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High resilience of plant species composition to coppice restoration – a chronosequence from the oak woodland of Gerolfing (Bavaria)

Hohe Resilienz der Pflanzenartenzusammensetzung gegenüber Stockausschlagsbetrieb – eine Chronosequenz aus dem Gerolfinger Eichenwald (Bayern)

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Abstract

In the oak forest of Gerolfing (near Ingolstadt, Germany), regular coppicing has been reintroduced after approximately 30 years of abandonment to enhance biodiversity and provide fuel to private households. Based on 42 vegetation plots in six strata (5-year harvesting intervals plus an untreated control) a chronosequence representing a full coppice cycle is studied using measurements of vegetation structure, light availability, topsoil chemistry and indicator species analysis.

Coppicing triggers a succession in forest structure and radiation regime. Canopy openings are filled with a dense shrub layer of resprouts after 10 years, which subsequently grow into a closed tree canopy, which reaches its maximum density 15–20 yrs after the cut. The succession appears to be loosely paralleled by increased soil phosphorus and potassium after cutting, but this pattern may be confounded by land-use legacies.

The reaction of understorey species composition is remarkably weak and noisy, with increased cover of dominant forest species and patches of ruderal species occurring shortly after the cutting, and very few target plant species of conservation interest. Despite imposing a distinct disturbance and succession of vegetation structure, coppicing as currently practiced in Gerolfing alters understorey community composition only inconspicuously and for a short time.

Keywords: conservation biology, coppice-with-standards, disturbance, forest herb layer, historical forest use, restoration

Erweiterte deutsche Zusammenfassung am Ende des Artikels

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1. Introduction

Biodiversity is a central component of sustainable forest management. There are two mainstream approaches to the conservation of forest species, communities and landscapes. The first and apparently dominant strategy is to allow natural processes untrammelled by human interference, as realised in wilderness areas, national parks and strict forest reserves (MÜLLER et al. 2010). The second, somewhat less frequently discussed approach, is to continue or emulate the traditional forest uses that could have given rise to the observed biodiversity patterns (RACKHAM 2001). The importance of historical legacies for understanding current ecosystems and devising efficient management has recently been stressed by FOSTER et al. (2003).

Coppicing, i.e. the repeated harvesting of woody shoots sprouting from tree stools, figures as the most important historical forest use in the long-inhabited lowland areas of Europe, which has left multiple legacies in the structure and composition of present-day forests (e.g. BUCKLEY 1992). Coppicing persists in a limited extent in some regions of Western, Eastern and Southern Europe, but has been almost completely abandoned during the 19th – 20th centuries throughout Central Europe. Thus, our knowledge about the specific biodiversity and dynamics of Central European coppices depends on few relic sites (REIF 1996, LUX 2000) and on abandonment studies that document changes after cessation of coppicing.

In a systematic review of 17 abandonment studies from temperate and submediterranean Europe, EWALD et al. (2017) showed that conversion to high forest regularly led to a decline in soil pH, but only rarely decreased nutrient concentrations or increased forest floor thickness. Significant vegetation responses included the decline of species richness, especially of heliophilous and oligotrophic (sometimes red-listed) understorey plants and the increase of Ellenberg nutrient values. Reports on the reaction of typical forest plants to coppice abandonment are contradictory: Thus, DEBUSCHE et al. (2001) reported an increase in Southern, but DECOQ et al. (2005) a decrease of typical forest plant species in Northern France. Likewise, BARTHA et al. (2008) found an increase, but GARADNAI (2010) a decline in beech forest specialist plants in the Italian Apennines. According to CAMPETELLA et al. (2016) abandonment effects on plant diversity depend on the scale considered.

Even fewer researchers have been able to study the effects of coppice restoration. In contrast to abandonment studies, these experiments cover only relatively short observation periods and initial effects of clearcutting (VILD et al. 2013, HÉDL et al. 2017, ŠIPOŠ et al. 2017) rather than long-term effects on coppice systems (cf. KWIATKOWSKA & WYSZOMIRSKI 1990).The prevailing finding is an initial increase of biodiversity mainly due to annual nutrient-demanding species (ruderals), while the species diversity and composition development over more than a decade remains virtually unknown.

The lack of long-term series can be partly overcome by taking chronosequences of coppice systems under operation. EWALD et al. (2017) reviewed 10 chronosequences from deciduous coppices in Europe. The rare chronosequences of soil conditions (COLIN-BELGRAND et al. 1996, RUBIO & ESCUDERO 2003, BRUCKMAN et al. 2011) demonstrated marked cyclical reactions of nutrient availability and humus quality (C/N-ratio), but not of organic matter. Studies of plant species composition and functional groups revealed a marked peak of species richness after cutting, that may include neophytes (RADTKE et al. 2013), followed by a gradual decline in older stages (BARTHA et al. 2008, CATORCI et al. 2011). CAMPETELLA et al. (2011) and CANULLO et al. (2011) showed the prominent role of sexually reproducing, short-lived transient ruderals in freshly-cut as opposed to clonally reproducing plants in mature coppice stands.

The oak forest at Gerolfing ("Gerolfinger Eichenwald") represents one of the rare examples where, after a period of abandonment, coppicing has been reintroduced successfully, and performed according to a long-term management plan up to the present day (HANSBAUER et al. 2015). After 25 years of more or less annual cutting of new parcels the full mosaic from fresh cut to mature regrowth has been restored and the second cutting cycle is about to start. This unique situation offers the chance to reconstruct a full chronosequence of vegetation succession and answer the following research questions: (1) How do understorey composition, diversity and importance of functional groups change through the coppice cycle? (2) Does the plant community composition converge to the mature stage during one cutting cycle?

2. Material and Methods

2.1 Study area

The "Gerolfinger Eichenwald" is situated near the village of Gerolfing, 7 km south-west of the city of Ingolstadt in Bavaria (Germany). It forms the northern part of a large area of floodplain forest accompanying the river Danube.

The following site description relates to the northern portion of the forest, which forms the object of the present study. Situated on a postglacial fluvial terrace, nutrient-rich pararendzina soils have developed from gravel overlain by ca. 30 cm of fluvial loam, both rich in carbonates owing to the catchment that extends to the Calcareous Alps (AUSSENDORF et al. 2002). The terrace has been beyond the reach of regular flooding since the middle Holocene (approx. 5000 BP, KLEINSCHNITZ & KROEMER 2003). According to the nearby gauge at Gerolfing, its surface is 3.48 m above the average groundwater table, which has risen to 50 cm below surface at the centennial floodwater of 1999 (INGOLSTÄDTER KOMMUNALBETRIEBE AÖR 2016). Fine scale variance in soil conditions can be attributed to the local absence of loam cover (natural levees deposited under high flow velocity, locally termed "Brennen") and microtopographical depressions (former flooding channels) approaching the groundwater.

The climate is temperate with 8.4 °C mean annual temperature (January: -1.5 °C, July: 17.7 °C), 740 mm annual precipitation (February: 41 mm, June: 96 mm) and suboceanic to subcontinental features with a thermal amplitude of 19.2 °C and pronounced summer peak in rainfall (reference period 1982–2012, AMBIWEB GMBH 2016).

As indicated by Bronze Age burial mounds, the study area represents an ancient cultural landscape (GABEL 1981). The modern mosaic of predominantly deciduous woodland and grassland is interpreted as a remnant of silvopastoralism, as indicated by several field names referring to goats, cattle, sheep and meadows ("Riedwiesen") as well as to groves ("Schachen") and coppice ("Stocket"). Coppice-with-standards management with *Quercus robur* as the dominant overstorey species is reported up to the 1950s. The oak forest served the local peasants as a source of building timber, fuelwood, pig mast, litter and fodder.

Until 1972 the forest was owned by the parish of Gerolfing, which then became a district of the city of Ingolstadt. Parish and city council had the right to use the overstorey, private beneficiaries ("Rechtler") to extract fuelwood. The latter rights were suspended by council rule and amended by granting private property in 1960. Private owners organized themselves in a cooperative, while the central part remained community/city land and was managed by the city forester under supervision of the state forest authority of Beilngries until 1995. Since then forest planning and management have been in the city forester's hands.

Conforming with the forest policy of the period, which regarded the legacy of multiple uses as deficient, post-war management plans were designed to convert coppice to more productive high forest. The 1977 inventory mentions the following tree species distribution: 22.7% *Quercus robur*, 11.9% *Ulmus* spp., 11.3% *Fraxinus excelsior*, 8.1% *Populus* hybrids, 7.6% *Populus alba*/×*canescens*, 3.7% *Acer pseudoplatanus*/*platanoides*, 2.6% *Tilia cordata*, 2% *Acer campestre*, and 1.4% *Carpinus betulus*.

The plan projected conversion to *Acer-Fraxinus-Tilia* stands on moist and maintenance of mixed oak stands on drier sites. In 1975 the forest was designated as water protection area. Three deep wells situated in the forest deliver drinking water from the lower groundwater story of karstic origin to the city. In 1977 it became legally protected as a landscape conservation area to secure recreation and natural scenery.

