetation can be caused by initial natural conditions rather than previous land-use. Moreover, historical events often occur on specific sites (for example, forests in the vicinity of villages were cleared first); therefore, the spatial autocorrelation could be significant.

That there might be a correlation between historical factors and initial natural conditions was neglected in some previous studies (Koerner et al. 1997, Wulf 2004), or selected environmental characteristics were used to define the initial conditions (e.g. Grashof-Bokdam & Geertsema 1998, Graae et al. 2004). Historical sources are usually not very detailed, therefore usually only current variables, which are unlikely to have been influenced by human activities over the respective time span, are used. For example, phosphorus content of soil is not appropriate when comparing ancient forests with recent ones because this variable can be influenced by cultivation. On the other hand, various geomorphological characteristics or geological properties are appropriate as they are unlikely to have changed. Geomorphological and geological characteristics are easily obtained from recent maps and various indices (such as slope, orientation, potential direct radiation, heat load index and wetness index) calculated. Variables that indicate the initial conditions and persist into the present are named here "ancient environmental variables" because they reflect the ancient state of the landscape.

Unfortunately, there is a high risk that the available ancient environmental variables are not the most important for vegetation. When analyzing the influence of historical factors on the variability of secondary forest vegetation (e.g. the influence of previous land-use) it is possible to compare vegetation gradients associated with historical development in secondary forests with those determined by natural factors in ancient forests. If the gradients do not fully overlap it is possible to state that historical factors influence the vegetation. On the other hand, historical factors can influence vegetation in a similar way to natural gradients (for example residues of previous fertilizer applications can shift vegetation in the direction of existing analogous vegetation). Some effects of historical factors can be hidden by natural gradients, therefore it is important to estimate the proportion of vegetation variability that is affected separately by historical factors, natural gradients, and ancient environmental variables.

Ancient environmental variables as well as natural gradients indicated by vegetation in ancient forests were used to define the initial conditions in this study. The aim was to identify the main factors, including historical factors, influencing secondary forests in abandoned villages.

The objectives were to (i) compare species composition and variability of secondary forests in abandoned villages with ancient forests; (ii) detect main environmental factors influencing the vegetation in abandoned villages; (iii) test the hypothesis that soil properties in abandoned villages are influenced by historical land-use or by general village structure; and (iv) test the hypothesis that village forests are influenced by historical factors (land-use and village structure) and that these factors give rise to gradients that differ from natural ones.

Materials and methods

Study area

The survey was carried out in the Doupovské hory mountains (Duppauer Gebirge in German), which lie in W Bohemia, Czech Republic, near the border with Germany (Fig. 1). The massif covers a large, nearly round area close to the towns Ostrov, Kadaň, Podbořany and Lubenec.

The Doupovské hory mountains are of tertiary volcanic origin. Bare rock consists mainly of basaltic tuffs and basalt-like rocks that are frequently redeposited in screes and alluviums. The bedrock is very homogeneous throughout the area. The bedrock is basic and readily breaks down to form deep and nutrient rich soils (mollic cambisols are the most frequent). In sites influenced by water gleys and alluvial soils are formed. Shallow soils (rankers) occur less frequently on rocky outcrops. Climatic conditions vary mainly between the east and west, the eastern part being warmer and drier; the annual precipitation in the central part is 671 mm. The average annual temperature is 6.1°C (Vesecký et al. 1961).

A large military area was created in the Doupovské hory mountains in 1953. Nearly all the inhabitants were cleared from the region; one town and more than 60 villages were abandoned by May 1954 (Augustin 1994). The military area covers 33,015 ha, but only about one third is used for military training (Komár 1993).

Unmanaged grasslands and shrubby vegetation are the most noticeable types of land cover in the area. Approximately one third of the military area is covered by forests. The most common are herb-rich beech forests. The other forest types (ravine forests, alluvial forests, oak-hornbeam forests and thermophilous oak forests) are mostly confined to the rugged terrain in valleys. Noticeably different vegetation grows on the sites of abandoned villages, which are currently covered mainly by secondary forests. The tree layer is dominated mainly by ash (*Fraxinus excelsior*); other woody species form the canopy less

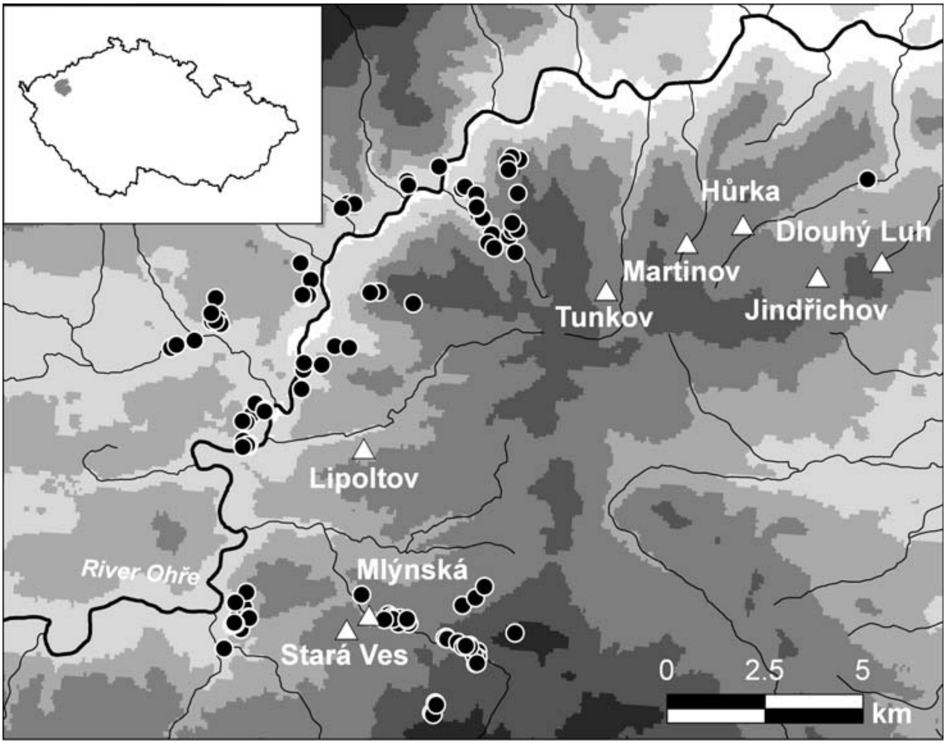

Fig. 1. – Locations of the eight abandoned villages (white triangles) and sites of the phytosociological relevés of ancient forests (black circles). The altitude is indicated by the shading. The location of Doupovské hory mountains is the grey area on the overview map in the upper left corner.

frequently (*Acer pseudoplatanus*, *Acer platanoides*) or under specific conditions (*Alnus glutinosa*, *Acer campestre*, *Populus tremula*, *Crataegus* sp. div., *Sambucus nigra* etc.). The herb layer is dominated by nitrophilous species such as *Urtica dioica*, *Geum urbanum* or *Anthriscus sylvestris* (Vojta & Kopecký 2006). Some exotic, formerly cultivated species are typical of the villages (*Viola odorata*, *Hesperis matronalis*, *Symphoricarpos albus* and *Syringa vulgaris* are the most frequent). Specific vegetation, dominated by *Salix caprea* and *Sambucus nigra*, grows in the ruins of buildings.

Data sampling

Two datasets were used in the analyses:

(1) Phytosociological relevés from eight abandoned villages were made in 1998–2000 in the W and NW part of the Doupovské hory mountains (Fig. 1). The 81 relevés were from areas outside ruins of buildings, which were homogeneous and with more than 50% canopy cover. All the relevés were of a standard area of 100 m^2. The species cover was estimated using the Braun-Blanquet semiquantitavive scale modified by Reichelt & Wilmanns (1973) (sec. Dengler 2003). The relevés were recorded in summer. Species that are at their optimum development in spring were recorded during a second inspection of the sampling sites in spring (April–May).

(2) Reference dataset were phytosociological relevés from ancient forests. The relevés were sampled in places, which had been forested for more than 220 years (Fig. 1). Forest continuity was verified using maps of the I. and II. Military mapping (Data source: Ministry of the Environment of the Czech Republic, http://oldmaps.geolab.cz). Seventeen relevés were taken from the literature (Moravec 1974, 1977, 1979), 111 relevés were recorded by the author in 1996–2004 using the standard method of Zürich-Montpellier school (preferential sampling, see e.g. Moravec 1994). The Braun-Blanquet semiquantitative scale modified by Reichelt & Wilmanns (1973) (sec. Dengler 2003) was used to record species cover. The relevés varied in area from 50 to 600 m^2 (median = 300 m^2). The complete dataset was used only in DCA analysis for the classification of ancient forest and comparison of ancient and village forests. The 17 previously published relevés were omitted from other analyses because their exact geographical position was unknown.

