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REGENERATION OF *OSTRYA CARPINIFOLIA* SCOP. FOREST AFTER COPPICING: MODELLING OF CHANGES IN SPECIES DIVERSITY AND COMPOSITION

ABSTRACT: In temperate forest ecosystems, management is one of the most relevant factors that can drive the temporal pattern of species. As species in an ecosystem show susceptibility to stress and disturbance, it is useful to take into account the plant community "compositional dimension", which derives from species behaviour and ecological attributes and provides information on the mechanisms underlying species assemblages. Taking into account the influence of environmental factors on species diversity and composition, in order to determine the most suitable ecological behaviour type of each species, the research aim was to generate a model for *Ostrya carpinifolia* coppiced woods (central Italy) that describes forest ecosystem regeneration after coppicing by the assessment of change in the composition of ecological behaviour types.

Vascular species cover percentage, field data, soil data, light intensity at the undergrowth, dominant tree layer cover and time since last logging were recorded for 63 plots covering 400 m^2 each (20 × 20 m), randomly selected within a set of homogeneous macro-environmental conditions. Low species richness is related to stressing factors (acid soil, high soil skeleton percentage), while high species richness is linked to high light intensity at the undergrowth level due to scarce canopy cover soon after coppicing. The driving forces affecting floristic composition, highlighted through multi-response permutation procedures (MRPP) were light intensity at the undergrowth, regenerative phase, dominant tree layer cover, acidity, presence/absence of outcropping rock or rock fragments and total nitrogen content. Six species groups, each one characterized by homogeneous ecological behaviour, were defined by indicator species analysis (ISA) and tested using bioindication values analysis. Floristic successional change, related to time since last coppicing, turned out to follow an ecological cycling process characterized by cyclical occurrence/disappearance of species belonging to the six groups.

KEY WORDS: forest management, forest regeneration, *Ostrya carpinifolia* forest

1. INTRODUCTION

Plant diversity is the result of species interaction or community adaptation to its environment over evolutionary time (Rice and Westoby 1983). Ecologists have long sought to explain why species can coexist and how they are distributed into plant communities. Niche differentiation (Giller 1984), species competition (Huston 1979, Tilman 1984, Wilson and Tilman 1993) and disturbance (Grubb 1977, Denslow 1980, 1987, Tilman and Pacala 1993) have been proposed as driving forces for high species diversity; an unifying model was hypothesized by Grime (1979). In temperate forest ecosystems, management is however one of the most relevant factors that can drive the temporal pattern of species (Denslow 1980, Picket and White 1985, van der Maarel 1993, Decocq *et al.* 2004), with different social and ecological behaviours (Bartha *et al.* 2008). Moreover, it has been hypothesized that long-term forest management and historical land use can play a significant role, particularly forest cover continuity over time (Decocq 2003, Hérault *et al.* 2005). Floristic diversity is also scale-dependent (Palmer 1994), showing stronger edaphic effects at finer scales and stronger geographic distinction at broader scales (Chytry *et al.* 2002, Wang *et al.* 2008). For many broad-scale data sets, however, edaphic, local topo-climatic and geographical factors can be of comparable importance and interact in a complex way (Bergmeier and Dimopoulos 2001, Kuzelovà and Chytry 2004, Vitanzi *et al.* 2009). As all species are not equivalent in an ecosystem (Tilman *et al.* 1997) and with the aim to understand the relationship between ecosystem environmental constraints/management and plant diversity, it is useful to take into account the biodiversity "compositional dimension" (Noss 1990) deriving from species behaviour and ecological attributes at a given observation level (Scheiner 1992, Borhidi 1995). As a matter of fact, compositional dimension, considering species in regard to their auto-ecology, morphology and physiological performances, provides information on the mechanisms underlying species assemblages (Kolasa and Rollo 1991, Alard and Poudevigne 2000).

On the basis of this theoretical framework and taking into account the influence of environmental factors on species diversity and composition, in order to determine the most suitable ecological behaviour type of each species, our research aim was to generate a model for hop-hornbeam (*Ostrya carpinifolia* Scop.) forest landscape that describes forest ecosystem regeneration after coppicing by the assessment of change in compositional dimension.

2. STUDY AREA

The study area is a mountainous territory in the Umbria-Marches Apennines (central Italy) (coordinates 43°14'–42°57'N; 12°57'–13°16'E). It is characterized mainly by calcareous substrata and included within a submediterranean context, on the border between temperate and mediterranean bioclimatic regions (Rivas-Martínez and Rivas-Saenz 1996–2009).