The natural history and biodiversity of the forest were studied by GABEL (1981) and BUSSLER (1994). The latter author identified the forest area as one of three outstanding Bavarian hotspots of dead wood-dwelling beetles, which comprise a remarkable number of endangered taxa and 11 virgin forest relics (BUSSLER 2010). He related this remarkable coleopteran diversity to the abundance of deadwood requisites and biotope trees and recommended to favour strong solitary overstorey trees, accumulate deadwood and leave bizarre trees with microstructures.

The revival of coppicing was induced by the wish to maintain the park-like structure for recreation as well as the diversity of tree species and thermophilous xylobionts. It was economically favoured by the revived interest of nearby locals in fuelwood, which they were willing to harvest manually. Thus, first experimental cuts were performed in the 1990s and in 2000, and the city forester issued the plan to reinstall a coppicing regime with cutting ca. every 25 yr. on 30 ha. In 2004, the regime was extended to 170 ha. Since then, yearly cuts were allocated to residents, giving rise to the present-day mosaic of developmental stages.

2.2 Sampling design

Vegetation plots were established in the study area in 2015 in order to capture compositional gradients related to stand disturbance and succession. Age of resprouts since coppicing was estimated from forestry records (roughly delimited on a 1:10.000 management plan) and divided into five strata of five-year intervals (0–5, 5–10, 10–15, 15–20 and 20–25 yr.). Seven plots per stratum were designated in the field by a team consisting of a vegetation scientist (J. Ewald) and a forester (H. Krenzler). Seven control plots without recent coppicing were randomly scattered across adjacent deciduous high forest. All 42 plots were marked with a *Robinia* pole and a magnet buried at ca. 30 cm depth. GPS coordinates were recorded using a Mobile Mapper 7 device. The spatial distribution of plots reflects the non-random cutting pattern of the last 25 years (Fig. 1), resulting in a clumping of plots belonging especially to the strata cut 10–15 and 15–20 years ago as well as the reference in the eastern study area, whereas strata cut 0–5, 5–10 and 20–25 years ago were somewhat more evenly distributed.

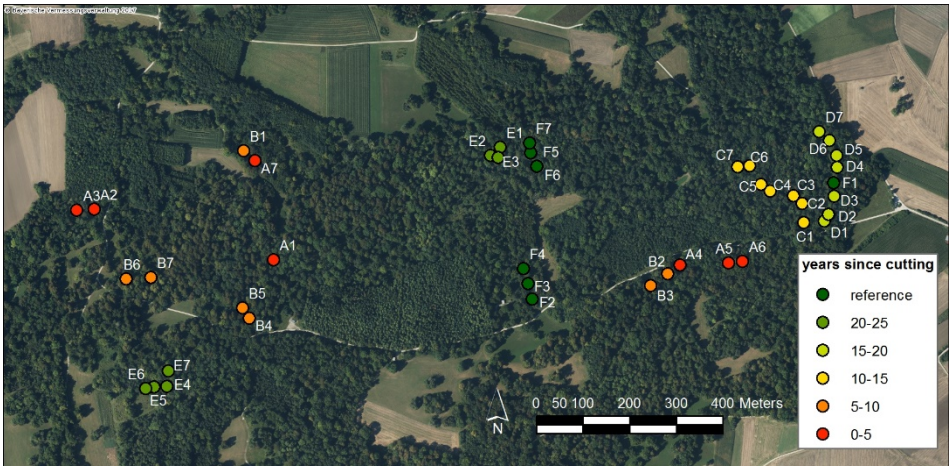

Fig. 1. Distribution of plots assigned to sampling strata defined by years since last cutting.

Abb. 1. Verteilung der Probeflächen mit Zuordnung zu den durch die Jahre seit dem letzten Holzeinschlag definierten Straten der Probenahme (Luftbild © Bayerische Vermessungsverwaltung).

2.3 Vegetation sampling and data editing

Circular 225 m² plots (r = 8.46 m) were laid out around the marked centre. Within the plot all vascular plant species were recorded, assigned to layers (moss, herb < 1 m, shrub 1 to 5 m, tree > 5 m height) and attributed cover values on the modified Braun-Blanquet scale according to WILMANNS (1998, 2m: <5% cover, >50 plant individuals, 2a: 5–15%, 2b: 15–25% cover). Composition and cover of spring geophytes was visually assessed on 23 and 24 March 2015. Full summer species composition and cover were recorded on 30 June and 1 July 2015 - at this date percentage total cover of the vertical layers was estimated visually. Nomenclature of plants follows WISSKIRCHEN & HAEUPLER (1998). Plot data were entered into a Turboveg 2 database (HENNEKENS & SCHAMINÉE 2001) using the German species list (JANSEN & DENGLER 2008). Before analyses, spring and summer data were pooled; in case the same species was recorded both in spring and summer in a plot, the higher of two cover values was taken.

2.4 Canopy shading sampling and analysis

Canopy shading was recorded by taking five hemispherical photographs (Canon Coolpix digital camera with fisheye lens mounted on a tripod one m above ground level) at the plot centre and 4 m to its north, east, south and west. Photos were analysed by Gap Light Analyser software (GLA 2.0, FRAZER et al. 1999) for canopy openness (in % of the fully opened canopy). The five values per plot were used for computation of average values entering statistical analyses.

2.5 Soil sampling and analysis

Soil properties (acidity and concentration of nitrogen, potassium and phosphorus) were measured in the upper 5 cm of the topsoil (after removing humus layers). Five cores were taken in a regular pattern from each plot, mixed and air dried at room temperature. After sieving to obtain < 2mm fraction, 42 soil samples were analysed in the Analytic Laboratory of the Institute of Botany, The Czech Academy of Sciences, in Brno. All units are mg kg^{-1}, except for soil acidity.

Soil acidity was measured in water suspension (pH-H_2O) following ZBÍRAL (1995). 5 ml of dry soil was diluted in 25 ml of demineralized water in a beaker, shaken for one hour, let sedimented for another hour and measured using a glass electrode.

Nitrogen was determined as extractable nitrates (NO_3^-) and ammonium (NH_4^+). 5 g of soil was shaken in 50 ml of 1M potassium chloride (KCl) solution in a polyethylene bottle for one hour and filtered. Phosphorus was determined as extractable orthophosphate (PO_4^{3-}). 5 g of soil was shaken in 100 ml of Olsen extracting solution for 30 minutes, filtered and measured. The choice of extracting solution was due to neutral soil acidity and calcareous character of analysed soils. Extraction methods followed HOUBA et al. (1988), ammonium and nitrate and phosphate contents were determined by continuous flow analysis (ISO 13395, ISO 15681–2) using Skalar SAN++ apparatus in an automated procedure.

Potassium was determined as exchangeable K^+. 10 g of soil was shaken in 100 ml of 0.01M calcium chloride ($CaCl_2$) for two hours. 60 ml of decanted extract was centrifuged and measured by using flame photometry (FIETZEK et al. 1972).

2.6 Data analysis

For each plot we counted species richness for the species groups as defined by SCHMIDT et al. (2011), see Table 1. We further computed unweighted average Ellenberg values for light, moisture and nitrogen (ELLENBERG et al. 2001). We compared strata by boxplots and Kruskal-Wallis tests (Statistica 7.1) of plot-related richness, cover and environmental variables.

We compared strata by measuring their compositional distances (Bray-Curtis distance after square-root transformation of cover) to untreated reference plots. We searched for diagnostic species limited to certain phases of the coppicing cycle using Multilevel Pattern Analysis (function multipatt in the R-Package indicspecies; DE CÁCERES et al. 2010, DE CÁCERES & JANSEN 2013, R-Version 2.15.2 R DEVELOPMENT CORE TEAM 2013). Significant indicator species were highlighted and sorted into groups of diagnostic species in a vegetation table (Supplement S1).

Table 1. Study variables; species group classification is after SCHMIDT et al. (2011).

Tabelle 1. Untersuchungsvariablen; Klassifizierung der Artengruppen nach SCHMIDT et al. (2011).

	name	Unit	min	mean	sd	Max
pH_H2O	soil pH in water	–	7.64	7.81	0.06	7.92
NH4	extractable soil ammonium	mg kg^{-1}	6.32	9.08	1.79	13.55
NO3	extractable soil nitrates	mg kg^{-1}	12.36	21.34	5.58	44.67
K_CaCl	exchangeable soil potassium	mg kg^{-1}	22.76	42.51	11.51	69.20
P_Olsen	exchangeable soil phosphorus	mg kg^{-1}	6.52	11.74	2.47	17.73
open_avg	canopy openness	%	3.61	12.35	7.69	37.06
Cov_tree	cover of tree layer	%	0.00	80.12	27.37	100.00
Cov_shr	cover of shrub layer	%	0.00	21.95	18.58	70.00
Cov_herb	cover of herb layer	%	10.00	42.38	22.15	95.00
Cov_moss	cover of moss layer	%	0.00	19.60	21.59	70.00
richn	understorey sp. richness		21.00	34.60	5.39	48.00
fs_tree	tree sp.	%	7.69	17.97	4.68	26.92
fs_1.1	strict forest sp.	%	20.59	34.77	7.02	50.00
fs_1.2	clearing sp.	%	0.00	4.22	2.85	9.68
fs_2.1	forest and open-land sp.	%	23.08	40.17	5.69	51.35
fs_2.2	open-land sp.	%	0.00	2.10	2.88	11.63
mL	mean Ellenberg light value for plots	–	4.36	4.96	0.27	5.66
mN	mean Ellenberg nutrient value for plots	–	5.52	5.88	0.23	6.43

To assess confounding by spatial structure, we partitioned the total amount of variation in the understorey data matrix into fractions representing spatial structure (GPS coordinates), soil parameters (nitrogen and phosphorus content), canopy structure (leaf area index), forest management (coppicing cycle) and their shared effect. This partitioning was performed by using (partial) Redundancy Analysis (BORCARD et al. 1992) and results were plotted as Venn diagrams. Spatial structure was numerically represented by geographic longitude and latitude of plot position and their square root transformation allowing identification of linear and non-linear trends.