The samples were stored in the TURBOVEG database (Hennekens & Schaminée 2001). The nomenclature of species follows Kubát et al. (2002). The species were further classified as canopy species (trees and shrubs, which are taller than 2 m and form more than 15% of canopy in at least one relevé) or as undergrowth (herb layer and low shrubs). The two groups were analyzed separately in most cases. Previously planted species (including fruit trees) were kept in the dataset. Species that are mainly present in spring and hard to find later in summer (for example *Ficaria verna*, *Gagea lutea*, *Corydalis cava*) were deleted from analyses of both ancient and village forests because information on early developing species was lacking for ancient forests. It was not possible to determine the species of some genera in all the samples. Therefore, all *Crataegus* species (mostly *C. ×fallacina*, *C. praemonticola*, *C. ×macrocarpa*, *C. monogyna* etc.) were treated as single "species" as were some *Galeopsis* species (*G. pubescens*, *G. bifida*, and *G. tetrahit*). Finally, species present in less than three samples were omitted from all RDAs.

Ancient environmental variables were obtained using GIS for all the samples from the abandoned villages (n = 81) and for all the samples from the ancient forests for which the exact location was known (n = 111). Only geomorphological variables were used as ancient environmental variables because the bedrock is very homogeneous across the whole area. The basic source for the analysis was the digital elevation model (DEM) with 15 × 15 m pixel resolution. The DEM was derived from the contours obtained from the CENIA ArcIMS Server (data source: Ministry of Environment of the Czech Republic, http://geoportal.cenia.cz/, contour vertical distance 5 m) using Spatial Analyst extension for ESRI ArcGIS 9.0 software (Topo to Raster tool). The slope and orientation rasters were subsequently calculated in Spatial Analyst. The heat load index (HLI) was then calculated according to McCune & Keon (2002). HLI modifies the value of potential direct radiation with respect to the fact that western slopes are warmer than eastern slopes (in the Northern Hemisphere). The HLI was calculated using equation 3 of McCune & Keon (2002) and OpenOffice software. Further, terrain shape index (TSI) was calculated according to McNab (1989). TSI according to McNab is simply the difference between sample altitude and mean altitude of points on the boundary of a circle of given radius. The use of GIS enabled the TSI calculation to be modified. Not only the values on the circle boundary, but all pixel values inside the circle were used for the mean altitude calculation (standardization by dividing the value by circle radius was not necessary). TSI was calculated for two different radii, 150 m and 750 m; the obtained variables were designated as TSI150 and TSI750. TSI150 reflects rather minor features (e.g. small gorges), while TSI750 reflects major features (e.g. valleys). The last geomorphological characteristic was the wetness index (WTI). The SAGA GIS software (http://www.saga-gis.uni-goettingen.de) was used to calculate this index. The wetness index is defined as: $WTI = \ln(A/\tan \beta)$, where A is catchment area and β is slope (Moore et al. 1992). Catchment area was also calculated from SAGA GIS using the kinematic routing algorithm method (Lea 1992).

Unweighted mean Ellenberg indicator values (Ellenberg et al. 1992) for ancient forest samples (n = 111) and all village samples (n = 81) were calculated using the computer program JUICE (Tichý 2002).

The next variables were measured only for the samples from abandoned villages. Canopy age was estimated by counting tree rings obtained by boring into the largest tree or shrub the canopy of which was in or at least partly overlapping the relevé area. The largest tree can be older than 50 years if present before abandonment, therefore this variable can indicate habitats that were microenvironmentaly suitable for shade tolerant species before the villages were abandoned. The last known type of land-use before abandonment was obtained by examining the records in the land registry in Karlovy Vary. The old written records for the villages Stará Ves and Dlouhý Luh were missing, therefore maps from the end of the 19th century were used as source of this information in these two cases (source: Czech Office for Surveying, Mapping and Cadastre). The types of land-use obtained from the maps and written sources were the following: meadows (n = 17), pastures (n = 10), arable fields (n = 9), gardens (n = 38) and public places (places in villages not used for specific economic purposes, mainly village squares and roads, n = 7). Further, the samples were classified according their position in the village, further referred to as "sample position" variable. The samples in previously built-up areas are classified as "village centre" (n = 31); these areas are expected to be more influenced by previous human activity. These samples lie among the ruins, therefore, there is also some debris present on soil surface. In contrast, the relevés that were recorded outside built-up areas are denoted as "village periphery" (n = 50).

Soil samples were taken in autumn from all the relevé sites in the villages. On each site three small pits were dug symmetrically around the relevé centre and a sample of soil from the depth of ca 15 cm was collected. The three samples were mixed together, homogenized and dried at room temperature, and then crushed and sifted to obtain a fraction smaller than 2 mm. Available phosphorus content was determined according to adapted Mehlich (II) method. Soil reaction was measured in a water extract (10 g of soil was suspended in 10 ml of distilled water, and the pH of the filtrate measured). Organic matter content was determined by weight loss after heating 5 g of soil for 5 hours at 550 °C. Three measurements were made on each sample, and means of the values were used in subsequent analyses. All variables measured are summarized in Table 1. Values of available phosphorus content and organic matter content were further logarithmically transformed in order to obtain variables with normal distributions.

Natural gradients were approximated using the ancient forest dataset and the following procedure. DCA of the herb layer in the ancient forests was performed (down-weighting of rare species was set and the other settings were used as default) and the relevés from the abandoned villages were added as passive samples in order to extract their sample scores on the first four axes (i.e. the gradients identified in the ancient forests were transferred to the secondary forests on the basis of species similarity). The same procedure was followed using the dataset that included both canopy and undergrowth species, because canopy

Table 1. – Basic statistics of the variables measured. Note that the values for phosphorus and organic matter content were log transformed in further analyses. TSI150 and TSI750 – terrain shape index were calculated for a radius of 150 and 750 m, respectively; WTI – wetness index; HLI – heat load index (see text for details); SD – standard deviation; Number of observations for forests and ancient forests was 111 and 81, respectively. Soil chemistry was estimated for three samples from ancient forests but not used in further analyses.

	Forests				Secondary forests			
	Mean	Minimum	Maximum	SD	Mean	Minimum	Maximum	SD
Ancient variables								
TSI150 (m)	1.22	–18.56	34.58	10.06	–3.39	–9.79	7.63	3.27
TSI750 (m)	1.74	–76.92	130.05	44.81	–19.81	–47.16	18.73	16.15
Altitude (m a.s.l.)	529.49	342.21	906.38	123.19	577.17	465.67	667.51	54.46
Slope (degrees)	20.26	3.28	36.28	8.9	9.59	1.55	19.60	3.29
WTI	6.61	4.27	15.55	1.83	7.88	4.83	13.18	1.71
HLI	0.81	0.40	0.95	0.12	0.79	0.69	0.91	0.05
Indicator values								
Light	4.70	3.29	6.63	0.74	5.24	4.00	6.00	0.31
Temperature	5.21	4.57	5.79	0.3	5.40	4.80	6.33	0.18
Moisture	5.14	3.75	7.25	0.59	5.55	4.72	7.00	0.35
Acidity	6.19	5.00	7.10	0.45	6.63	6.00	7.00	0.22
Nutrients	5.67	2.75	7.12	0.85	6.84	5.56	7.70	0.46
Cover of E2 + E3 (%)	90.33	35	140	19.27	89.54	60	130	15.09
Age of canopy (years)	N/A	N/A	N/A	N/A	39.04	18.00	88.00	12.38
Soil chemistry								
pH	5.05	5.03	5.07	0.02	5.69	5.02	7.10	0.36
Phosphorus (mg/100g)	5.19	4.38	5.63	0.71	24.58	0.49	151.74	35.15
Organic matter (%)	11.44	8.96	15.85	3.83	14.43	9.45	39.06	3.70

Table 2. – Correlation coefficients between ANG (scores of samples from abandoned villages treated as passive samples in the DCA analysis of ancient forests), environmental variables, and Ellenberg indicator values. Significant correlations (P = 0.05) are marked with an asterisk. A1–A4 – sample scores on the first four axes of the DCA analysis of undergrowth (ANG); AC1–AC4 – sample scores on the first four axes of the DCA analysis of undergrowth and canopy (ANG); WTI – wetness index; HLI – heat load index; indicator values: L – light, T – temperature, M – moisture, A – acidity, Nut – nutrients.