The forest landscape is composed of mixed woods in which *Ostrya carpinifolia* Scop., *Fraxinus ornus* L. subsp. *ornus*, *Acer opalus* Mill. subsp. *obtusatum* (Waldst. & Kit. ex Willd.) Gams, *Quercus cerris* L. and *Quercus pubescens* Willd. s.l. play a dominant or a co-dominant role. These woods are managed as coppice with standards (mature trees retained through two or three coppicing rotation cycles) and cut down every 20–25 years. From a phytosociological point of view, they are referred to the *Querco-Fagetea* class, *Quercetalia pubescenti-petraeae* order and *Carpinion orientalis* alliance (Catorci and Orsomando 2001, Catorci *et al.* 2003, Blasi *et al.* 2004).

3. MATERIAL AND METHODS

3.1. Experimental design

To plan data collection, the study area was divided into homogeneous ecological units, from a bioclimatic, geological and morphological point of view, according to the Blasi *et al.* (2000) method, using the geodatabase (G.I.S.) of the Marche region plant landscape (Catorci *et al.* 2007, Pesaresi *et al.* 2007). In order to reduce the number of environmental variables, *Ostrya carpinifolia* woods growing on calcareous substrata and north-facing slopes at altitudes ranging from 600 to 900 m a.s.l. were selected. Within this set of homogeneous macro-environmental conditions, 63 sampling plots, covering 400 m^2 each (20 × 20 m), were randomly chosen.

3.2. Data collection

Floristic and environmental data were collected in the period 2007–2008. Species cover in each sampling plot was expressed in percent values. Floristic nomenclature follows Conti *et al.* (2005). Field data on slope, morphology, outcropping rock or rock fragment cover and dominant tree layer cover were gathered. Soil samples, collected in five locations in each plot within a depth ranging from 10 to 40 cm and thoroughly mixed, were analysed in the laboratory for pH, total nitrogen content (g·kg^{-1} of the soil dry matter) and texture (skeleton and sand %) measurements. Soil depth (cm) in each plot was measured using a graduated pole. Measurements of light intensity (PHAR – photosynthetically active radiation) at the undergrowth (μmol·m^{-2}·s^{-1}) were performed in June/July, at 50 cm above soil level using a ceptometer. Information about time since last logging was obtained from coppicing registers (Corpo Forestale dello Stato database).

3.3. Data elaboration

Field and soil data, light intensity at the undergrowth, canopy cover and time since last coppicing were expressed in classes, as reported in Table 1. Species richness was calculated for each relevé, then multi-response permutation procedures (MRPP) were applied using Sørensen distance, and two matrices, relevés × species (cover %) and relevés x environmental data (classes), were run to determine parameters affecting species composition (driving forces).

Two matrices, relevés x species (cover %) and relevés x environmental data (classes of parameters highlighted by MRPP), were processed using indicator species analysis (ISA) to assess the relation between species and environmental parameters classes. The statistical significance of observed maximum indicator values for species was verified for each parameter through the Monte Carlo test based on 5000 permutations. Species highlighted as indicators of more than one environmental parameter class were listed only as indicators of the class showing the highest indicator value.

In order to test the ecological homogeneity of the outcoming species groups, the frequency distribution of bioindication values (Pignatti 2005) within each of them was synthesized by quartiles calculation. Outliers were relocated to the most ecologically appropriate group. The hypothesis of no difference among groups in relation to species distribution and abundance in the relevés data set was tested through MRPP on two matrices, species x relevés (cover %) and species x ecological species groups (classes).

In order to generate a model for forest recovery over the time, relevés were ordered on the basis of the stretch from the last coppicing and divided into four age classes: 1–8, 9–16, 17–24, more than 24 years. These classes were analysed with respect to ecological species group composition.

Table 1. Classes of the environmental parameters used for statistical elaborations.

Parameter	Label	Class				
		1	2	3	4	5
Slope (°)	Slope	31–45	16–30	< 15	–	–
Morphology	Morph	Watershed	Slope	Impluvium	–	–
Outcropping rock	Rock	Presence	Absence	–	–	–
Rock fragments cover (%)	Rockfrag	> 5	1–5	0	–	–
Regenerative phase (years)	Regen	1–8	9–16	17–24	> 24	–
Light intensity (μmol·m^{-2}·s^{-1})	Light	> 100	76–100	51–75	26–50	0–25
Soil pH	pH	<5.0	5.1–6.0	6.1–7.0	> 7.0	–
Soil depth (cm)	Soildep	0–15	16–30	31–45	–	–
Soil texture (sand %)	Sand	> 60	41–60	<40	–	–
Soil texture (skeleton %)	Skel	76–100	51–75	26–50	0–25	–
Total nitrogen content (g·kg^{-1} soil d.m.)	Nitr	<2	2–4	> 4	–	–
Dominant tree layer cover (%)	Domtree	0–20	21–40	41–60	61–80	81–100

Numerical analyses were performed using PCORD 5.0 (McCune and Mefford 2006) and SPSS 8.0 (SPSS Inc. 1997).