3. Results

Soil conditions in plots were rather uniform with respect to pH, but varied considerably for potassium and both forms of nitrogen (Table 1). Phosphorus even showed significant differences between strata (Fig. 2c). However, all plots of stratum 15–20 yr. with the lowest P contents were concentrated at the eastern fringe of the study area. Apart from an increase of P under open canopies with dense herb layer, soil variables showed rather weak relationships with vegetation (Table 2). Stratum 15–20 had unusually low P and K concentrations (Fig. 2c), whereas stratum 20–25 stood out with elevated NH_4^+-concentrations (Fig. 2b).

As imposed by the sampling design, visually estimated tree cover was lowered to 0–75% in freshly cut plots, whereas it was close to 100% in advanced development stages (Supplement S1; relevé headers). Hemispherical photos reflected the chronosequence remarkably closely, with canopy openness decreasing from average 23% after cutting to 5% in 15–20 yr.

Table 2. Correlation matrix of study variables (for definitions see Table 1); Pearson coefficients > |0.5| are shown in bold.

Tabelle 2. Korrelationsmatrix der Untersuchungsvariablen (Definitionen s. Tab. 1); Pearson-Koeffizienten > |0.5| sind in Fettdruck dargestellt.

	NH4	NO3	K_CaCl$_2$	P_Olsen	open_avg	Cov_tree	Cov_shr	Cov_herb	Cov_moss	richn	fs_tree	fs_1.1	fs_1.2	fs_2.1	fs_2.2	mL	mN
pH_H2O	-0.36	-0.38	-0.06	-0.24	0.16	-0.09	-0.14	0.18	-0.17	0.03	0.24	-0.21	0.11	0.03	-0.12	0.01	-0.21
NH4		0.33	0.49	0.21	0.08	0.06	-0.15	-0.12	-0.29	-0.01	**-0.53**	0.22	0.29	-0.06	0.05	-0.15	0.06
NO3			0.48	0.39	0.24	-0.12	0.13	0.27	-0.07	-0.03	-0.46	0.02	0.30	0.11	0.10	0.09	0.38
K_CaCl$_2$				**0.55**	0.37	-0.36	0.06	0.30	-0.46	0.13	-0.31	-0.20	0.37	0.22	0.24	0.14	0.02
P_Olsen					**0.64**	**-0.62**	0.36	**0.56**	-0.15	0.23	-0.39	-0.39	0.41	0.45	0.34	0.43	0.15
open_avg						**-0.71**	0.00	**0.80**	-0.42	0.32	-0.23	-0.41	0.42	0.42	0.02	0.33	0.23
Cov_tree							-0.26	**-0.58**	0.38	-0.43	0.09	0.44	-0.38	-0.32	-0.26	-0.48	-0.07
Cov_shr								0.16	-0.05	0.25	-0.09	-0.49	0.21	0.34	**0.60**	**0.65**	-0.12
Cov_herb									-0.20	0.39	-0.19	-0.43	0.31	0.46	0.02	0.40	0.23
Cov_moss										-0.19	0.00	0.32	-0.22	-0.23	-0.12	-0.18	0.14
richn											-0.22	**-0.51**	0.11	**0.55**	0.27	**0.54**	-0.24
fs_tree												0.01	-0.45	-0.43	-0.12	-0.15	-0.17
fs_1.1													-0.47	**-0.71**	**-0.53**	**-0.84**	0.37
fs_1.2														0.25	0.25	0.42	-0.03
fs_2.1															0.14	**0.58**	-0.18
fs_2.2																**0.71**	-0.26
mL																	-0.28

old plots; after 20–25 yr. canopy openness rose slightly to 10%, corresponding to the reference stands (Fig. 2a). Herb layer cover peaked at ca. 80% in freshly cut plots and was minimal in 15–20 yr. old cuts (Fig. 3a). Shrub cover peaked 5–10 (Fig. 3b), moss cover 10–15 yr. after cutting. Understory richness of plots was quite variable within strata, with a weak and insignificant minimum in 15–20 yr. old regrowth (Fig. 3c). The proportion of strict forest species reached 30–50% in older stands and was conspicuously lowered up to 10 yr. after cutting (Fig. 3d), while mean Ellenberg light values exhibited the complementary pattern (Fig. 3e). Mean Ellenberg nutrient values varied mostly within the eutrophic range according to EWALD & ZICHE (2017), mesotrophic plots were mostly found in 5–10 yr. old cuts and reference stands, however, differences between strata were not significant (Fig. 3f).

The tree layer of the plots (Supplement S1) was diverse, with *Corylus avellana* as the most frequent woody species, and appeared transitional between *Carpinion* (*Tilia cordata*, *Carpinus betulus*), *Alno-Ulmion* (*Ulmus minor*, *Populus alba*), and *Tilio-Acerion* (*Acer pseudoplatanus*). The most important tree species *Fraxinus excelsior*, *Acer campestre* and *Quercus robur* have affinities to several of these alliances. Under the tree layer a remarkably diverse shrub community with dominant *Lonicera xylosteum*, *Cornus sanguinea*, *C. mas* and *Ligustrum vulgare* was developed. The herb layer consisted of an equally diverse (Fig. 3c) matrix of mesophytic and hygrophytic forest herbs and graminoids equally distributed across all sampling strata.

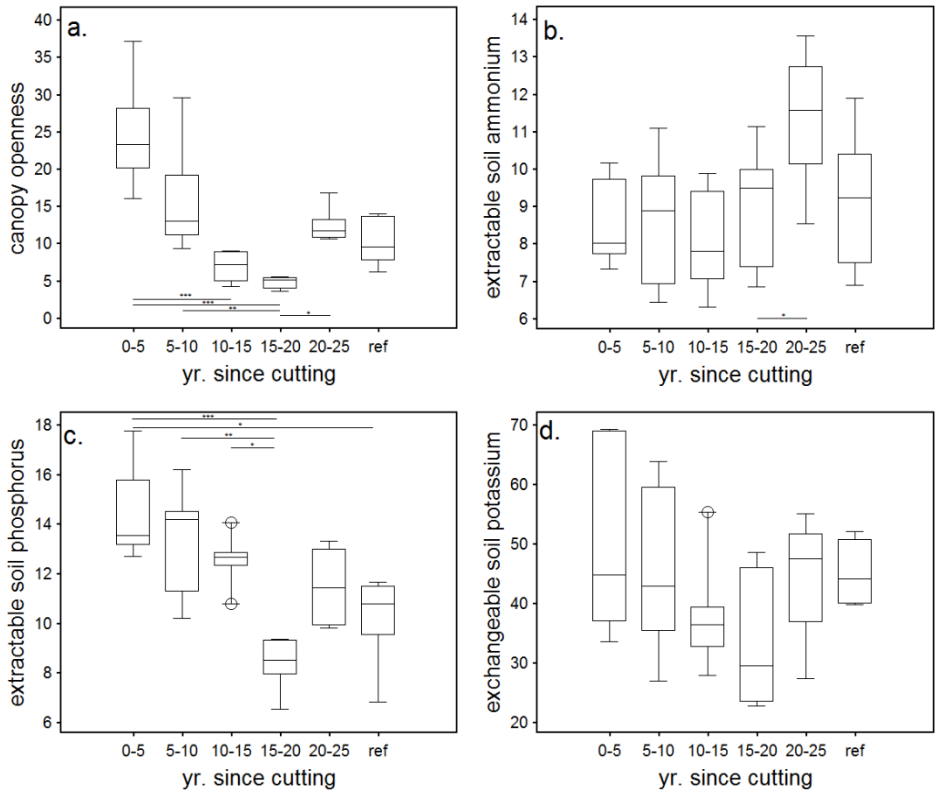

Fig. 2. Boxplots (box: 25–75% percentile, whiskers: 5 and 95% percentile, circle: outlier outside 1.5 interquartile range) of environmental variables measured in five coppicing strata and reference; variable definitions are in Tab. 1; pairwise significant differences according to Kruskall-Wallis test are indicated by horizontal lines; p-levels * <0.05, ** <0.01, *** <0.001.