ANG	TSI150	TSI750	Altitude	Slope	HLI	WTI	L	T	M	A	Nut
A1	0.20	0.17	–0.40*	0.37*	0.16	–0.40*	0.21	0.41*	–0.76*	–0.19	–0.51*
A2	0.03	–0.07	–0.06	0.20	0.10	–0.14	0.22*	–0.01	–0.12	–0.13	–0.35*
A3	–0.30*	–0.36*	0.44*	–0.33*	–0.20	0.38*	–0.24*	–0.22	0.66*	0.15	0.60*
A4	–0.17	–0.20	0.39*	–0.08	–0.24*	0.18	0.02	–0.18	0.37*	0.25*	0.25*
AC1	0.17	0.12	–0.47*	0.21	0.13	–0.33*	0.00	0.16	–0.52*	–0.10	–0.39*
AC2	–0.32*	–0.29*	0.23*	–0.24*	0.07	0.31*	–0.06	–0.12	0.49*	0.28*	0.45*
AC3	0.06	0.15	–0.06	–0.11	–0.02	0.11	0.03	–0.39*	0.29*	–0.10	–0.05
AC4	0.00	–0.14	0.52*	–0.14	–0.34*	0.14	0.04	–0.01	0.31*	0.04	0.26*

composition can reflect environmnetal gradients that differ from those revealed for the undergrowth. The eight sample scores obtained are designated as "approximated natural gradients" (ANG) below. The sample scores correlate with many important environmental factors in abandoned villages (see Table 2).

Data analysis

The relevés from ancient forests were classified using the Twinspan method (Hill 1979) in the JUICE software (Tichý 2002). Following settings were used: values of cut levels: 0–5–25, minimum group size: 5, maximum level of divisions: 3. This analysis resulted in eight groups. In two cases two clusters on the same hierarchical level were merged in order to obtain ecologically interpretable groups. The groups were briefly described according to their ecology. This classification helped in the interpretation of the results of the following DCA (all multivariate analyses of species composition were performed using software CANOCO for Windows 4.5, ter Braak & Šmilauer 2002). Undergrowth from abandoned villages was analysed along with undergrowth from ancient forests in the DCA (downweighting of rare species was set; other settings were used as default). The vegetation groups (based on the previous classification of ancient forest) were visualized in a DCA scatter plot.

Floristic differences between ancient and village forests were analysed using CCA. Ancient environmental variables, cover of canopy species (cover of tree layer plus cover of shrub layer), and geographical coordinates were used as covariates in the CCA in order to filter out initial conditions and spatial gradients (Borcard et al. 1992, Fortin & Dale 2005), and obtain pure village effect on species composition. Significance of all covariates was first tested by manual forward selection with the P-value = 0.05. Canopy species were excluded from this analysis because differences in the herb layer are more interesting than differences in the canopy layer and the analysis is intended to detect small ecological differences that are indicated by many species of herbs, and low-growing shrubs rather than by the few canopy species.

RDA was used to analyze the relationship between various sets of variables (chemical soil properties, ancient environmental variables, and shrub and tree layer cover and age) and vegetation in abandoned villages. Forward selection in RDA was performed separately for undergrowth and canopy species data (the canopy cover and age was omitted from the analysis of canopy species). The nominal variable "locality" (village) was used in all analyses as a covariate in order to filter out the spatial autocorrelation. Spatial gradients were filtered out using geographical coordinates (only coordinates that were significant in manual forward selection were used; x coordinates for undergrowth and y coordinates for canopy). Significance of variables at each step of the forward selection was estimated by Monte Carlo permutation tests (P-value threshold 0.05).

Relative importance of historical factors (historical land-use and village structure – sample position) was estimated as the ratio of the variance explained by canonical axes in RDA (sum of all canonical eigenvalues) to the total variance in a series of analyses with different sets of covariates (geographical coordinates and locality, ancient environmental variables, approximated natural gradients). Moreover, the sample position was used as covariate when estimating the pure effect of land-use and vice versa. Effect of ancient environmental variables and ANG was estimated after fitting only geographical variables (coordinates and locality) as covariates. The procedure follows the variance partitioning method (Lepš & Šmilauer 2003) but only the most important results are presented. Significance of all canonical axes was estimated using Monte Carlo permutation tests (blocks for permutations were defined by all the categorical covariates, P-value threshold 0.1).

Differences in Ellenberg indicator values between ancient forests and villages and of soil variables among land-use types were tested using ANCOVA in the generalized linear models module in Statistica 7.0 software (StatSoft, Inc. 2006). Geomorphological characteristics (ancient environmental variables) were used as covariates in order to filter out initial environmental conditions (and to compare only the vegetation growing in similar conditions in the analysis). Appropriate sets of linear predictors were selected prior to using multiple regression in general regression models module in Statistica 7.0 software (backward selection with P-value threshold 0.05). Differences between the ancient and village forests were tested using one-way ANCOVA with a simple categorical predictor. Effects of a previous land-use and sample position were tested using factorial ANCOVA that best reflects the data structure. Moreover, locality was used as the main factor with random effect to ensure that the values are similar among localities.

Results

Variability of ancient forests

The classification of ancient forests resulted in the following groups[1], a detailed account of which will be published elsewhere (J. Vojta, in prep.): (1) Alluvial forests (5 relevés) are strongly influenced by springs and water courses. The tree layer is dominated by *Alnus glutiosa* or *Fraxinus excelsior*. This vegetation can be phytosociologicaly denoted as *Arunco sylvestris-Alnetum glutiosae* and *Stellario-Alnetum glutinosae*. (2) Ravine forests (16 relevés) occur on scree slopes or on fine-grained deluvial sediments. The tree layer is dominated by *Fraxinus excelsior*, other tree species sometimes occur (*Acer pseudoplatanus*, *Acer platanoides*, *Tilia cordata*, *Fagus sylvatica* etc.). The soils are sometimes wetter due to springs; therefore, some relevés contain hydrophilous species and can be phytosociologically denoted as *Carici remotae-Fraxinetum*, while others belong to *Tilio-Acerion* and probably to the association *Mercuriali-Fraxinetum* and in some cases the association *Aceri-Carpinetum*. (3) Beech forests of higher altitudes (35 relevés) grow on relatively wet sites with good conditions for litter decomposition. The communities belong to associations *Violio reichenbachianae-Fagetum* and *Dentario enneaphylli-Fagetum*. (4) Beech forests of lower altitudes (38 relevés) grow on drier and nutrient-poorer sites than the previous group. This community can be denoted as *Tilio cordatae-Fagetum*. (5) Oak-hornbeam forests (26 relevés) are dominated by *Carpinus betulus*, *Quercus petraea* or *Fraxinus excelsior*. These communities occur mainly at lower altitudes and on south-facing slopes and can be denoted as *Melampyro nemorosi-Carpinetum*, although some samples are transitional between this and beech or thermophilous oak forests. (6) Thermophilous oak forests (8 relevés) are found on extreme sites mainly on rankers on south-facing rock edges. This community can be phytosociologically denoted as *Sorbo torminalis-Quercetum*.

Comparison of village and ancient forests

The ancient forests were grouped together with village forests in the DCA scatterplot, which indicates that the vegetation of abandoned villages is relatively homogeneous when

[1] The nomenclature of syntaxa follows Moravec (1995).

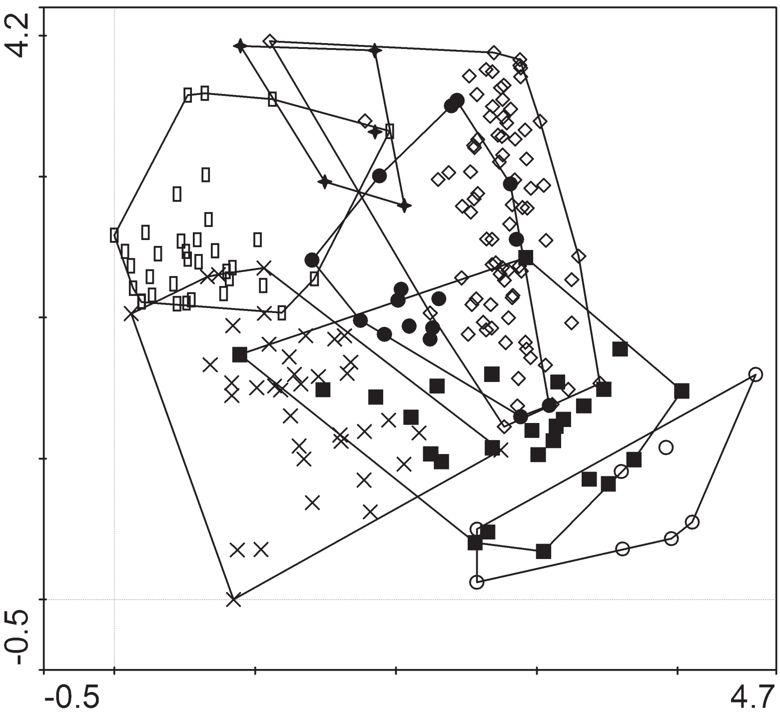

Fig. 2. – Variability of ancient and secondary forests. The first two axes of the DCA ordination plot are shown. The two ordination axes explain 12.4% of the species variability (the first axis explains 7.3%). Symbols: ◇ – abandoned villages, ✦ – alluvial forests, ▯ – beech forests at high altitudes, × – beech forests at low altitudes, ● – ravine forests, ○ – thermophilous oak forests, ■ – oak-hornbeam forests.

compared to that of ancient forests (Fig. 2). The vegetation of abandoned villages is most similar to ravine and alluvial forests and partly overlaps that of oak-hornbeam forests. The vegetation of abandoned villages covers nearly all the variability represented by the second axis, which can be interpreted as a moisture gradient. Only the thermophilous oak forests and oak-hornbeam forests in most extreme sites differ completely from vegetation in abandoned villages. The abandoned villages are shifted to the right on the first axis which most likely represents soil acidity or a nutrient gradient (Fig. 2).