4. RESULTS

A total of 175 species was collected; the mean species number per plot is 47.4. Relevés with the lowest species number (30.5–39.7) are linked to the most acid and skeleton-rich soil classes (pH <5.0 and skeleton content 76–100%). Richness values around the mean are pointed out for the last regenerative phase (more than 24 years since last coppicing), light intensity <50 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and dominant tree layer cover > 60%, while values ranging from 51.5 to 55.0 are linked to absence of rock fragments, slope angle <15° and sand percentage <40%. Relevés with the highest richness (60.0–68.0) are related to the deepest soil class and, considering forest structure and regenerative phase, to the brightest condition (1–8 years since last coppicing, light intensity > 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$, dominant tree layer cover <20%). Moreover, during the regenerative cycle, mean species richness declines from 60.0 (1–8 years from the last logging) to values ranging from 45.6 to 46.8.

Multi-response permutation procedures (MRPP) highlight that the parameters showing statistically significant floristic differences within classes are light intensity, regenerative phase, dominant tree layer cover, presence/absence of outcropping rock or rock fragments, soil pH and soil total nitrogen content (Table 2). Therefore, parameter classes asso-

Table 2. Summary statistics for multi-response permutation procedures (MRPP) and pairwise comparison. Codes for environmental variable classes – see Table 1. Only significant values (P <0.05) are reported (T – test statistics; A – chance-corrected within-group agreement; P – probability of a smaller or equal weighted mean within-group distance).

Parameter	Pairwise comparison	T	A	*P*
Regenerative phase		–8.746	0.056	0.000
	1 *vs.* 3	–5.627	0.048	0.000
	1 *vs.* 2	–5.386	0.043	0.001
	1 *vs.* 4	–5.614	0.082	0.000
	3 *vs.* 4	–6.971	0.058	0.000
	2 *vs.* 4	–5.071	0.037	0.000
Light intensity		–6.695	0.048	0.000
	1 *vs.* 5	–3.913	0.018	0.004
	1 *vs.* 4	–2.134	0.076	0.035
	1 *vs.* 3	–3.347	0.106	0.007
	4 *vs.* 5	–2.138	0.011	0.039
	3 *vs.* 5	–5.603	0.027	0.000
	3 *vs.* 4	–3.432	0.254	0.010
Soil pH		–4.840	0.037	0.000
	1 *vs.* 4	–2.019	0.273	0.000
	2 *vs.* 3	–2.950	0.011	0.011
	1 *vs.* 3	–6.007	0.072	0.000
	1 *vs.* 2	–3.690	0.037	0.008
Outcropping rock		–3.604	0.013	0.005
Rock fragments cover		–1.869	0.011	0.048
	1 *vs.* 3	–2.497	0.067	0.022
	2 *vs.* 3	–2.879	0.013	0.013
Total nitrogen content		–1.976	0.010	0.041
	1 *vs.* 3	–2.003	0.012	0.043
Dominant tree layer cover		–5.857	0.039	0.000
	1 *vs.* 4	–2.649	0.032	0.021
	1 *vs.* 5	–8.521	0.044	0.000
	3 *vs.* 5	–3.055	0.018	0.009
	4 *vs.* 5	–3.105	0.014	0.008

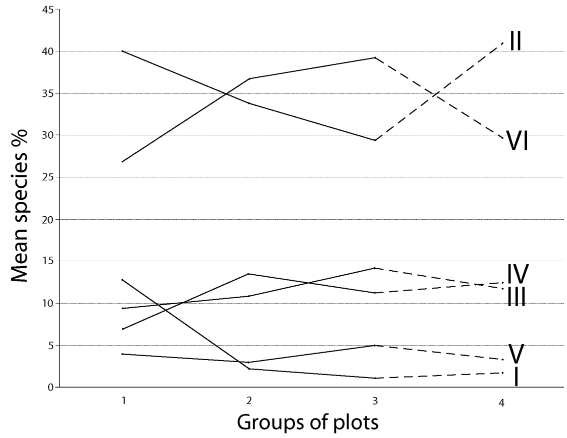

Fig. 1. Trends of ecological species groups (I–VI) mean percent values per plot throughout a regenerative cycle after coppicing (1: 1–8 years after coppicing; 2: 9–16 years; 3: 17–24 years; 4: more than 24 years). Species groups – see APPENDIX II.

Table 3. Results of bioindication analysis of species groups (I–VI, see APPENDIX II).