Abb. 2. Boxplots (Box: 25–75 % Perzentil, Antenne: 5 und 95 % Perzentil, Kreis: Ausreißer außerhalb des 1.5 Interquartilranges) von Umweltvariablen gemessen in fünf Stockausschlagsbetriebs-Straten und ungenutzter Referenz; Variblendefinitionen s. Tabelle 1; paarweise signifikante Differenzen entsprechend Kruskall-Wallis-Test sind durch horizontale Linien gekennzeichnet; Signifikanzniveaus *p* * <0,05; ** <0,01; *** <0,001.

Bray-Curtis distances to reference plots ranged between 0.22 and 0.61 (Fig. 4). Plots that had been coppiced 5–10 yrs. ago tended to be most dissimilar from untreated reference plots ($z = 5.24$, $p < 0.001$). Freshly coppiced plots were less dissimilar, but still significantly different from the reference ($z = 3.20$, $p = 0.02$). Compositional distances of older stands did not differ from those within the group of reference plots.

The first section of Supplement S1 shows the structure of the diverse tree layer and its rejuvenation: *Fraxinus excelsior*, *Tilia cordata*, *Acer campestre* and *Quercus robur* form the canopy matrix, in which a remarkable variety of other tree species persist. The second table section highlights quantitative (cover-based) and qualitative (presence-absence-based) diagnostic understorey species with their respective indicator values and significance levels.

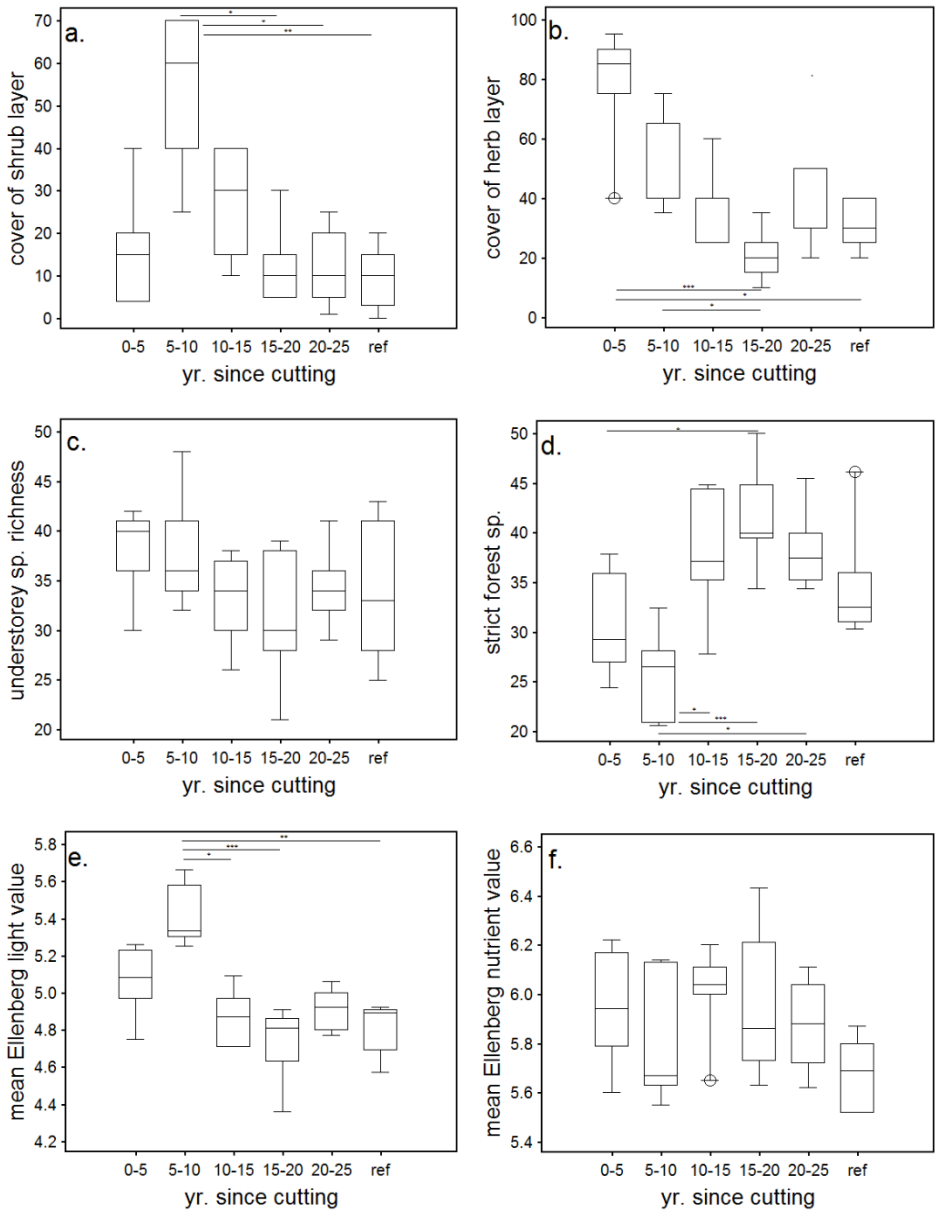

Fig. 3. Boxplots (definitions see Fig. 2) of vegetation variables observed in strata; variable definitions in Tabele 1; pairwise significant differences according to Kruskall-Wallis-test indicated by horizontal lines and p-levels * <0.05, ** <0.01, *** <0.001.

Abb. 3. Boxplots (Definitionen s. Abb. 2) von in den Straten beobachteten Vegetationsvariablen; Variablendefinitionen s. Tabelle 1; paarweise signifikante Differenzen entsprechend Kruskall-Wallis-Test sind durch horizontale Linien gekennzeichnet; Signifikanzniveaus *p* * <0,05; ** <0,01; *** <0,001.

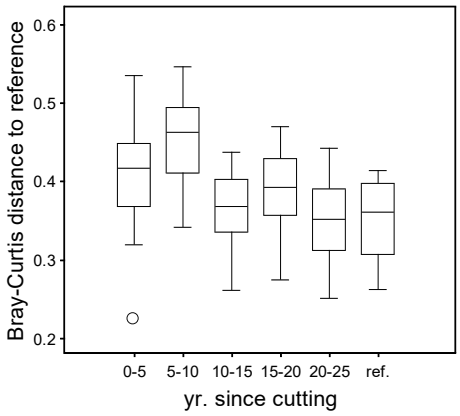

Fig. 4. Boxplot of pairwise compositional Bray-Curtis distances between coppiced plots and untreated reference plots.

Abb. 4. Boxplot der paarweisen kompositorischen Bry-Curtus-Distanzen zwischen Flächen mit Stockausschlagsbetrieb und unbehandelten Flächen.

The highest number of unique diagnostic species were found in 5–10 yr. old cuts and comprised resprouts and rejuvenation of the shrubs *Rhamnus cathartica* and *Frangula alnus*, the forest fringe herbs *Fragaria vesca* and *Solidago gigantea* (a neophyte of North-American origin) as well as the meadow herbs *Lathyrus pratensis* and *Galium album*. Freshly cut plots were characterized by *Sanicula europaea* and *Galium aparine*. With *Anemone ranunculoides* and *Allium ursinum* 15–20 yr. old cuts (all situated at the eastern fringe of the study area, Fig. 1) were the only older stratum with unique diagnostic species.

We found 12 additional understorey species significantly diagnostic of more than one stratum (Supplement S1). Only one of them, *Populus tremula*, linked two temporally non-contiguous strata. The others characterized various segments of the successional cycle, ranging from *Ajuga reptans* and *Carpinus betulus* rejuvenation as species linking reference and freshly-cut plots, through species like *Convallaria majalis*, *Deschampsia cespitosa*, *Elymus caninus* and *Cornus mas* rejuvenation that were only missing in the thicket phase of plots cut 10 to 20 years ago, to *Glechoma hederacea* and highly covering *Aegopodium podagraria* that were only absent from the untreated reference. *Polygonatum multiflorum* was the only species diagnostic of closed canopy stands, that was absent from freshly-cut plots.

We found more diagnostic species groups for freshly-cut (eight and six groups, respectively) and reference (nine) than for regenerated coppices (five each). In summary, freshly cut plots had larger numbers of diagnostic species (14 for 5–10 and 12 for 0–5 yr. old cuts) than the reference (nine) and regenerated coppices (eight species each).