The ancient forests are affected by a wider range of abiotic conditions defined by ancient environmental variables than the village forests (Table 1). Except for slope, all the minima for the ancient forests are lower than those for the village forests and all the maximal values are higher for the ancient forests. That means that the higher vegetation variability in ancient forests may be caused by the higher variability in geomorphological properties in forested areas. However, the overlap in initial conditions allows the comparison of ancient with village forests when ancient environmental variables are used as covariates.

All Ellenberg indicator values, except that for moisture, are significantly higher in the abandoned villages than in the ancient forests (ancient environmental variables were used as covariates). Adjusted means of Ellenberg indicator values are shown in Table 3. Thus, the vegetation in the villages indicates more basic and nutrient-rich soils than in the ancient

Table 3. – Means of Ellenberg indicator values (adjusted by covariate means) for ancient forests and villages. Mean ± SE and significance of differences in ANCOVA are shown (F-statistic, P-value). Variables used as covariates are marked by x. Number of observations: 111 (forests) and 81 (villages)

	Light	Temperature	Moisture	Acidity	Nutrients
Forests	4.58±0.06	5.15±0.02	5.31±0.04	6.22±0.04	5.88±0.07
Villages	5.40±0,07	5.47±0.03	5.32±0.05	6.60±0.05	6.55±0.08
F	68.6	71.5	0.0	31.7	34.7
P-value	< 0.0001	< 0.0001	0.85	< 0.0001	< 0.0001
Covariates:					
TSI150		x			
TSI750			x	x	x
Altitude	x	x	x	x	x
Slope	x	x	x	x	x
HLI	x		x		x
WTI			x		

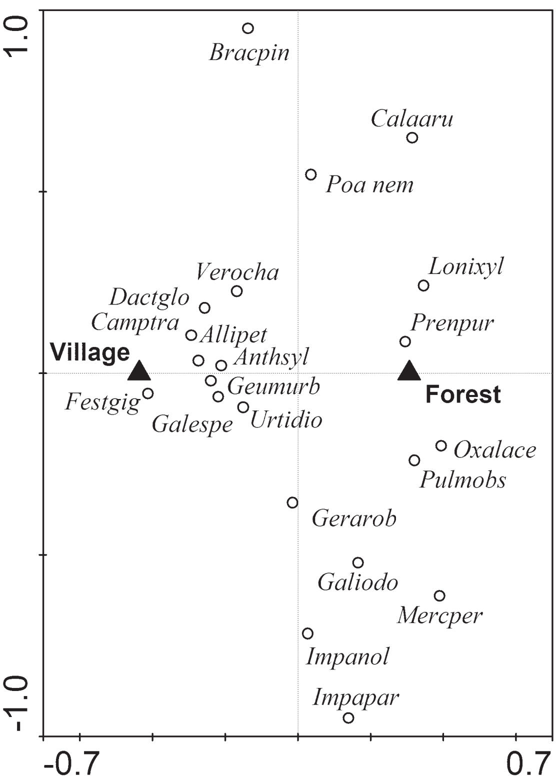

Fig. 3. – Result of the CCA analysis. The village effect was tested as a categorical variable while the environmental properties (slope, altitude, HLI, TSI150, TSI750, WTI, canopy cover) and geographic coordinates were used as covariates in order to filter out initial environmental conditions and possible spatial gradients. The village effect was significant at P = 0.002 and explained 2.1 % of species variability. The diagram shows the first two ordination axes. Species: Allipet – *Alliaria petiolata*, Anthsyl – *Anthriscus sylvestris*, Bracpin – *Brachypodium pinnatum*, Calaaru – *Calamagrostis arundinacea*, Camptra – *Campanula trachelium*, Dactglo – *Dactylis glomerata*, Festgig – *Festuca gigantea*, Galespe – *Galeopsis* sp., Galiodo – *Galium odoratum*, Gerarob – *Geranium robertianum*, Geumurb – *Geum urbanum*, Impanol – *Impatiens noli-tangere*, Impapar – *I. parviflora*, Lonixyl – *Lonicera xylosteum*, Mercper – *Mercurialis perennis*, Oxalace – *Oxalis acetosella*, Poa nem – *Poa nemoralis*, Prenpur – *Prenanthes purpurata*, Pulmobs – *Pulmonaria obscura*, Urtidio – *Urtica dioica*, Verocha – *Veronica chamaedrys*.

forests and that there is a lighter and warmer environment there than in the ancient forests. In addition, it indicates that previous human activity does not affect the moisture conditions.

The results are supported by the CCA (Fig. 3), which indicates that the nitrophilous species (*Alliaria petiolata, Anthriscus sylvestris*, *Geum urbanum*, *Urtica dioica* etc.) are associated with abandoned villages. The ancient forests are characterized by typical species of deciduous broadleaved forests (*Oxalis acetosella*, *Pulmonaria obscura*, *Galium odoratum, Mercurialis perennis, Prenanthes purpurea*, *Calamagrostis arundinacea*). The second ordination (unconstrained) axis obviously represents the moisture gradient that affects the vegetation in abandoned villages and ancient forests in a similar way.

Environmental factors influencing vegetation in abandoned villages

The effect of several environmental factors (logarithm of available phosphorus content in soil, soil pH, logarithm of organic matter content in soil, slope, heat load index, terrain shape index, wetness index, altitude, age of the canopy) on the herb layer was tested using

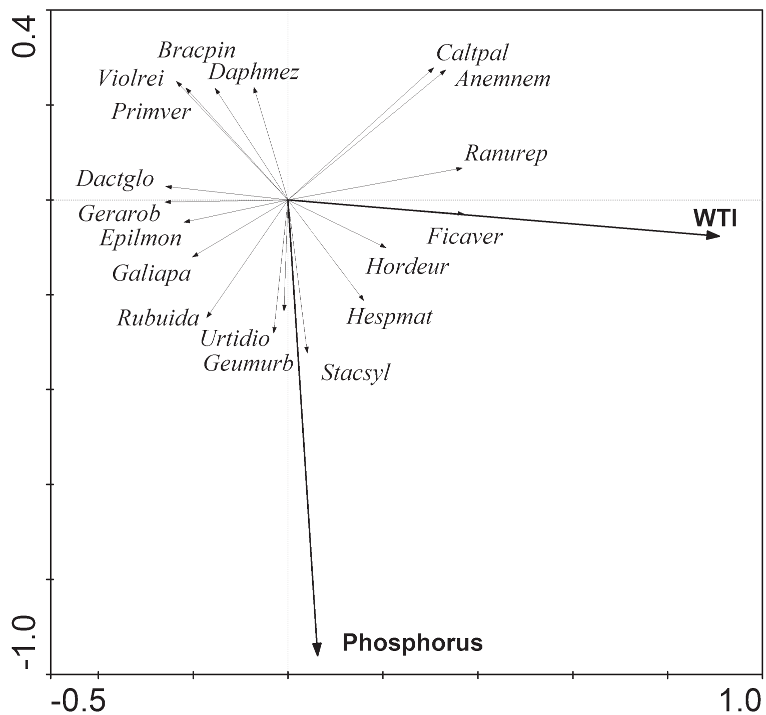

Fig. 4. – Influence of soil and terrain properties on the herb layer in abandoned villages. The effects of several factors were tested by forward selection in RDA ($P < 0.05$). The two significant variables explained 7.9 % of the species variability. Symbols: Phosphorus – natural logarithm of available phosphorus content of the soil, WTI – wetness index. Species: Anemnem – *Anemone nemorosa*, Bracpin – *Brachypodium pinnatum*, Caltpal – *Caltha palustris*, Dactglo – *Dactylis glomerata*, Daphmez – *Daphne mezereum*, Epilmon – *Epilobium montanum*, Ficaver – *Ficaria verna*, Galiapa – *Galium aparine*, Gerarob – *Geranium robertianum*, Geumurb – *Geum urbanum*, Hespmat – *Hesperis matronalis*, Horeur – *Hordelymus europaeus*, Primver – *Primula veris*, Ranurep – *Ranunculus repens*, Rubuida – *Rubus idaeus*, Stacsyl – *Stachys sylvatica*, Urtidio – *Urtica dioica*, Violrei – *Viola reichenbachiana*.