Variable	Group	I	II	III	IV	V	VI
Light	1st quartile	7.00	5.00	4.00	5.00	2.00	3.75
	Median	7.00	6.00	4.50	5.00	4.00	4.00
	3rd quartile	8.00	7.00	6.00	6.00	4.50	5.00
Temperature	1st quartile	5.00	5.00	5.00	5.00	4.00	5.00
	Median	6.00	6.00	5.00	5.50	5.50	6.00
	3rd quartile	7.00	7.00	5.00	7.00	8.00	7.00
Moisture	1st quartile	4.00	4.00	5.00	3.00	4.00	4.00
	Median	4.00	4.00	5.00	3.50	6.00	5.00
	3rd quartile	5.00	5.00	5.00	5.25	6.50	5.00
Soil reaction	1st quartile	5.00	5.25	5.00	5.25	2.00	5.25
	Median	7.00	7.00	7.00	7.00	4.00	7.00
	3rd quartile	8.00	8.00	7.00	7.75	4.00	7.00
Nutrients	1st quartile	3.00	3.00	5.00	3.00	4.00	4.00
	Median	4.00	4.50	6.00	4.00	4.00	5.00
	3rd quartile	6.00	5.00	6.00	5.00	5.00	7.00

ciated with the highest floristic composition difference are closely related to the following environmental constraints: light intensity (linked to regenerative phase and dominant tree layer cover) and soil chemical and physical features (acidity, total nitrogen content, presence/absence of outcropping rock or rock fragments). We considered these environmental constraints as the main species diversity driving forces of the studied forest ecosystem.

Indicator species analysis (ISA) showed the presence of species significantly related to the environmental variables classes (APPENDIX I). Indicator species of the same class were grouped together; the resulting sets were further grouped according to the above mentioned driving forces. Species not highlighted by ISA were grouped together. These elaborations led to the identification of six species groups (APPENDIX II). Bioindication values analysis of the species sets made it possible to define the ecological features of each group (Table 3).

The detected six species groups can be characterized as follows. *Group I (transient species)* – species showing pioneer behaviour, generally demanding full light (median light bioindication value 7.0) and growing mainly on nutrient-poor, neutral to basic soils. *Group II (fringe species)* – species growing in half-shadowed conditions (median light bioindication value 6.0) and on nutrient-poor, neutral to basic soils. *Group III (nutrient-rich and cool soil niche forest species)* – species living on cool, deep, neutral-basic soils, well watered and nutrient-rich (moisture and nutrient median values 5.0 and 6.0, respectively), mostly on concave morphologies such as *impluvia* or soil depressions, in not very shadowed conditions. *Group IV (drained soil niche forest species)* – species living on drained, clast-rich, neutral-basic, water- and nutrient-poor soils, characterized by high rock fragment cover or presence of outcropping rock, mainly on convex morphologies such as watersheds (soil moisture and nutrient values 3.5 and 4.0, respectively). *Group V (acid soil niche forest species)* – species living in shadowed conditions, exclusively on acid, moist and nutrient-poor soils (soil reaction value 4.0). *Group VI (generalist forest species)* – species growing under closed forest canopy, in quite shadowed conditions, on well watered and moderately nutrient-rich, neutral to basic soils. They show intermediate median values and/or wide interquartile ranges, overlapping with the other species groups.

The hypothesis of no difference among species groups in relation to species distribution and abundance in the relevés data set, tested through MRPP, was rejected (test statistic T = –27.196; A = 0.065; P = 0.000).

The 63 plots, divided into four groups linked to the above mentioned age classes, were analysed in terms of ecological species sets composition, obtaining the trend of each species group depending on the time since last coppicing (Fig. 1).

5. DISCUSSION

Average species richness values (51.5–55.0) above the mean are pointed out in unstressed habitats (low slope angle and sand percentage, absence of rock fragments), while in more stressed habitats (acid soil, high presence of soil skeleton) mean species richness is quite lower (30.5–39.7). These results are consistent with the conclusions of Pausas and Carreras (1995), Burnett *et al.* (1998) and Decocq (2000). The highest species richness (60.0–68.0) is linked to the high light intensity at the undergrowth after coppicing. This result is consistent with many other experiences (*e.g.* Kirby 1990, Kirby and Thomas 2000, Debussche *et al.* 2001, Nash Suding 2001, Mason and Macdonald 2002, Bartha *et al.* 2008) and allows to state that forest canopy cover and regenerative phase strongly define species richness (Denslow 1980, Stone and Wolfe 1996, Campetella *et al.* 2004, Decocq *et al.* 2004).

As emphasised by several authors (*e.g.* Franklin 1982, Metzger and Schultz 1984, Peet and Christensen 1988, Decocq *et al.* 2004), species diversity increases to a peak shortly after disturbance and declines under closed canopy in the subsequent part of regenerative process, up to values which approximate the mean species number per plot. This trend seems to be a general pattern in temperate forests (Bormann and Likens 1979, Roberts and Gilliam 1995, Howard and Lee 2003).