According to Redundancy Analysis (RDA) spatial position, soil nutrient content and time since last coppicing explained 19.6% (canopy openness 18.6%) of the total variance in understorey composition (Fig. 5). The bulk of explained variation was attributable to unique predictor groups, with only moderate joint prediction by coppicing and nutrients (6.8%) and canopy structure and space (4.4% of explained variance). Most of the compositional variability was attributable to plot layout, i.e. spatial position in the study area. However, the spatial structure in species composition overlapped only weakly with the one induced by

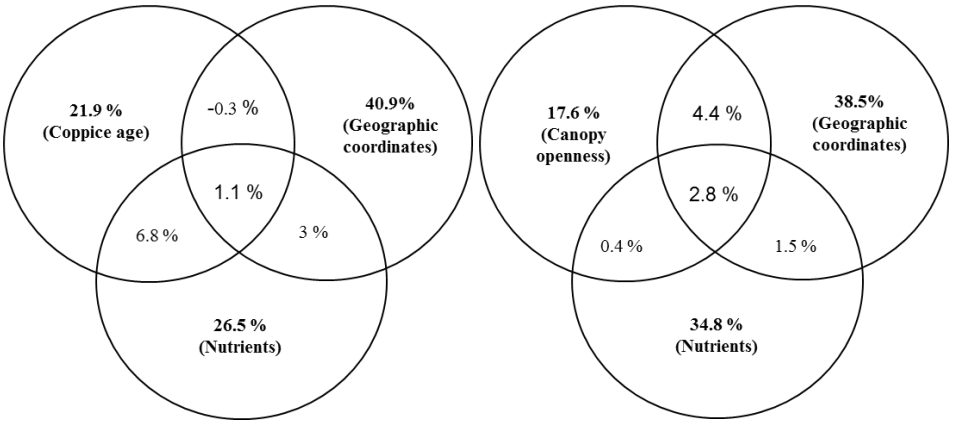

Fig. 5. Venn diagrams of explained variance attributable to unique and shared effects of predictor groups space (geographic coordinates), nutrients (soil conditions) and canopy openness.

Abb. 5. Venn-Diagramme erklärter Varianz, die einzelnen und gemeinsamen Effekten der Prediktorgruppen geographische Koordinaten (Raum), Nährstoffe (Bodenbedingungen) und Beschirmung zuzuordnen ist.

nutrients and canopy openness and almost not at all with coppicing age. Both in terms of total explanation and partial contribution, time since coppicing appeared to slightly be superior to canopy structure observed in the year of sampling.

4. Discussion

Besides monitoring on permanent plots and experiments, chronosequences are an obvious approach to study cyclical vegetation succession induced by silvicultural regimes. Considering their particular suitability, it is surprising that EWALD et al. (2017) found only nine chronosequence studies from coppice systems, mostly from southern European *Fagus* (BARTHA et al. 2008, CAMPETELLA et al. 2011, CANULLO et al. 2011), *Ostrya* (CATORCI et al. 2011, 2012, RADTKE et al. 2013) and *Castanea* coppices (COLIN-BELGRAND et al. 1996, RUBIO & ESCUDERO 2003). To our knowledge, the present study is the first complete chronosequence performed in a system where coppicing has recently been restored to promote biodiversity.

The reintroduction of coppicing has opened transient canopy gaps to which vegetation structure has reacted closely by the development of a dense herb and, with a time lag of ca. 5 yr., shrub layer. Structural changes can be interpreted as a relay played out in a competitive hierarchy of deterministic top-down control (cf. SHIPLEY & KEDDY 1994): The impact of tree removal translates into an immediate reaction of the herb layer; five years later resprouts and saplings form a dense shrub layer, which in turn initiates the decline of the herb layer, which goes through a minimum in 10–20 yr. old thickets. After 15 yr. the bulk of woody regrowth has reached the tree layer or declined through self-thinning, and the shrub layer reaches its minimum. Beyond 20 yr. mature coppices approach the structure of a gothic hall, under which the cover of the herb (Fig. 3b), but not of the shrub layer (Fig. 3a) recovers from the suppression of the thicket phase.

Concentrations of extractable phosphorus, and to a lesser extent potassium, appeared to be clearly related to the coppicing cycle. The lowest P and K concentrations were recorded in 15–20 yr. old regrowth, while the highest values occurred in freshly cut plots. This measured pattern would support results based on plant indicator values from other European chronosequences as reviewed by EWALD et al. (2017), but is not paralleled by a corresponding pattern in indicator values in Gerolfing. On the other hand, the 15–20 yr. stratum stands out by its spatial position close to the eastern fringe of the forest (Fig. 1), where it currently borders a remnant of oligotrophic calcareous grassland. Thus, low P supply may in this case be a legacy of extractive former land-use or caused by some other spatially autocorrelated factor in the physical environment. This uncertainty of causal attribution demonstrates the problem imposed by an imperfect spatially clumped design as is typical of observations based in "found experiments" in nature conservation (SAGARIN & PAUCHARD 2012). However, as variance partitioning (Fig. 5) showed small overlap between compositional variation attributable to spatial position and ecological factors, spatial autocorrelation is unlikely to confound the main findings of our study.

Plant species composition reflects the high resilience of the system by returning to the pre-disturbance state within 10 yr. Two conditions in Gerolfing are favourable to the fast regeneration of the forest: Water and nutrient supply are reliable and high tree species richness buffers for local dieback of stools. In terms of structure and productivity, the system appears highly sustainable. Besides, although closely following changes in canopy structure, the forest understorey community in Gerolfing is remarkably robust against disturbances. The dominant forest species react with an increase in cover and are merely joined by a loose and highly transient flock of ruderals – thus, the resource pulse reaching the forest floor seems to be partitioned between resident (usually clonal and perennial) and transient (often sexual and short-lived) plant species (EWALD et al. 2017). Similar unspectacular regeneration cycles have been reported from *Fagus sylvatica* coppices in the Apennines (BARTHA et al. 2008, CAMPETELLA et al. 2011, CANULLO et al. 2017) and in unsalvaged windfalls in Bavarian Forest National Park (FISCHER & FISCHER 2009). DECOCQ et al. (2005) even found that many so-called "true forest plants" thrived better in coppice woodlands than in comparable high forests in France, which they interpreted as the result of many centuries of co-adaptation. CERVELLINI et al. (2017) argue that human interest in a regular harvest of fuel crops and the requirements of forest plant specialists largely overlap. Thus, like other coppice-with-standards forests the intermediate disturbance regime, or in other words the balance between dominance reduction (WOHLGEMUTH et al. 2002) and habitat continuity (KRIEBITZSCH et al. 2013), in Gerolfing is very favourable to the maintenance of vascular plant species diversity.

Mesic and nutrient-rich conditions as well as the resulting vigour of the shrub and tree layer in the Gerolfing forest are not favourable to endangered, oligotrophic and light-demanding species that are among the principal targets of conservation-oriented coppicing (e. g. VILD et al. 2013). Except for *Ulmus minor* (distributed across strata, red-listed due to its decline caused by Dutch elm disease), two occurrences of *Carex tomentosa* (light-demanding) on freshly cut plots and one occurrence of *Carex cespitosa* (oligotrophic, light-demanding) in a freshly cut plot in vicinity to an oxbow wetland, no endangered plant species (cf. SCHEUERER & AHLMER 2002) were recorded in the forest (Table 3), although the pool of species is present in adjacent calcareous grassland, oligotrophic meadows and fringes (as documented by biotope mapping).

Table 3. Endangered, oligotrophic (Ellenberg N-value ≤ 4) and light-demanding (Ellenberg L-value ≥ 6) plant species; d strata: diagnostic status for sampling strata according to Supplement S1.

Tabelle 3. Gefährdete oligotraphente (Ellenberg-N-Wert ≤ 4) und lichtbedürtige (Ellenberg-L-Wert ≥ 6) Pflanzenarten; d Strata: Diagrnostische Artengruppen für Straten der Probenahme entsprechend Beilage S1.

	red list status	N-value	L-value	d strata
Ulmus minor	endangered	X	X	
Carex tomentosa	endangered	X	7	d0–10
Carex cespitosa	endangered	4	6	
Carex flacca	-	1	7	d5–10
Ligustrum vulgare	-	3	7	-
Berberis vulgaris	-	3	7	-
Vincetoxicum hirundinaria	-	3	6	d0–10
Deschampsia cespitosa	-	3	6	
Crataegus monogyna	-	4	7	
Viburnum lantana	-	4	7	d0–10
Rhamnus cathartica	-	4	7	d5–10
Angelica sylvestris	-	4	7	
Hypericum perforatum	-	4	7	
Cornus mas	-	4	6	

According to their Ellenberg values for nitrogen and light, 12 species, half of them shrubs, can be regarded as oligotrophic and light-demanding by broad standards (only *Carex flacca*, *Ligustrum vulgare* and *Berberis vulgaris* fulfil strict criteria, Table 3). Five of them were identified as diagnostic for fresh cuts in Supplement S1. This concentration is clearly reflected in elevated mean light values, but not in lower nitrogen values in freshly cut strata (Fig. 4). Therefore, our results do not contradict positive effects on the target groups, but these are too small and noisy to be significant.

While the reintroduction of coppicing has caused the expected changes in light conditions and has initiated a succession of vegetation structure, the floristic succession associated with it – slight reduction in cover of dominant forest herbs, transient appearance of ruderals and few oligotrophic, light-demanding plant species – remains remarkably indistinct. This weakness of floristic patterns may be associated with the local practice of protecting fresh resprouts from sunburn and roe deer browsing by covering up the stools with leftover branches, which reduces nutrient export, excess nitrification and germination of ruderals (Fig. 6). When combined with limited skidding by tractors, this practice bears resemblance to unsalvaged windthrows in the Bavarian Forest, where FISCHER & FISCHER (2009) found a negligible development of ruderals. Such a moderate version of clearcutting leaves the understory community intact and allows only few species of open habitats. Conversely, we have to conclude that former management practices that favoured a rich oligotrophic, light demanding flora, that can be still be found along forest margins and in adjacent meadows must have involved additional interventions such as extraction of twigs, grass and herbage by forest grazing, mowing or litter raking. In addition, the replacement of extracted nitrogen from atmospheric deposition may balance nutrient extraction.