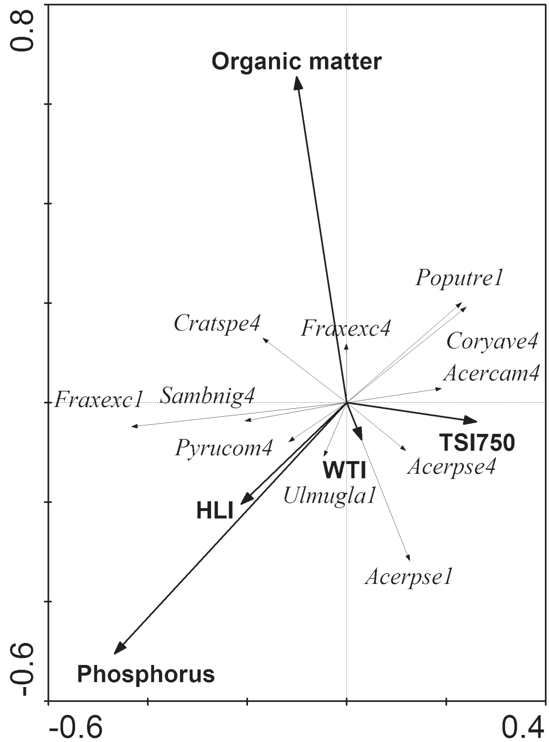

Fig. 5. – Influence of soil and terrain properties on the canopy layer in abandoned villages. The effects of several factors were tested by forward selection in RDA ($P < 0.05$). The significant variables explained 8.6 % of the species variability. Symbols: Phosphorus – natural logarithm of available phosphorus content of the soil, Organic matter – natural logarithm of organic matter content in the soil, Altitude – height above sea level. Species: Acercam – *Acer campestre*, Acerpse – *Acer pseudoplatanus*, Coryave – *Corylus avellana*, Cratspe – *Crataegus* sp., Fraxexc – *Fraxinus excelsior*, Poputre – *Populus tremula*, Pyrucom – *Pyrus communis*, Sambnig – *Sambucus nigra*, Ulmugla – *Ulmus glabra*. Numbers in species abbreviations denote the vegetation layer (1 – tree layer, 4 – shrub layer).

forward selection in the RDA analysis. As shown in Fig. 4, two variables are significant at $P < 0.05$: available phosphorus and wetness index. These results indicate that the vegetation of village forests is differentiated mainly in terms of the moisture gradient (for example *Ficaria verna*, *Ranunculus repens* and *Anemone nemorosa* are positively correlated with WTI). The presence of a second gradient indicates that variability in soil nutrient content is also reflected in the vegetation.

The most important factors influencing the canopy are TSI750 (terrain shape index, Fig. 5), available phosphorus content and organic matter content of the soil. HLI (heat load index) and wetness index are less important. Species growing predominantly in depressions in the terrain (negative TSI) are associated with high nutrient content of the soils (*Fraxinus excelsior*, *Sambucus nigra*), whereas those growing on sites with higher TSI are associated with poorer soils (*Populus tremula*, *Corylus avellana*, *Acer campestre*). One tree species is strongly negatively correlated with organic matter content (*Acer pseudoplatanus*).

Influence of historical factors on the chemical properties of soil

Relationship between chemical properties of soil (pH, available phosphorus and organic matter content), historical land-use, sample position, and locality was tested using ANCOVA (ancient environmental variables were used as covariates; see Table 4). Available phosphorus content is significantly higher at the centre than in the periphery of villages. A similar effect was found for soil pH. In contrast, the sample position had no significant effect on organic matter content. Importantly, organic matter content varied nearly significantly among localities (P = 0.057, F = 2.1). Adjusted means of the respective soil variables are presented in Table 4.

Table 4. – Adjusted means of soil chemistry variables (adjusted by covariate means) for the centre (n = 31) and periphery (n = 50) of villages. Mean ± SE and significance of differences between means are shown (F-statistic, P-value). P – natural logarithm of available phosphorus content of the soil, ORG – natural logarithm of the organic matter content in the soil. Note that no effect of historical land-use was found therefore is not displayed. Variables used as covariates are marked by x.

	pH	P	ORG
Village periphery	5.59±0.07	–2.40±0.21	2.65±0.04
Village centre	5.84±0.10	–1.45±0.28	2.63±0.05
F	4.7	7.9	0.1
P-value	0.03	0.006	0.73
Covariates:			
Altitude			x
Slope		x	x
WTI	x		

Influence of historical factors on the vegetation in abandoned villages

The effect of historical factors (land-use and sample position in village) is relatively high on both canopy and undergrowth species but decreases significantly after fitting ancient environmental variables and ANG as covariates (Table 5). Ancient environmental variables explain 6.8 % of the total variability in canopy species and together with ANG explain 39.3 %, whereas all the historical factors together explain 10.3% before fitting ancient environmental variables and ANG (Table 5A). The effect of historical land-use on the composition of the canopy disappears when ANG were fitted, whereas the effect of sample position remains significant after fitting all the covariates (Table 5A). RDA diagrams show the effect of historical land-use (Fig. 6) and the effect of sample position (Fig. 7) on the composition of the canopy after fitting ancient environmental variables as covariates. Public places and arable fields are clustered together in the diagram and are characterized mainly by *Acer platanoides* and *A. pseudoplatanus*. Meadows are clustered with pastures, whereas abandoned gardens form a unique group of relevés that is characterized by *Fraxinus excelsior* and *Sambucus nigra* (Fig. 6). Three species (*Sambucus nigra*, *Acer platanoides* and *Fraxinus excelsior*) on the diagram (Fig. 7) are more or less associated with village centres, some other species are associated with the periphery of villages (*Acer campestre*, *Prunus avium*, *Corylus avellana*), and some occur independently of the sample position in villages (Fig. 7).

Table 5. – Partial effects of historical factors after fitting covariates for canopy (A) and undergrowth species (B). The percentage of variability explained by each historical factor (sample position and land-use) after subtracting the effect of the other historical factor and after fitting covariates (listed in headers of the rows) is shown. Asterisks indicate that the historical variable was significant at P < 0.1. ANG – approximated natural gradients; WTI – wetness index; HLI – heat load index; A1–A4 – sample scores on the first four axes of the DCA analysis of the undergrowth; AC1–AC4 – sample scores on the first four axes of the DCA analysis of the undergrowth and canopy.

Covariates	Sample position	Land-use	Land-use and sample position
A. Canopy species:			
1. y-coordinates, locality	3.0%*	7.3%*	10.3%*
2. Ancient variables (altitude, WTI, HLI), y-coordinates, locality	2.9%*	5.3%*	8.5%*
3. ANG (AC1,AC2,AC3,AC4, A1,A4), ancient variables (altitude, WTI, HLI), y-coordinates, locality	1.7%*	2.1%	3.9%*
B. Undergrowth species:			
1. x-coordinates, locality	1.8%*	5.1%*	7.2%*
2. Ancient variables (WTI), x-coordinates, locality	1.1%	5.0%*	6.3%
3. ANG (A1,A2,A3,A4), ancient variables (WTI), x-coordinates, locality	0.8%	2.4%	3.2%

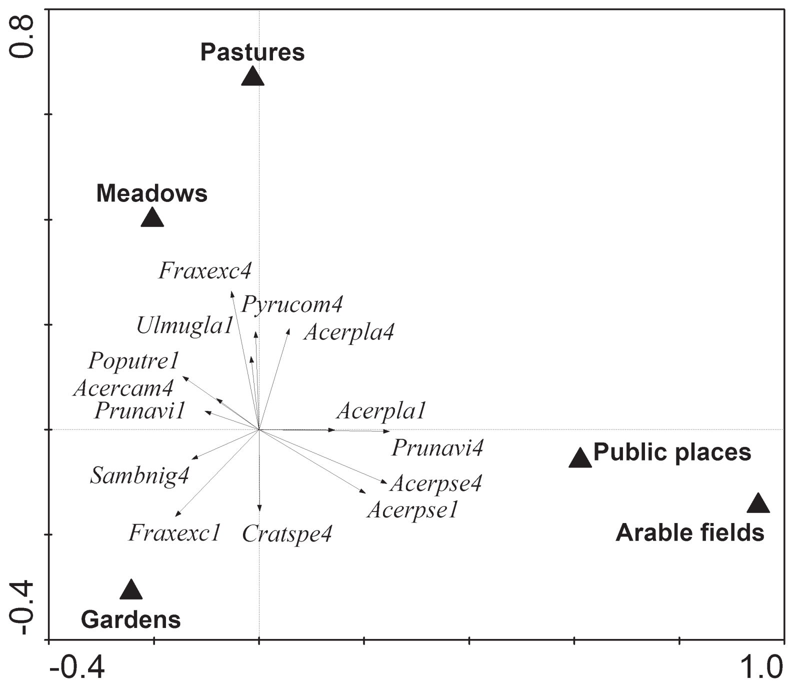

Fig. 6. – Influence of historical land use on canopy species in abandoned villages. The RDA was significant at P < 0.1 (Monte Carlo permutation test, 499 permutations) after fitting covariates (sample position, ancient variables, locality and y coordinate). Species: Acercam – *Acer campestre*, Acerpla – *Acer platanoides*, Acerpse – *Acer pseudoplatanus*, Cratspe – *Crataegus* sp., Fraxexc – *Fraxinus excelsior*, Poputre – *Populus tremula*, Prunavi – *Prunus avium*, Pyrucom – *Pyrus comunis*, Sambnig – *Sambucus nigra*, Ulmugla – *Ulmus glabra*. Numbers in species abbreviations denote the vegetation layer (1 – tree layer, 4 – shrub layer).