From an ecological point of view, floristic successional change related to coppice management does not follow a linear gradient, but rather, a cycling process (Fig. 1), in which the different species groups peak in different phases of the regenerative cycle. This is consistent with the findings of Aubert *et al.* (2003) and Bartha *et al.* (2008). After logging fringe species are the most frequent ones, followed by generalists, (presenting their minimum percent value of the whole regenerative cycle), and transient species, (which in turn are present in their highest value). Transient species, generally showing low frequencies (less than 5% in the study area), spread rapidly throughout forest undergrowth by means of the local seed-bank or the seed-rain from the surrounding landscape, as a result of tree felling and the consequent increase of light at the soil level (Grime 2001). As the regenerative process goes on (9–16 years after logging), fringe and transient species decrease, while generalist species increase and drained soil niche forest ones reach their peak. Drained soil species peak is probably due to the high level of solar radiation hitting the soil, which increases evapotranspiration rate, and to soil dryness, especially on shallow soils and steep slopes. Furthermore, 17–24 years after logging, full light, half-shadow and dry soil niche species decrease their percent values with respect to the previous phase; transient species have almost completely disappeared, while shade-tolerant ones (generalist forest species) colonise the understory again, reaching the maximum value. Nutrient-rich and cool soil niche forest species show a slow increasing trend after coppicing, thus in accordance with that of late-successional species (Decocq and Hermy 2003), they may be considered as "ancient forest species" (Peterken 1974, Rackham 1980, Whitney and Foster 1988, Putman 1994). Hermy *et al.* (1999) defined this kind of species as preferring "fresh" and moist soils (avoiding both wet and dry sites) with intermediate pH and nitrogen availability. This could explain why, in the study area, they are related to the most deep, cool, moist and nitrogen-rich soils, associated with the most conservative morphologic conditions that could be considered as shelter niches. This hypothesis is strengthened by the presence of *Fagus sylvatica* L. subsp. *sylvatica* within this species group. As van der Warf (1991) and Nagaike *et al.* (2003) reported, cutting and coppicing cause a decline of *F. sylvatica* L. or *F. crenata* Blume and, probably, of all ancient forest species. In fact, as Bengtsson *et al.* (2000) affirm, not all species are equally affected by forestry; some species, primarily generalist, are often little or even positively affected, while others (specialist) are very sensitive to forestry disturbance and habitat fragmentation. In the submediterranean hop-hornbeam woods, the low number of specialist species is probably related to a too short forest time rotation. Moreover, these species are probably negatively affected by the summer drought period that takes place in submediterranean forest ecosystems (Orsomando and Catorci 2000), enhanced by the combination of canopy opening and high slope angle that in turn cause soil erosion.

6. CONCLUSIONS

The research pointed out that in *Ostrya carpinifolia* coppiced woods low species richness is related to stress factors (acid soil, high soil skeleton percentage), while high species richness is linked to high light intensity at the undergrowth level. The driving forces affecting floristic composition were light intensity (linked to regenerative phase and dominant tree layer cover) and soil chemical and physical features (acidity, total nitrogen content, presence/absence of outcropping rock or rock fragments). Indicator species analysis led to the identification of six species groups, each one characterized by homogeneous ecological behaviour.

Floristic successional change along a regeneration cycle turned out to follow an ecological cycling process characterized by cyclical occurrence/disappearance of species belonging to the six groups.

On the basis of the research results, in coppiced stands, species that do not tolerate shade, as well as half-shadow and dry soil niche species, occur after canopy disturbance, while shade tolerant species probably persist under standard trees, shrubs or neighbouring uncoppiced stands. Ancient forest species are restricted to shelter niches and have a low ability to colonise the forest understory again. Thus, it is possible to assume that the studied *Ostrya carpinifolia* woods could be considered as secondary forest ecosystems rising from mixed beech woods degradation, as hypothesized for other European countries (Piskernik 1985, Sercelj 1996). This hypothesis seems to be supported by historic studies on landscape evolution in central Apennines (Catorci *et al.* 2003).

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APPENDIX I. Indicator species analysis results. Only significant values (P <0.05) are reported. Maxgrp.: group identifier for group with maximum observed indicator value. Obs. I.V.: observed indicator value. P: proportion of randomized trials with indicator value equal to or exceeding the observed indicator value, $P = (1 + \text{number of runs} \geq \text{observed})/(1 + \text{number of randomized runs})$. Codes for environmental variable classes – see Table 1. Codes for species names – see APPENDIX II.