Fig. 6. Spring aspect of a coppice-with-standards stand cut the previous year (stratum A); piles of leftover branches protect stools from sunburn and game browsing; fuelwood pile in the background (Photo: J. Ewald, March 2015).

Abb. 6. Frühlingsaspekt eines im vorherigen Jahr geschlagenen Mittelwalds (Stratum A); Stapel übrig gelassener Äste schützen Stöcke vor Sonnenbrand und Wildverbiss; Feuerholzstapel im Hintergrund. (Foto: J. Ewald, März 2015).

Erweiterte deutsche Zusammenfassung

Einleitung – Die Biodiversität der mitteleuropäischen Wälder wird durch natürliche Prozesse, aber auch durch jahrhundertelange Nutzungen geprägt. Vor diesem Hintergrund gewinnen die Erhaltung, Wiedereinführung und Nachahmung traditioneller Nutzungen im Waldnaturschutz an Bedeutung. Im Gerolfinger Eichenwald bei Ingolstadt (Bayern) wurde der Stockausschlagbetrieb nach ca. 30 Jahren Überführung in Hochwald wiedereingeführt. In der vorliegenden Studie werden die Auswirkungen dieser Maßnahmen auf die Biodiversität der Gefäßpflanzen untersucht.

Material und Methoden – In dem seit 25 Jahren als Mittelwald genutzten Waldgebiet wurde eine Chronosequenz angelegt, indem fünf Altersklassen zu je fünf Jahren (0–5 bis 20–25 Jahre nach letzter Nutzung) und eine ungenutzte Referenz (im Folgenden als Straten bezeichnet) mit je 7 Vegetationsaufnahmen nach Braun-Blanquet (separate Erfassung der Frühjahrsephemeren im März) erfasst wurden. In jeder Aufnahmefläche wurden an Bodenproben pH-Werte und Gehalte an pflanzenverfügbarem N, P und K gemessen, Kronenschlussgrad mittels Hemisphärenphotos gemessen und Gesamtdeckungen der Schichten visuell geschätzt. Aus den Vegetationsaufnahmen wurden für die Bodenvegetation die Artenzahl der Gefäßpflanzen, der Anteil der Waldartengruppen nach SCHMIDT et al. (2011) an der Artenzahl und die mittleren Ellenberg-Zeigerwerte für Licht und Nährstoffe berechnet.

Die Vegetationsaufnahmen wurden nach Straten, Schichten und Trennartengruppen der Straten manuell sortiert. Die Ausprägung der Prüfvariablen in den Straten wurden mittels Boxplots und Wilcoxon-Test verglichen.

Ergebnisse – Die Verteilung der Aufnahmen im Gebiet folgte dem Hiebsmuster und wies deshalb gewisse räumliche Klumpungen (räumliche Autokorrelation) innerhalb von Straten auf. Die Eingriffe in den Baumbestand spiegelten sich deutlich in der Kronendichte wider. Sie sank durch Sukzession der Gehölzschichten nach dem Hieb von 25 % auf 5 % und erreichte nach 20 Jahren mit 10 % das Niveau

ungenutzter Referenzflächen. Unter den Nährstoffen wies nur der extrahierbare Phosphor im Schlagzyklus eine deutliche absteigende Tendenz auf, wobei ein Einfluss früherer Landnutzung nicht ausgeschlossen werden konnte.

In den ersten fünf Jahren erreichten die Krautschicht (85 %), im anschließenden Fünfjahreszeitraum die aufwachsende Strauchschicht (60 %) ihr Deckungsmaximum, um in der Folge auf Werte um 20–30 bzw. 10 % zurückzugehen. Während die Gesamtartenzahlen und mittlere Nährstoffzahlen über alle Straten hinweg variierten, reagierten der Anteil streng an Wald gebundener Arten und die Ellenberg-Lichtzahl deutlich auf die Hiebe. Gegen die Referenzbestände war die Artenzusammensetzung nur in den ersten 10 Jahren signifikant verändert. Diese Unterschiede bestanden in erster Linie in einer vorübergehenden Deckungszunahme bereits vorhandener Waldarten, während in der pflanzensoziologischen Tabelle nur wenige, überwiegend ruderale Trennarten für die frühen Stadien identifiziert wurden. Für den botanischen Artenschutz interessante gefährdete Licht-, Wärme und Magerkeitszeiger wurden nur ganz vereinzelt in frischen Hiebsflächen festgestellt, obwohl in der Umgebung entsprechende Offenlandbiotope vorhanden waren.

Diskussion – Chronosequenzen sind gerade in Stockausschlagwäldern gut geeignet um den Einfluss von Störungen und zyklische Sukzessionsprozesse mit vertretbarem Aufwand darzustellen. Da es nur noch wenige funktionierende Mittelwaldsysteme gibt, haben solche Studien eine hohe Bedeutung. Während im Mittelwaldsystem von Gerolfing die quantitativen Strukturgrößen Kronenschluss und Schichtdeckung direkt durch den Schlagzyklus gesteuert werden, unterliegen qualitative Indikatoren wie Artenzahl und Artenzusammensetzung innerhalb der Straten so großen Schwankungen, dass ihre Reaktion schwach erscheint und wenig Raum für das Auftreten spezialisierter und seltener Arten lässt. In eutrophen Waldökosystemen wie dem Gerolfinger Eichenwald reicht die Mittelwaldnutzung nicht aus, um für den botanischen Artenschutz relevante Effekte zu erzielen. Die Naturschutzwirkung ist hier eher in der Erhaltung der Baumarten- und Strukturvielfalt sowie der davon abhängigen Lebensgemeinschaften zu sehen.

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Supplements

Supplement S1. Vegetation table sorted by the sampling strata and their diagnostic species.

Beilage S1. Vegetationstabelle, sortiert nach den Straten der Probenahme und ihren diagnostischen Arten.

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Supplement S1. Vegetation table sorted by the sampling strata and their diagnostic species; ; t1: upper tree layer, t2: lower tree layer, s: shrub layer, jl: juvenile tree or shrub, hl: herb layer, d: diagnostic species.

Beilage S1. Vegetationstabelle, sortiert nach den Straten der Probenahme und ihren diagnostischen Arten; ; t1: obere Baumschicht, t2: untere Baumschicht, s: Strauchschicht, jl: Baum- bzw. Strauchjungwuchs, hl: Krautschicht, d: diagnostische Art.