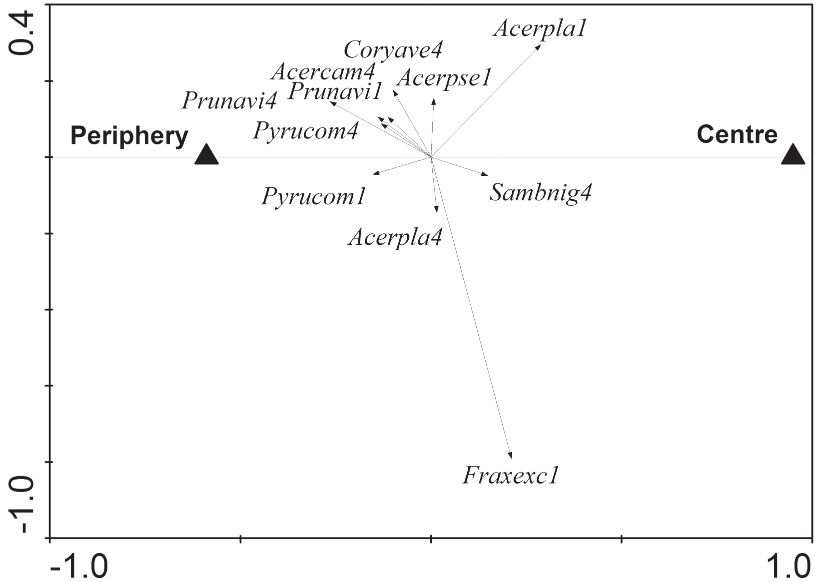

Fig. 7. – Influence of sample position (village structure) on canopy species in abandoned villages. The RDA was significant at P < 0.1 (Monte Carlo permutation test, 499 permutations) after fitting covariates (land use, ancient variables, locality and x coordinate). Species: Acercam – *Acer campestre*, Acerpla – *Acer platanoides*, Acerpse – *Acer pseudoplatanus*, Coryave – *Corylus avellana*, Fraxexc – *Fraxinus excelsior*, Prunavi – *Prunus avium*, Pyrucom – *Pyrus comunis*, Sambnig – *Sambucus nigra*. Numbers in species abbreviations denote the vegetation layer (1 – tree layer, 4 – shrub layer).

Ancient environmental variables explain 4.2% of total variabilty of undergrowth species, together with ANG they explain 33.7%, whereas all historical factors together explain 7.2% before fitting ancient environmental variables and ANG (Table 5B). The effects of sample position on undergrowth were not significant after fitting ancient environmental variables whereas the effect of historical land-use was (Fig. 4). The RDA diagram (Fig. 8) shows the effect of historical land-use on undergrowth species. Arable fields are characterized by the presence of *Moehringia trinervia*, *Hypericum perforatum* and some other species. Most of the species are connected with public places (e.g. *Impatiens parviflora*, *Chaerophyllum aromaticum*, *Viola odorata*). Abandoned gardens are characterized by many spring geophytes and hemicryptophytes. Only a small number of species is associated with former meadows and pastures.

Discussion

The vegetation of village forests forms a relatively homogeneous group in contrast to that of ancient forests. Although the vegetation of abandoned villages covers nearly the same moisture gradient (Fig. 2, Table 1) as ancient forests, it is restricted to nutrient-rich and basic soils. This is shown by the analysis of the Ellenberg indicator values for nutrients and soil acidity, which are significantly different in secondary and ancient forests (Table 3). In their floristic composition, the village forests differ from the ancient forests mainly in the

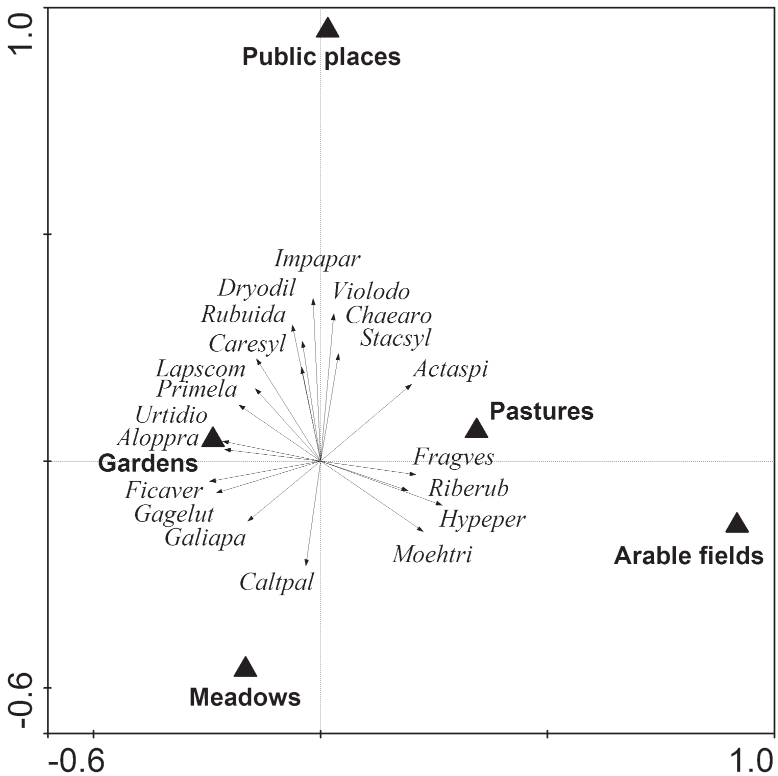

Fig. 8. – Influence of historical land use on undergrowth species in abandoned villages. The RDA was significant at P < 0.1 (Monte Carlo permutation test, 499 permutations) after fitting covariates (sample position, ancient variables and geography). Species: Actaspi – *Actaea spicata*, Aloppra – *Alopecurus pratensis*, Caltpal – *Caltha palustris*, Caresyl – *Carex sylvatica*, Chaearo – *Chaerophyllum aromaticum*, Dryodil – *Dryopteris dilatata*, Ficaver – *Ficaria verna*, Fragves – *Fragaria vesca*, Gagelut – *Gagea lutea*, Galiapa – *Galium aparine*, Hypeper – *Hypericum perforatum*, Impapar – *Impatiens parviflora*, Lapscom – *Lapsana communis*, Moehtri – *Moehringia trinervia*, Primela – *Primula elatior*, Riberub – *Ribes rubrum*, Rubuida – *Rubus idaeus*, Stacsyl – *Stachys sylvatica*, Urtidio – *Urtica dioica*, Violodo – *Viola odorata*.

presence of nitrophilous species (*Geum urbanum*, *Alliaria petiolata*, *Anthriscus sylvestris* etc). Nevertheless, some other relatively nitrophilous species occur with similar frequency in both the forests and villages (*Impatiens parviflora*, *Geranium robertianum*). This may indicate that the species pool in the villages is enriched by some ruderal species surviving from the past, whereas the pool of nitrophilous species in the ancient forests is relatively poor. Moreover, some typical forest species are mostly confined to ancient forests (*Mercurialis perennis*, *Galium odoratum*, *Pulmonaria obscura* etc.); this is usualy explained by the poor colonization ability of forest species (Dzwonko & Loster 1989, Matlack 1994, Peterken & Game 1984). The distribution pattern of some forest herb species in the Doupovské hory mountains confirms their poor colonization ability (Drhovská & Vojta 2006). One can hypothesize that the differences in Ellenberg indicator values are caused by differences in species pool rather than differences in soil properties because some species with high indicator values for nutrients and soil acidity survive from the past and others with lower indicator values have not yet arrived (for discussion see Dzwonko 2001). This may be partly true, but on the other hand the phosphorus content of the soils in the villages is unusualy high (the mean available phosphorus content in the soil from the villages was 24.6 mg/100 g, whereas the mean value for three samples from beech forests with a species composition typical of the area was 5.2 mg/100 g, see Table 1). Verheyen et al. (1999) document a correlation between cultivation duration, phosphorus content and pH. Also Koerner et al. (1999) reported that the phosphorus content of soils of previous pastures and arable fields is twice that of soils in ancient forests. It is likely that the differences in vegetation composition between village and ancient forests are at least partly caused by enrichment of soils by nutrients and cations in the past.