Species	Maxgrp.	Obs. I.V.	*P*	Species	Maxgrp.	Obs. I.V.	*P*
Ace mon	Light3	71.0	0.005	Lap com	Light1	50.0	0.005
Ace obt	Light4	53.8	0.033	Leu vul	Light1	50.0	0.006
Ace pse	Regen3	42.6	0.004	Lig vul	Regen1	50.0	0.022
Aju rep	Rock2	40.0	0.020	Lil cro	Rock1	53.1	0.027
Ara tur	Rock1	34.7	0.009	Lil mar	Nitr1	24.9	0.035
Arc min	Light1	50.0	0.006	Lon cap	Domtree1	61.4	0.018
Are ser	Light1	33.3	0.013	Lon xyl	Regen4	69.2	0.002
Asp acu	Rockfrag3	61.8	0.002	Lot cor	Light1	50.0	0.006
Asp qua	Rock1	51.5	0.000	Luz for	Light3	64.5	0.032
Bla per	Light1	33.3	0.015	Luz syl	Light5	58.0	0.041
Bra rup	Light3	79.8	0.002	Mel mel	Rock1	60.7	0.000
Bro ere	Light1	33.3	0.015	Mel uni	Regen4	49.7	0.042
Bro ram	Domtree1	42.9	0.007	Moe tri	Domtree1	28.6	0.015
Bug pur	Domtree1	61.4	0.001	Myo arv	Light1	33.3	0.015
Bun bul	Light3	50.4	0.028	Ost car	Domtree5	39.7	0.000
Bup pra	Light1	33.3	0.013	Pae ita	Rock1	15.0	0.029
Cam rap	Light1	49.6	0.009	Pic hie	Light1	66.7	0.001
Car bet	pH1	91.2	0.003	Pot mic	Rock1	22.9	0.011
Car gra	Rock1	45.3	0.000	Pru avi	Domtree1	45.5	0.022
Car hal	Rockfrag3	88.7	0.000	Pru mah	Domtree1	32.8	0.029
Car mac	Rock1	23.7	0.025	Pru spi	Light3	57.5	0.049
Cen ery	Light1	50.0	0.006	Pti str	Domtree1	45.6	0.006
Cep dam	Light4	45.7	0.047	Pul ape	Domtree1	54.8	0.005
Cep lon	Rock1	32.6	0.023	Pyr com	Domtree1	28.6	0.015
Cha pol	Light1	44.6	0.030	Que cer	pH1	75.1	0.002
Cir vul	Light1	33.3	0.015	Que ile	Light4	76.9	0.003
Cle vit	Domtree1	83.7	0.000	Ran bul	Light1	33.3	0.015
Cli vul	Domtree1	94.4	0.000	Ros arv	Rock2	67.1	0.040
Col arb	Domtree1	35.7	0.023	Ros can	Domtree1	52.8	0.006
Cor ave	Rock2	61.8	0.001	Rub ulm	Domtree1	42.9	0.008
Cor san	Domtree1	42.1	0.024	Rus acu	Light3	64.1	0.012
Cot tom	Rock1	22.9	0.011	San eur	Rock2	43.5	0.008
Cra mon	Domtree1	74.7	0.004	Sax rot	Rock1	30.0	0.001
Cre neg	Light1	50.0	0.007	Sca col	Light1	33.3	0.012
Cyc rep	Regen2	44.2	0.031	Sed cep	Light1	33.3	0.015
Dap lau	Regen3	33.5	0.034	Ses aut	Domtree1	44.6	0.014
Dau car	Light1	65.5	0.004	Ses nit	Rock1	61.2	0.003
Dig aus	Rock2	30.2	0.017	Sil alb	Light1	32.6	0.029
Eme eme	Domtree1	39.5	0.049	Sil ita	Regen4	65.6	0.015
Eup dul	Rockfrag3	68.5	0.002	Son asp	Light1	33.3	0.013
Fag syl	Rock2	34.9	0.034	Sor ari	Rock1	50.4	0.046
Fes het	Domtree1	43.6	0.039	Sor dom	Domtree1	62.8	0.003
Gal mol	Light1	33.3	0.015	Sta off	Light3	49.2	0.027
Ger col	Light1	33.3	0.015	Ste hol	Light3	65.9	0.001
Ger pur	Domtree1	42.9	0.009	Ste med	Light3	60.3	0.018
Ger rob	Light3	89.7	0.001	Tam com	Domtree1	66.4	0.006
Geu urb	Light3	71.2	0.006	Tan cor	Light3	41.7	0.049
Gle hir	Light3	48.1	0.020	Tan par	Light1	50.0	0.006
Hed hel	Regen3	56.0	0.002	Tor arv	Light1	33.3	0.015
Hel boc	Light3	79.7	0.001	Tri cam	Light1	50.0	0.006
Hel obs	Light1	33.3	0.011	Tri mol	Light1	33.3	0.015
Hie rac	Regen3	17.4	0.045	Tri och	Light1	31.4	0.035
Hyp per	Light1	64.9	0.002	Tri pra	Light1	49.0	0.009
Ile aqu	Regen4	30.9	0.004	Tri str	Domtree1	28.6	0.014
Inu con	Domtree1	16.7	0.044	Ver tha	Light1	33.3	0.015
Lac mur	Rock2	30.2	0.010	Vio deh	Light3	62.6	0.014
Lac ser	Light1	33.3	0.015	Vio rei	Rock2	51.2	0.021