Strat_nr		indicator value		A1	A2	A3	A4	A5	A6	A7	B1	B2	B3	B4	B5	B6	B7	C1	C2	C3	C4	C5	C6	C7	D1	D2	D3	D4	D5	D6	D7	E1	E2	E3	E4	E5	E6	E7	F1	F2	F3	F4	F5	F6	F7	
Cover tree layer (%)		cover	p/a															30	30	100					35	20	15	100				30	50	100					20	30	90					
Cover shrub layer (%)				80	20	60					10	40	60	40	30	40	50	30	25	15	100	40	20	100	20	35	10	100	20	15	5	30	30	5	10	20	10	30	3	0	86	5	40	35	5	100
Cover herb layer (%)					75	40	0	90	40	95	40	40	33	35	40	75	65	40	40	40	90	40	25	95	70	20	50	100	10	25	20	50	85	50	50	25	1	20	3	20	2	15	100	25	15	100
Cover moss layer (%)				5	10	3	85	15	4	5	1	10	1	10	20	30	5	30	50	50	70	50	50	70	35	70	70	-1	20	1	1	30	5	10	10	-1	25	10	20	5	2	5	40	20	95	
Tree layer																																														
Corylus avellana	t2			.	.	.	1	1	.	.	1	.	3	1	1	.	.	5	4	4	.	2a	4	3	5	3	2b	4	4	4	4	4	3	4	4	5	3	5	+	4	4	3	4	4	1	3	33
Corylus avellana	s			1	+	1	1	1	.	+	4	3	4	2a	3	+	.	+	2a	.	.	.	.	.	.	.	.	1	.	.	+	.	.	+	.	.	1	.	+	1	.	.	.	1	1	1	23
Corylus avellana	jl			+	+	1	1	.	+	+	.	.	1	1	+	+	+	.	.	+	+	r	.	.	.	+	.	+	.	r	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	18
Fraxinus excelsior	t1			1	2a	.	.	.	2a	1	1	+	.	1	3	.	1	2a	2b	.	2a	2a	2a	2a	.	.	.	+	2a	2b	2a	2b	3	3	2b	2a	2a	2a	2a	.	.	2b	2a	3	1	31
Fraxinus excelsior	t2			1	2m	.	.	1	.	.	2m	.	.	.	.	+	1	.	.	+	.	1	.	.	.	1	1	.	.	1	.	.	.	.	.	.	2a	.	2a	.	.	.	.	.	.	.	13
Fraxinus excelsior	s			.	+	.	.	.	.	+	1	.	1	1	.	+	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	7
Fraxinus excelsior	jl			1	1	1	+	+	+	+	1	+	+	2a	2a	1	2a	+	+	1	+	+	+	+	1	2a	2m	1	1	+	+	+	+	+	+	1	+	1	1	1	1	+	1	1	1	+	41
Acer campestre	t1			2b	1	.	4	1	.	.	2b	1	3	2a	2a	1	2b	2b	1	.	.	.	.	.	2b	.	2a	2b	.	2a	2b	2b	+	2a	.	2m	.	.	2b	3	.	.	.	.	.	.	24
Acer campestre	t2			1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	+	.	.	.	.	1	1	.	6
Acer campestre	s			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	.	.	.	.	+	.	3
Acer campestre	jl			+	+	1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	r	+	r	+	1	+	+	+	1	+	+	+	+	+	+	+	+	+	+	1	+	+	+	+	+	1	42
Quercus robur	t1			r	3	.	.	.	3	.	1	3	.	+	2a	2a	3	.	.	+	.	.	.	.	.	1	.	3	1	2m	.	.	.	.	.	.	2a	.	1	.	.	.	.	.	1	.	17
Quercus robur	t2			.	2m	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	4
Quercus robur	s			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	r	.	.	.	.	.	.	.	.	2
Quercus robur	jl			.	r	.	.	r	r	.	+	r	+	.	r	.	r	r	r	.	r	r	.	r	r	r	.	r	.	.	.	.	.	r	r	.	.	.	r	r	r	.	.	+	.	23
Acer pseudoplatanus	t1			2b	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2b	.	.	.	2a	1	.	1	.	2a	.	.	.	.	.	.	.	.	2a	2b	.	.	.	3	.	2b	10
Acer pseudoplatanus	t2			.	.	.	.	.	.	.	.	.	.	.	.	.	1	2b	2b	.	4	4	1	2a	.	2a	3	2a	1	2a	.	.	.	.	2b	3	.	2b	+	.	.	.	.	1	.	17
Cornus sanguinea	t1			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	1
Cornus sanguinea	t2			.	.	.	.	.	1	.	.	1	1	.	.	.	.	1	1	+	.	.	1	1	.	1	.	.	.	.	.	1	2a	1	2b	1	.	.	.	.	3	.	.	.	.	.	15
Cornus sanguinea	s			.	2a	.	.	+	1	.	.	+	+	.	.	1	1	.	.	1	.	.	.	.	.	.	1	1	.	1	+	1	+	2m	.	.	.	.	.	.	.	.	.	+	1	2m	18
Cornus sanguinea	jl			.	2m	.	.	+	1	.	+	2a	+	+	.	+	1	+	+	+	.	.	+	+	.	+	+	+	+	+	+	+	+	+	+	1	+	.	.	r	.	.	+	.	r	.	28
Tilia cordata	t1			.	.	.	.	.	.	.	.	+	.	3	.	2b	2a	.	.	2a	.	2a	2b	.	2a	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	9
Tilia cordata	t2			.	2b	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2m	4
Tilia cordata	s			+	.	.	.	.	.	.	1	2a	2a	.	.	.	.	+	+	+	+	.	+	.	.	.	+	.	.	r	+	.	+	r	1	1	.	.	.	.	.	.	.	.	.	+	17
Tilia cordata	jl			+	+	1	+	+	r	r	1	+	1	.	+	.	+	.	r	+	+	r	.	+	r	r	.	.	r	.	r	.	+	+	.	+	+	.	.	+	+	.	.	.	r	+	29
Cornus mas	t2			.	2a	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	1	1	2a	.	.	.	.	.	.	.	.	2a	.	.	.	2m	.	3	.	.	.	8
Carpinus betulus	t1			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2a	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
Carpinus betulus	t2			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2b	3	.	2
Crataegus monogyna	t2			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2m	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	2
Crataegus monogyna	s			.	1	.	.	.	r	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1	6
Crataegus monogyna	jl			.	+	.	+	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	5
Crataegus species	t2			1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	2b	.	.	1	.	.	.	.	.	.	5
Crataegus species	s			.	.	.	.	.	.	r	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	1	1	.	.	+	.	.	.	.	r	+	.	8
Crataegus species	jl			+	.	+	.	+	.	+	+	+	+	+	+	.	.	+	+	+	+	+	+	+	+	.	+	+	+	+	+	r	r	+	+	r	.	+	+	+	+	r	.	r	.	33
Alnus incana	t1			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2a	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Alnus incana	t2			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Alnus incana	jl			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Malus sylvestris	t1			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	1
Malus sylvestris	t2			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	2b	2
Malus sylvestris	jl			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	2
Populus alba	t1			.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Populus alba	s			.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Populus alba	jl			.	+	.	.	.	1	.	.	.	.	.	.	.	.	+	r	r	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	7
Populus species	jl			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	1
Populus tremula	t1			.	.	.	.	.	2a	.	.	.	.	.	.	.	.	2a	.	2a	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	5
Populus tremula	t2			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1
Populus tremula	s			.	.	.	.	.	1	r	.	.	.	.	r	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4
Populus tremula	jl	0.749*	0.645*	.	.	.	.	+	+	r	.	.	.	.	.	.	.	.	.	r	.	.	.	.	+	.	.	r	+	r	+	.	.	.	.	.	.	.	.	.	.	+	.	.	.	10
Populus x canescens	t1			.	.	.	.	.	.	2b	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Pyrus pyraster	t1			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Salix caprea	t2			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1
Frangula alnus	t2			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	2
Tilia platyphyllos	s			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	1
Ulmus glabra	t2			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	1
Ulmus minor	t1			.	.	.	.	1	.	.	.	.	.	2m	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
Ulmus minor	t2			.	.	.	.	.	2b	.	.	.	.	.	.	.	.	.	.	.	1	.	2a	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	5
Ulmus minor	t2			.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Ulmus minor	jl			r	.	.	.	+	r	.	.	.	.	+	.	.	.	.	.	r	+	r	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	10
d reference + 0-5yr																																														
Ajuga reptans	hl	0.799**	0.761**	+	.	+	1	+	+	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	+	.	.	1	10
d 0-5yr																																														
Sanicula europaea	hl	0.779***	0.668*	.	r	r	.	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	r	r	.	.	.	8
Galium aparine	hl	0.700**	0.617*	.	.	r	+	.	+	r	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	6
d 10-reference + 0-5yr																																														
Viola mirabilis	hl	0.946*		+	+	+	.	+	r	+	+	r	+	.	.	.	.	+	+	+	+	+	+	+	+	+	.	r	+	r	r	+	+	+	+	+	+	+	+	+	.	+	+	+	1	35
d reference + 0-10yr																																														