The undergrowth in the abandoned villages is mostly influenced by soil moisture, which is approximated by the wetness index (WTI), and by available phosphorus content of the soils (Fig. 4). Species that grow in moist soils are associated with high WTI (*Ficaria verna*, *Ranunculus repens*). Competitive nitrophilous species (*Urtica dioica*, *Stachys sylvatica* etc.) are associated with soils with a high phosphorus content. The typical forest species are mostly negatively influenced by soil phosphorus (*Viola reichenbachiana, Daphne mezereum*, *Anemone nemorosa*), with some exceptions (*Hordelymus europaeus*). This indicates that the restricted occurrence of forest species in the village forests may be influenced by soil fertility. The composition of the canopy is influenced mainly by phosphorus content, organic matter content and terrain shape (Fig. 5). Woody species, such as *Fraxinus excelsior*, *Ulmus glabra* and *Sambucus nigra*, are associated with nutrient rich soils while *Corylus avellana*, *Populus tremula* and *Acer campestre* are associated with poorer soils at sites with higher TSI.

The hypothesis is that the variability in soil properties is caused mainly by differences in previous agricultural use, as shown in some previous studies (Koerner et al. 1999, Prévosto et al. 2004). This hypothesis is not confirmed for abandoned villages, but the soil chemistry is clearly dependent on where samples are collected (Table 4). Soils from the built-up areas have a higher pH and contain more available phosphorus than those from the periphery of villages. Higher intensity of human influence in village centres and enrichment by basic ions from the mortar of ruins are probably the reasons. This effect overrides that of previous specific land-use.

Correlations between both undergrowth and canopy layer composition and historical factors were found. The variability explained by the historical factors is relatively high compared with the effects of ancient environmental variables. Although the effects of ancient environmental variables and historical factors partly overlap (Table 5), the effects of the historical factors are detectable regardless of the initial conditions (except for the effect of sample position on undergrowth). Nevertheless, the historical factors generated similar gradients to those found in the ancient forests (with one exception, the effect of sample position on canopy; Table 5). Thus, past human influence only shifts environmental conditions in the direction of an existing gradient. Only those effects that were significant regardless of the initial conditions (ancient environmental variables) are discussed further because ancient environmental variables need to be interpreted as the primary factors influencing vegetation. After a more detailed examination of the canopy species characteristic of particular land-use types (Fig. 6), it appears that it is mainly the conditions occurring immediately after the abandonment that determine the differences. The presence of *Acer* *pseudoplatanus* and *Acer platanoides* in the former arable fields and public places can be explained in terms of competition. These species are rarely observed germinating in grassland, whereas abandoned fields and disturbed public places can offer an opportunity for them. Note that *Acer platanoides* occurs also in previous meadows, but only in the shrub layer, therefore the conditions immediately after the abandonment are not important in this case because the spread of *Acer platanoides* in abandoned meadows has probably been enhanced by the decrease in competition pressure in the herb layer due to shading by older trees. Moreover, the presence of *Acer pseudoplatanus* correlates with soils with a low organic matter content (Fig. 5), which can be caused by previous ploughing (Koerner et al. 1999, Verheyen et al. 1999). Also the presence of *Populus tremula* in former meadows supports this hypothesis. *Populus tremula* is a clonal species capable of spreading despite competition, a potentially important factor in meadows after abandonment. The presence of *Pyrus communis* and *Prunus avium* in grasslands can indicate that fruit trees were tolerated in pastures and meadows. This is consistent with the results of Stover & Marks (1998) who explain vegetation differences in terms of the survival of plants typical of pastures before abandonment or differences in the suitability of ploughed versus unploughed areas for woody species germination shortly after abandonment. Nevertheless, the presence of *Fraxinus excelsior* and *Sambucus nigra* in the previous gardens can be explained in terms of soil properties (enrichment by nutrients). There are important differences between the centre and periphery of the village (Fig. 7). Village centres are occupied mainly by nitrophilous species and species that were previously tolerated in villages (*Fraxinus excelsior*, *Acer platanoides*, *Sambucus nigra*). Note that *Sambucus nigra* had some economic importance in the past. At the periphery of villages grow species that demand less by way of nutrients (*Acer campestre*, *Corylus avellana* etc.) and often species of economic importance, which were planted or tolerated (*Prunus avium*, *Pyrus communis*, *Corylus avellana*). The effect of sample position is relatively strong. It was the only effect that remained significant after fitting ANG as covariates.

The effect of historical factors on the undergrowth of abandoned villages has to be interpreted with caution because the effect was nearly insignificant after fitting ancient environmental variables and disappears after fitting ANG. Nitrophilous species are typical of the former gardens and public places, whereas arable fields and pastures are occupied by species that demand less nutrient-rich soils (Fig. 8). Although the differences were not confirmed by soil analyses, it is probable that gardens and public places were enriched with nutrients in the past, whereas they were removed from arable fields and pastures. Gardens were probably manured and public places were influenced by domestic animals (mainly poultry). In contrast, biomass was removed from arable fields and pastures. Some of the species that are typical of public places are also invasive species (*Impatiens parviflora*) or previously planted species and able to spread to natural communities (*Viola odorata*) or species that often spread from their native environment into anthropogenous stands (*Chaerophyllum aromaticum*, *Stachys sylvatica*). All these species are common in inhabited villages in the area and are denoted as nitrophilous species. The presence of perennial nitrophilous species (*Urtica dioica*, *Alopecurus pratensis*) is typical of former gardens. Striking is the presence of early flowering geophytes and hemicryptophytes (*Ficaria verna*, *Gagea lutea*, *Primula elatior*). This is associated with the fact that the abandoned gardens are dominated by *Fraxinus excelsior* in the tree layer. Ash develops leaves later than other trees, which enables many early-flowering plants to survive. Nevertheless, some differences may be attributed to the effect of historical disturbances. The effect of disturbance is discussed in previous studies. Motzkin et al. (1996) report the effect of ploughing on many herb species, which only slowly recolonize an area after abandonment. Wulf (2004) argues that the lower proportion of perennial plants in former croplands than former grasslands is due to destruction by ploughing in the past. In this study there were also some species that can survive the disturbance associated with former arable fields or public places (*Impatiens parviflora*, *Stachys sylvatica*, *Hypericum perforatum*, *Moehringia trinervia,* and *Viola odorata*; see Fig. 8). The arable fields were exposed to deep periodic soil disturbance, whereas public places were disturbed irregularly and mainly only the soil surface.

It can be concluded, that the secondary forests that develop in abandoned villages significantly differ from ancient forests. The differences are at least partly caused by soil conditions influenced by previous human activity. The changed soil properties will probably influence the vegetation over decades and maybe centuries, and enhance species and vegetation variability. The variability of village forests is influenced by soil factors, which are believed to be widely influenced by previous human activity (soil phosphorus, organic matter content). Nevertheless, previous land-use did not appear to influence soil factors. On the other hand, some variables exhibit a dependence on village zonation (soil phosphorus, pH). Vegetation reflects historical village structure as well as historical land-use.

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Souhrn

Historické lidské vlivy mohou být významným faktorem ovlivňujícím složení vegetace v sekundárních lesích. Vedle přirozených podmínek prostředí mohou historické faktory obohacovat variabilitu stanovišť a tím zvyšovat diverzitu rostlin. Vliv dřívějšího hospodaření na současnou vegetaci však není dostatečně prozkoumán. Cílem této studie bylo porovnat vegetaci kontinuálně existujících lesů se sekundárními lesy na místě zaniklých vesnic v Doupovských horách (vojenský výcvikový prostor Hradiště) a pokusit se separovat vliv historických faktorů od vlivu přírodního prostředí. Výsledky ukazují, že vegetace sekundárních lesů v zaniklých vesnicích je výrazně odlišná od vegetace kontinuálních lesů, liší se zejména výskytem druhů indikujících vysoký obsah živin v půdě a vysoké pH. Příčinou jsou pravděpodobně vysoké vstupy živin a basických iontů v minulosti. Variabilita sekundárních lesů je ovlivněna zejména gradientem přístupného fosforu v půdě, půdní vlhkostí (odhadnutou tzv. vlhkostním indexem) a obsahem humusu. Prostorové rozložení obsahu fosforečnanů a pH v rámci vesnice lze interpretovat jako rozdíly v intenzitě lidských vlivů v centru a na okraji vesnice. Variabilita vegetace je ovlivněna historickým hospodařením a také, podobně jako obsah živin v půdě, historickou strukturou zaniklé vesnice. Efekt historických faktorů je relativně vysoký a nemůže být vysvětlen jejich korelací s výchozími podmínkami prostředí.

References

Augustin M. (1994): Akce D – vysídlení Doupovska v letech 1953–1954 [Action D – displacement of Doupov region in 1953–1954]. – In: Augustin M. (ed.), Historický sborník Karlovarska II [Contributions to history of Karlovy Vary region], p. 295–315, Státní okresní archiv v Karlových Varech.

Bielek P. (1984): Dusík v pôde a jeho premeny [Soil nitrogen and its changes]. – Príroda, Bratislava.