APPENDIX II. Groups of species highlighted by indicator species analysis. In brackets abbreviations used in APPENDIX I are reported.

***Group I.* Species highlighted for light intensity class 1 and regenerative phase 1**: *Arabis sagittata* (Ara sag), *Arctium minus* (Arc min), *Arenaria serpyllifolia* (Are ser), *Blackstonia perfoliata* (Bla per), *Bromus erectus* (Bro ere), *Bupleurum praealtum* (Bup pra), *Campanula rapunculus* (Cam rap), *Centaurium erythraea* (Cen ery), *Chamaecytisus hirsutus* subsp. *polytrichus* (Cha pol), *Cirsium vulgare* (Cir vul), *Crepis neglecta* (Cre neg), *Dactylis glomerata* (Dac glo), *Daucus carota* (Dau car), *Galium mollugo* (Gal mol), *Geranium columbinum* (Ger col), *Helianthemum nummularium* subsp. *obscurum* (Hel obs), *Hypericum perforatum* (Hyp per), *Lactuca serriola* (Lac ser), *Lapsana communis* (Lap com), *Leucanthemum vulgare* (Leu vul), *Lotus corniculatus* (Lot cor), *Myosotis arvensis* (Myo arv), *Picris hieracioides* (Pic hie), *Ranunculus bulbosus* (Ran bul), *Scabiosa columbaria* (Sca col), *Silene alba* (Sil alb), *Sonchus asper* (Son asp), *Tanacetum parthenium* (Tan par), *Torilis arvensis* (Tor arv), *Trifolium campestre* (Tri cam), *Trifolium incarnatum* subsp. *molinerii* (Tri mol), *Trifolium ochroleucum* (Tri och), *Trifolium pratense* (Tri pra), *Verbascum thapsus* (Ver tha).

***Group II.* Species indicated for dominant tree layer cover class 1 and light intensity class 3**: *Acer campestre* (Ace cam), *Acer monspessulanum* (Ace mon), *Brachypodium rupestre* (Bra rup), *Bromus ramosus* (Bro ram), *Buglossoides purpurocaerulea* (Bug pur), *Bunium bulbocastanum* (Bun bul), *Campanula persicifolia* (Cam per), *Carex flacca* (Car fla), *Clematis vitalba* (Cle vit), *Clinopodium vulgare* (Cli vul), *Colutea arborescens* (Col arb), *Cotinus coggygria* (Cot cog), *Cornus sanguinea* (Cor san), *Crataegus monogyna* (Cra mon), *Cruciata laevipes* (Cru lae), *Cytisophyllum sessilifolium* (Cyt ses), *Dactylorhiza maculata* subsp. *fuchsii* (Dac fuc), *Galium aparine* (Gal apa), *Emerus majus* subsp. *emeroides* (Eme eme), *Euonymus europaeus* (Euo eur), *Festuca heterophylla* (Fes het), *Fragaria vesca* (Fra ves), *Geranium robertianum* subsp. *purpureum* (Ger pur), *Geranium robertianum* subsp. *robertianum* (Ger rob), *Geum urbanum* (Geu urb), *Glechoma hirsuta* (Gle hir), *Helleborus bocconei* (Hel boc), *Helleborus foetidus* (Hel foe), *Inula conyzae* (Inu con), *Juniperus communis* (Jun com). *Juniperus oxycedrus* (Jun oxy), *Ligustrum vulgare* (Lig vul), *Lonicera caprifolium* (Lon cap), *Luzula forsteri* (Luz for), *Malus sylvestris* (Mal syl), *Moehringia trinervia* (Moe tri), *Primula veris* subsp. *suaveolens* (Pri sua), *Prunus avium* (Pru avi), *Prunus mahaleb* (Pru mah), *Prunus spinosa* (Pru spi), *Ptilostemon strictum* (Pti str), *Pyrus communis* (Pyr com), *Rosa canina* s.l. (Ros can), *Rubus ulmifolius* (Rub ulm), *Ruscus aculeatus* (Rus acu), *Sesleria autumnalis* (Ses aut), *Sorbus domestica* (Sor dom), *Stachys officinalis* (Sta off), *Stellaria holostea* (Ste hol), *Stellaria media* (Ste med), *Tamus communis* (Tam com), *Tanacetum corymbosum* (Tan cor), *Trifolium striatum* (Tri str), *Veratrum nigrum* (Ver nig), *Veronica officinalis* (Ver off), *Viburnum lantana* (Vib lan), *Viola alba* subsp. *dehnhardtii* (Vio deh).