Carpinus betulus	jl		0.619**	+	r	+	.	1	.	.	r	.	.	r	r	r	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	r	+	+	.	+	+	.	14
d 20-reference + 0-10yr																																														
Deschampsia cespitosa	hl	0.837*	0.829*	+	+	+	.	+	+	+	+	.	.	+	+	+	.	+	.	.	.	.	.	.	+	.	.	.	r	r	.	+	+	+	.	+	+	+	+	r	+	r	.	r	26
Cornus mas	s			.	2m	.	.	r	.	2a	1	.	.	2m	2a	1	2a	.	.	.	.	.	.	.	.	.	.	.	.	+	.	1	.	.	+	2a	.	+	.	1	.	2a	+	1	.	17
Cornus mas	jl	0.822*	0.793*	.	+	+	r	+	.	1	+	.	.	+	2a	1	+	.	.	.	.	.	.	.	r	.	+	.	.	+	.	r	.	.	.	.	.	.	.	.	+	+	.	.	.	16
d 5-10yr																																														
Rhamnus cathartica	s			.	.	.	.	.	.	.	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3
Rhamnus cathartica	jl	0.924***	0.717**	r	.	.	.	.	.	.	r	+	.	r	+	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	r	r	.	9
Fragaria vesca	hl			.	1	.	.	.	.	.	+	.	.	+	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	6
Solidago gigantea	hl	0.733**	0.676*	.	.	.	.	.	.	.	.	r	.	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	5
Lathyrus pratensis	hl	0.627*		r	.	.	.	.	.	.	+	.	+	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4
Galium album	hl	0.634*		.	.	.	.	.	.	.	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	4
Frangula alnus	s	0.655*	0.655*	.	.	.	.	.	.	.	+	+	2m	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3
d 20-reference + 0-15yr																																														
Convallaria majalis	hl	0.956***	0.942***	1	+	.	+	2b	1	2b	1	+	+	.	+	+	1	+	+	1	+	+	+	1	r	.	.	.	.	.	.	2b	+	3	1	1	1	+	.	1	1	1	+	1	1	33
Elymus caninus	hl	0.775*	0.775*	+	+	+	+	.	+	+	+	+	r	.	.	+	+	.	r	+	.	+	+	.	r	.	.	.	.	.	.	.	+	.	.	r	.	+	r	.	.	.	+	+	.	21
d reference + 0-20yr																																														
Acer pseudoplatanus	s			2a	3	.	.	.	+	.	+	.	.	4	2a	1	3	1	2a	1	2a	2a	2b	.	1	1	1	2m	1	+	+	.	.	.	.	1	.	.	+	.	.	1	.	.	.	24
Acer pseudoplatanus	jl	0.934*		2a	3	+	.	.	1	+	+	+	.	2b	2a	+	2b	+	1	1	1	1	+	+	+	+	+	+	.	+	.	.	+	.	.	.	.	+	+	1	1	3	2a	+	1	32
d 10-25yr + reference																																														
Polygonatum multiflorum	hl		0.655*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	+	r	.	r	.	.	.	+	.	r	r	r	.	.	r	r	.	.	.	.	r	12
d 15-20yr																																														
Anemone ranunculoides	hl	0.883**		.	.	.	.	+	+	.	.	+	.	.	.	.	.	.	+	.	.	+	.	+	1	+	+	+	+	.	+	.	.	.	.	.	+	.	+	.	.	.	.	.	.	14
Allium ursinum	hl	0.655*	0.655*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3
d 0-25yr																																														
Aegopodium podagraria	hl	0.97***		+	2a	4	4	1	2a	1	2a	2a	2a	1	1	1	3	2a	2a	2m	2a	2b	2a	3	1	+	.	.	+	1	+	2a	1	1	1	2a	1	2b	.	.	r	+	+	r	+	38
Glechoma hederacea	hl		0.88*	1	2m	2a	2b	+	2a	1	1	1	1	+	+	+	1	.	r	1	+	1	+	2a	+	+	.	.	+	.	+	+	.	+	.	+	1	+	.	.	.	.	+	+	.	31
Other understorey species																																														
Brachypodium sylvaticum	hl			2a	2a	2a	2a	+	3	3	1	+	1	1	+	2a	2a	+	+	1	+	+	2a	1	+	+	+	1	1	+	+	1	1	1	+	+	+	+	+	+	+	1	1	1	42
Primula elatior	hl			+	1	1	1	2a	1	1	+	+	1	1	+	+	+	2m	+	2a	+	2a	1	2a	1	+	2m	2a	+	1	1	2m	1	1	1	1	+	1	1	2m	1	1	1	1	2m	42
Scilla bifolia	hl			+	+	+	1	1	+	+	+	+	+	+	+	+	+	1	+	1	+	1	1	+	1	1	1	1	+	+	+	+	+	+	+	+	+	+	+	2	1	+	+	+	+	+	42
Carex alba	hl			2b	2m	1	+	+	3	1	2a	2b	2m	1	2b	+	2a	+	+	1	2b	1	1	1	+	2b	1	+	+	+	1	2m	1	2m	1	+	1	1	2a	1	+	2m	1	2a	2b	42
Pulmonaria obscura	hl			+	+	1	+	+	1	+	r	+	.	+	+	+	+	1	+	1	+	1	+	1	1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	.	+	+	1	40
Asarum europaeum	hl			+	+	1	1	1	1	+	1	+	1	1	+	.	2m	1	1	2a	1	2a	2a	2a	1	+	+	+	+	+	+	2m	+	1	1	+	2a	+	+	.	+	2a	+	+	1	40
Viola reichenbachiana ag.	hl			+	+	+	+	+	1	+	+	+	+	+	+	+	.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	1	+	+	+	+	+	+	+	.	+	+	+	+	+	40
Carex sylvatica	hl			+	1	1	+	.	1	+	+	+	+	.	+	.	+	2a	+	1	+	1	+	1	1	1	+	1	+	+	+	1	+	1	+	1	+	1	+	+	+	+	+	+	+	2m	39
Anemone nemorosa	hl			r	+	1	+	1	+	.	+	r	+	.	r	r	.	+	+	+	+	1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	.	r	+	1	+	+	+	+	+	38
Paris quadrifolia	hl			.	.	+	.	r	+	+	1	+	+	+	.	.	+	1	+	+	+	+	+	1	1	+	r	r	+	+	+	+	+	+	+	1	+	+	+	+	+	+	+	+	+	37
Lonicera xylosteum	s			2a	1	.	2a	.	2a	2a	2b	2a	2b	2m	1	1	2a	2b	1	3	+	2a	1	.	2a	1	2a	2b	1	2a	1	1	1	2m	+	2a	+	2a	+	.	.	2a	.	1	1	36
Lonicera xylosteum	jl			+	1	1	1	+	1	1	.	.	.	1	+	.	+	.	+	1	+	+	+	1	+	+	.	+	.	+	.	1	+	.	+	+	+	+	+	+	+	1	+	+	1	33
Geum urbanum	hl			.	+	1	+	1	r	+	r	.	.	+	+	+	1	+	.	+	+	+	+	+	r	+	r	+	+	+	+	+	.	r	.	+	+	.	r	.	+	+	r	.	+	+	33
Euonymus europaea	s			.	1	.	.	.	.	.	+	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	+	.	.	+	+	.	.	.	.	+	1	r	+	.	.	.	.	.	.	.	10
Euonymus europaea	jl			+	r	r	r	+	.	+	r	.	+	r	.	+	+	+	r	+	r	.	.	.	+	+	.	+	r	r	r	.	.	.	.	.	+	.	.	r	r	+	.	+	r	+	32
Aconitum napellus	hl			+	+	r	r	+	+	+	r	r	.	.	r	.	+	.	+	r	+	+	+	+	+	.	.	+	.	.	r	+	+	+	+	r	r	r	.	r	r	.	+	+	+	32
Stachys sylvatica	hl			+	1	+	.	.	.	+	+	+	.	.	.	+	.	.	.	+	+	1	+	1	r	+	.	r	.	+	+	r	+	+	.	.	+	.	r	.	.	.	+	.	.	23
Circaea lutetiana	hl			.	.	2a	2a	+	r	+	.	.	.	+	+	2b	2m	.	.	.	.	.	.	1	.	.	.	+	+	+	r	+	.	+	.	+	r	1	.	.	r	.	.	.	.	20
Ligustrum vulgare	s			r	.	.	.	.	.	.	+	+	+	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	+	.	.	.	.	.	.	.	6
Ligustrum vulgare	jl			+	+	.	.	.	.	r	+	+	+	+	r	.	.	r	.	r	.	.	.	.	+	r	.	.	r	r	.	.	r	.	.	.	.	+	.	.	.	.	+	r	.	18
Filipendula ulmaria	hl			r	.	.	.	.	.	.	+	.	.	.	.	r	.	+	.	+	+	r	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	+	15
Campanula trachelium	hl			r	.	r	.	.	.	.	r	r	.	.	.	.	.	r	r	.	+	r	.	r	.	r	.	.	.	.	.	r	.	r	.	.	.	.	.	.	r	.	r	r	.	15
Maianthemum bifolium	hl			.	.	.	.	+	+	+	.	.	.	.	+	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	+	+	1	.	.	r	.	.	r	+	.	+	+	+	15
Lysimachia nummularia	hl			r	.	.	.	+	.	.	.	.	.	.	.	+	+	.	.	.	.	+	.	+	.	.	.	.	.	.	.	+	+	+	.	.	.	.	.	.	.	r	+	+	+	13
Bromus benekenii	hl			.	r	r	.	r	.	.	r	.	.	+	.	.	.	.	.	.	.	+	+	+	.	r	.	.	.	.	.	.	.	.	.	.	r	r	.	.	.	r	.	.	.	12
Clematis vitalba	hl			.	.	.	.	.	1	+	.	.	1	1	+	+	1	.	.	.	.	.	.	.	.	+	.	.	.	+	+	.	.	1	.	.	.	.	.	.	.	.	.	.	1	12
Carex tomentosa	hl			+	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
Vincetoxicum hirundinaria	hl			r	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
Rubus caesius	hl			.	.	.	.	.	2a	2a	.	.	.	.	.	.	.	.	.	.	r	r	.	r	.	.	.	.	+	+	+	+	r	.	.	.	.	.	.	.	.	.	.	.	+	11
Galeopsis tetrahit ag.	hl			.	.	r	+	+	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	r	.	.	.	.	.	r	r	.	r	.	r	.	.	.	.	.	r	.	.	10
Viburnum opulus	s			.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Viburnum opulus	jl			.	.	+	.	+	+	.	.	.	.	.	.	.	r	.	.	r	.	r	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	+	.	.	.	.	r	9
Hypericum hirsutum	hl			+	.	.	.	.	.	.	+	+	+	.	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	r	.	.	.	.	+	.	.	9
Melica nutans	hl			r	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	r	.	+	r	r	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8
Festuca gigantea	hl			.	.	.	r	.	.	.	.	.	.	.	.	+	+	.	.	r	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	r	.	.	.	.	.	.	8
Viburnum lantana	s			r	.	.	.	.	.	.	+	r	+	.	.	.	.	.	.	.	.	+	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	7
Viburnum lantana	jl			r	.	.	.	r	.	.	r	.	.	.	.	.	.	.	.	.	.	+	.	.	r	.	.	.	.	.	.	+	.	.	.	.	.	r	.	.	.	.	.	.	.	7
Ranunculus auricomus ag.	hl			.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.

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Artikel/Article: High resilience of plant species composition to coppice restoration – a chronosequence from the oak woodland of Gerolfing (Bavaria) 61-78