Bleck R. (1969): Phosphatanalytische Untersuchungen vor der Hauptburg der Pfalz Tilleda. – Zeitschrift für Archäologie 3: 118–121.

Blume H. & Sukopp H. (1976): Ökologische Bedeutung Anthropogener Bodenveränderungen. – Schriftenreihe für Vegetationskunde 10: 75–89.
Borcard D., Legendre P. & Drapeau P. (1992): Partialling out the spatial component of ecological variation. – Ecology 73: 1045–1055.
Dengler J. (2003): Entwicklung und Bewertung neuer Ansätze in der Pflanzensoziologie unter besonderer Berücksichtung der Vegetationsklassifikation. – Martina Galunder-Verlag, Nümbrecht-Elsenroth.
Drhovská L. & Vojta J. (2006): Význam historické kontinuity vegetace pro výskyt lesních druhů [The importance of vegetation continuity for forest species occurence]. – In: Neuhöferová P (ed.), Historie a vývoj lesů v českých zemích [Forest history and development in the Czech countries], p. 129–134, Katedra pěstování lesů FLE ČZU v Praze, Praha.
Dzwonko Z. (2001): Assessment of light and soil conditions in ancient and recent woodlands by Ellenberg indicator values. – J. Appl. Ecol. 38: 942–951.
Dzwonko Z. & Loster S. (1989): Distribution of vascular plant species in small woodlands on the Western Carpathian foothills. – Oikos 56: 77–86.
Ellenberg H., Weber H. E., Düll R., Wirth W., Werner W. & Paulissen D. (1992): Zeigerwerte von Pflanzen in Mitteleuropa. Ed. 2. – Scr. Geobot. 18: 1–258.
Farina A. (1998): Principles and methods in landscape ecology. – Chapman & Hall, London.
Flinn K. & Vellend M. (2005): Recovery of forest plant communities in post-agricultural landscapes. – Front. Ecol. Environ. 3: 243–250.
Fortin M. J. & Dale M. (2005): Spatial analysis: a guide for ecologists. – Cambridge Univ. Press, Cambridge.
Fried M. & Broeshart H. (1967): The soil–plant system in relation to inorganic nutrition. –Academic Press, New York & London.
Graae B. J., Økland R. H., Petersen P. M., Jensen K. & Fritzbøger B. (2004): Influence of historical, geographical and environmental variables on understorey composition and richness in Danish forests. – J. Veg. Sci. 15: 465–474.
Grashof-Bokdam C. J. & Geertsema W. (1998): The effect of isolation and history on colonisation patterns of plant species in secondary woodlands. – J. Biogeogr. 25: 837–846.
Hennekens S. M. & Schaminée J. H. J. (2001): Turboveg, a comprehensive database management system for vegetation data. – J. Veg. Sci. 12: 589–591.
Hill M. O. (1979): TWINSPAN. A Fortran program for arranging multivariate data in an ordered two way table by classification of the individuals and attributes. – Cornell Univ., Ithaca.
Hill M. O. & Carey P. (1997): Prediction of yield in the Rothamsted park grass experiment by Ellenberg indicator values. – J. Veg. Sci. 8: 579–586.
Hrabě F. & Halva E. (1993): Limits of forage production and the efficiency of grassland management. – In: Rychnovská M. (ed.), Structure and functioning of seminatural meadows, p. 165–192, Academia, Praha.
Koerner W., Benoît M., Dambrine E. & Dupouey J. (1999): The influence of past agricultural practices on the vegetation and soils of reforested areas in the Vosges mountains. – Revue Forestiere Francaise 51: 231–238.
Koerner W., Dupouey J., Dambrine E. & Benoît M. (1997): Influence of past land use on the vegetation and soils of present day forest in the Vosges mountains, France. – J. Ecol. 85: 351–358.
Komár A. (1993): Vojenský újezd hradiště [Military area Hradiště]. – Sbor. Čes. Geogr. Společ. 2: 75–86.
Kubát K., Hrouda L., Chrtek J. jun., Kaplan Z., Kirschner J. & Štěpánek J. (2002): Klíč ke květeně České republiky [Key to the flora of the Czech Republic]. – Academia, Praha.
Lea N. L. (1992): An aspect driven kinematic routing algorithm. – In: Parsons A. J. & Abrahams A. D. (eds.), Overland flow: hydraulics and erosion mechanics, p. 147–175, Chapman & Hall, London.
Lepš J. & Šmilauer P. (2003): Multivariate analysis of ecological data using CANOCO. – Cambridge Univ. Press, Cambridge.
MacDonald D., Crabtree J., Wiesinger G., Dax T., Stamou N., Fleury P., Gutierrez Lazpita J. & Gibon A. (2000): Agricultural abandonment in mountain areas of Europe: environmental consequences and policy response. – J. Env. Manage. 59: 47–69.
Matlack G. (1994): Plant demography, land-use history, and the commercial use of forests. – Conserv. Biol. 8: 298–299.
McCune B. & Keon D. (2002): Equations for potential annual direct incident radiation and heat load. – J. Veg. Sci. 13: 603–606.
McNab H.W. (1989): Terrain shape index: quantifying effect of minor landforms on tree height. – Forest Sci. 35: 91–104.
Moore I. D., Grayson R. B. & Ladson A. R. (1992): Digital terrain modelling: a review of hydrological, geomorphological and biological applictations. – Hydrological Processes 5: 3–30.

Moravec J. (1974): Zusammensetzung und Verbreitung des *Dentario enneaphylli-Fagetum* in der Tschechoslowakei. – Folia Geobot. Phytotax. 9: 113–152.

Moravec J. (1977): Die submontanen krautreichen Buchenwälder auf Silikatböden der westlichen Tschechoslovakei. – Folia Geobot. Phytotax. 12: 121–166.

Moravec J. (1979): Das *Violo reichenbachianae-Fagetum* – eine neue Buchenwaldassoziation. – Phytocoenologia 6: 484–504.

Moravec J. (1994): Fytocenologie [Phytosociology]. – Academia, Praha.

Moravec J. (ed.) (1995): Rostlinná společenstva České republiky a jejich ohrožení [Red list of plant communities of the Czech Republic and their endangerment]. – Severočes. Přír., Suppl. 1995: 1–206.

Motzkin G., Foster D., Allen A., Harrod J. & Boone R. (1996): Controlling site to evaluate history: vegetation patterns of a New England sand plain. – Ecol. Monogr. 66: 345–365.

Peterken G. F. (1981): Woodland conservation and management. London, UK. – Chapman & Hall, London.

Peterken G. F. & Game M. (1984): Historical factors affecting the number and distribution of vascular plant species in the woodlands of central Lincolnshire. – J. Ecol. 72: 155–182.

Prach K. & Řehounková K. (2006): Vegetation succession over broad geographical scales: which factors determine the patterns? – Preslia 78: 469–480.

Prévosto B., Dambrine E., Moares C. & Curt T. (2004): Effects of volcanic ash chemistry and former agricultural use on the soils and vegetation of naturally regenerated woodlands in the Massif Central, France. – Catena 56: 239–261.

Reichelt G. & Wilmanns O. (1973): Vegetationsgeographie (Das Geographisher Seminar – Praktishe Arbeitsweisen). – Westernmann, Braunschweig.

Siegl A. (1998): Zum Einfluß Anthropogener Faktoren auf die Variabilität des Vegetationspotentials. – Ber. Reinhold-Tüxen-Gess. 10: 19–41.

StatSoft Inc. (2006). Electronic statistics textbook. – Statsoft, Tulsa, URL: [http://www.statsoft.com/textbook/stathome.html].

Stover E. & Marks P. (1998): Successional vegetation on abandoned cultivated and pastured land in Tompkins County, New York. – J. Torrey Bot. Soc. 125: 150–164.

ter Braak C. & Šmilauer P. (2002): CANOCO reference manual and CANODRAW for Windows user's guide: software for canonical community ordination. Version 4.5. – Microcomputer Power, Ithaca.

Tichý L. (2002): JUICE, software for vegetation classification. – J. Veg. Sci. 13: 451–453.

Verheyen K., Bossuyt B., Hermy M. & Tack G. (1999): The land use history (1278–1990) of a mixed hardwood forest in western Belgium and its relationship with chemical soil characteristics. – J. Biogeogr. 26: 1115–1128.

Vesecký A., Briedoň V., Karský V. & Petrovič Š. (1961): Podnebí ČSSR – tabulky [Climatic conditions of the ČSSR – tables]. – Český hydrometeorologický ústav, Praha.

Vojta J. & Kopecký M. (2006): Vegetace sekundárních lesů a křovin Doupovských hor [Vegetation of secondary forests and shrubs in the Doupovské hory hills]. – Zpr. Čes. Bot. Společ. 41/ Mater 21: 209–225.

Wulf M. (2004): Plant species richness of afforestations with different former use and habitat continuity. – For. Ecol. Manage. 195: 191–204.

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