***Group III.* Species highlighted for outcropping rock class 2, rock fragments class 3 and total nitrogen content class 3**: *Ajuga reptans* (Aju rep), *Corylus avellana* (Cor ave), *Crataegus laevigata* (Cra lae), *Digitalis lutea* subsp. *australis* (Dig aus), *Euphorbia dulcis* (Eup dul), *Fagus sylvatica* (Fag syl), *Lactuca muralis* (Lac mur), *Lathyrus vernus* (Lat ver), *Primula vulgaris* (Pri vul), *Pulmonaria apennina* (Pul ape), *Rosa arvensis* (Ros arv), *Sanicula europaea* (San eur), *Viola reichenbachiana* (Vio rei).

***Group IV*. Species indicated for outcropping rock class 1 and total nitrogen content class 1**: *Arabis turrita* (Ara tur), *Asparagus acutifolius* (Asp acu), *Asplenium trichomanes* subsp. *quadrivalens* (Asp qua), *Cardamine graeca* (Car gra), *Carex halleriana* (Car hal), *Carex macrolepis* (Car mac), *Cephalanthera longifolia* (Cep lon), *Cotoneaster tomentosus* (Cot tom), *Lilium bulbiferum* subsp. *croceum* (Lil cro), *Lilium martagon* (Lil mar), *Lonicera etrusca* (Lon etr), *Melittis melissophyllum* (Mel mel), *Paeonia officinalis* subsp. *italica* (Pae ita), *Polypodium interjectum* (Pol int), *Potentilla micrantha* (Pot mic), *Saxifraga rotundifolia* (Sax rot), *Sesleria nitida* (Ses nit), *Sorbus aria* (Sor ari).

***Group V*. Species highlighted for pH class 1**: *Carpinus betulus* (Car bet), *Carex sylvatica* (Car syl), *Hieracium racemosum* (Hie rac), *Luzula sylvatica* (Luz syl), *Quercus cerris* (Que cer), *Sedum cepaea* (Sed cep).

***Group VI.* Species not indicated by ISA or highlighted for regenerative phases 2, 3 and 4, light intensity class 4 and dominant tree layer cover class 5**: *Acer opalus* subsp. *obtusatum* (Ace obt), *Acer platanoides* (Ace pla), *Acer pseudoplatanus* (Ace pse), *Allium pendulinum* (All pen), *Anemone apennina* (Ane ape), *Aremonia agrimonioides* (Are agr), *Asplenium onopteris* (Asp ono), *Brachypodium sylvaticum* (Bra syl), *Campanula trachelium* (Cam tra), *Carex digitata* (Car dig), *Castanea sativa* (Cas sat), *Cephalanthera damasonium* (Cep dam), *Cephalanthera rubra* (Cep rub), *Cornus mas* (Cor mas), *Cruciata glabra* (Cru gla), *Cyclamen repandum* (Cyc rep), *Daphne laureola* (Dap lau), *Epipactis helleborine* (Epi hel), *Euonymus latifolius* (Euo lat), *Euphorbia amygdaloides* (Eup amy), *Fraxinus excelsior* (Fra exc), *Fraxinus ornus* (Fra orn), *Galium odoratum* (Gal odo), *Hedera helix* (Hed hel), *Hepatica nobilis* (Hep nob), *Hieracium bifidum* (Hie bif), *Hieracium murorum* (Hie mur), *Hypericum montanum* (Hyp mon), *Ilex aquifolium* (Ile aqu), *Laburnum anagyroides* (Lab ana), *Lathyrus venetus* (Lat ven), *Lonicera xylosteum* (Lon xyl), *Melica uniflora* (Mel uni), *Mercurialis perennis* (Mer per), *Neottia nidus-avis* (Neo nid), *Ostrya carpinifolia* (Ost car), *Platanthera chlorantha* (Pla chl), *Poa nemoralis* (Poa nem), *Polypodium vulgare* (Pol vul), *Quercus ilex* (Que ile), *Quercus pubescens* s.l. (Que pub), *Scutellaria columnae* (Scu col), *Silene italica* (Sil ita), *Solidago virgaurea* (Sol vir), *Sorbus torminalis* (Sor tor), *Stellaria nemorum* (Ste nem), *Tilia platyphyllos* (Til pla).