

How effective are clearcutting and topsoil removal in the de-eutrophication of mixed oak forests?

Wie effektiv sind Kahlschlag und Oberbodenabtrag
hinsichtlich De-Eutrophierung von Eichenmischwäldern?

Henry Preuß¹, Simon Thorn² & Jörg Ewald³ *

¹Birgstraße 2a, 91247 Vorra, Germany; ²Hessisches Landesamt für Naturschutz, Umwelt und Geologie, Dezernat N3 - Staatliche Vogelschutzwarte, Europastrasse 10, 35394 Giessen, Germany; ³Institut für Ökologie und Landschaft, Hochschule Weihenstephan-Triesdorf, Hans-Carl-von-Carlowitz-Platz 3, 85354 Freising, Germany

*Corresponding autor, e-mail: joerg.ewald@hswt.de

Abstract

The present work examines the extent to which clearcutting and topsoil removal lead to de-eutrophication of forest sites in the communal forest of Bad Windsheim (Bavaria/Germany). In addition, effects on microclimate were analysed. We used average Ellenberg indicator values for nutrients (mN) as a proxy of eutrophication status. 27 plots in two treatments (clearcutting, topsoil removal) and untreated controls in three forest compartments were sampled for vegetation composition, soil pH, canopy shading (global site factor) and temperature. While treatments increased light availability, temperature amplitude and late frosts, effects on nutrient status and prevalence of ruderal plant species were inconsistent across compartments, which could be attributed to differences in soil substrate and land use histories. The results of this experiment indicate that the effectiveness of ecological compensation measures depends on bedrock geology and management legacies.

Keywords: light forest, nutrient removal, restoration, vegetation

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

Light forest canopy structures receive increasing attention in biodiversity conservation (BÜRGI & WOHLGEMUTH 2002, MÜLLER-KROEHLING 2007, MÖLDER et al. 2019). Fine-scale variance in temperature and light favours structural diversity and ecological succession, which, in combination with a long biotope tradition, contribute to the nature conservation value (MÖLDER et al. 2019, MICHELS 2021). In pristine forests light canopy structures were associated with extreme site conditions (FISCHER et al. 2015) or, possibly, with combined fire and wild ungulate browsing (BOND 2005). However, they became widespread through historical land uses such as litter raking, forest pasture, coppices and coppice-with-standards (JOTZ et al. 2017), which have lost their economic importance in the modern age and became threatened habitats (RUPP 2010, KIRBY et al. 2017). Today, well-tended remnants of light

forests are rare, small and isolated (MICHELS 2021). In addition to the quantitative decrease in light forests, qualitative changes are observed due to progressive N-eutrophication (BUNZEL-DRÜKE et al. 2008, HÉDL et al. 2010, FISCHER et al. 2015, EWALD & PYTTEL 2016).

Nitrogen-eutrophication and darkening through canopy closure have emerged as the main drivers of change in plant composition in numerous local studies and meta-analyses (e.g. FISCHER 1999, VERHEYEN et al. 2012, EWALD et al. 2013). However, against expectations, eutrophication of forests does not depend on nitrogen immissions in a straightforward way (PERRING et al. 2018), but involves site conditions as well as past and present land-use (ROTH 2022).

HÖLZEL (2019) highlights the conservation and recreation of light and oligotrophic forests among the main goals of forest restoration. Light forest structures can be restored by reactivating historical forms of land use such as forest pastures (cf. RUPP 2010) or coppice-with-standards (MÜLLER-KROEHLING 2007), which combine timber extraction and lighting (BÜRGI & WOHLGEMUTH 2002). More thorough de-eutrophication is sought by removing litter (BEER & EWALD 2005) and humus layers (SCHMIDT et al. 2008, FISCHER et al. 2015) in order to create low-competition habitats for oligotrophic plants and long-lasting, structurally rich succession stages. As an endpoint in a continuum of measures against eutrophication (EWALD & PYTTEL 2016), topsoil removal in forests remains a contentious and understudied restoration method (GANN et al. 2019, ZERBE 2023).

In spring 2019, trial areas were set up in the Bad Windsheim communal forest to improve the habitat of the endangered butterflies *Euphydryas maturna* and *Eriogaster catax* with the treatments clear-cutting and clearcutting with topsoil removal. This experimental set-up offers the opportunity to test for heliophilizing and de-eutrophinating effects on microclimate, soil and vegetation (EWALD & PYTTEL 2016). The following effects of intervention intensity were expected (research questions 1–5): (1) increase in incoming radiation and heliophytic plant species, (2) creation of open-air microclimate with larger temperature amplitudes, (3) increase in topsoil pH, (4) increase of soil disturbance and ruderal plant species, and (5) maximum of nitrophytic plant species after intermediate disturbance (clearcutting), reduction of nutrient value and increase in stress strategists after soil removal.

2. Study area

The Kehrenberg (49.52616 N, 10.36897 E) is located in the county of Neustadt a. d. Aisch-Bad Windsheim in northwestern Bavaria/Germany (Fig. 1), belongs to growth region 5 Fränkischer Keuper and Albvorland and is part of the FFH area Vorderer Steigerwald mit Schwanberg (AELF AN 2016).

2.1 Climate and geology

The climate is temperate, warm and relatively dry with an annual average temperature of 8.4 °C and annual precipitation of 690 mm (reference period 1961–1990). At the nearby Kaubenheim weather station (BAYER. LFL 2023) an increase in average annual temperature of 1.7 °C has been observed since 1991. Geologically, the study area is characterized by sand, clay and marl rocks of the Lower and Middle Keuper (EMMERT 1969), giving rise to pseudo-gleyed two-layer soils with high base saturation and heavy clay soils (pelosols) on Estheria and Myophoria Layers (WALENTOWSKI et al. 2020).

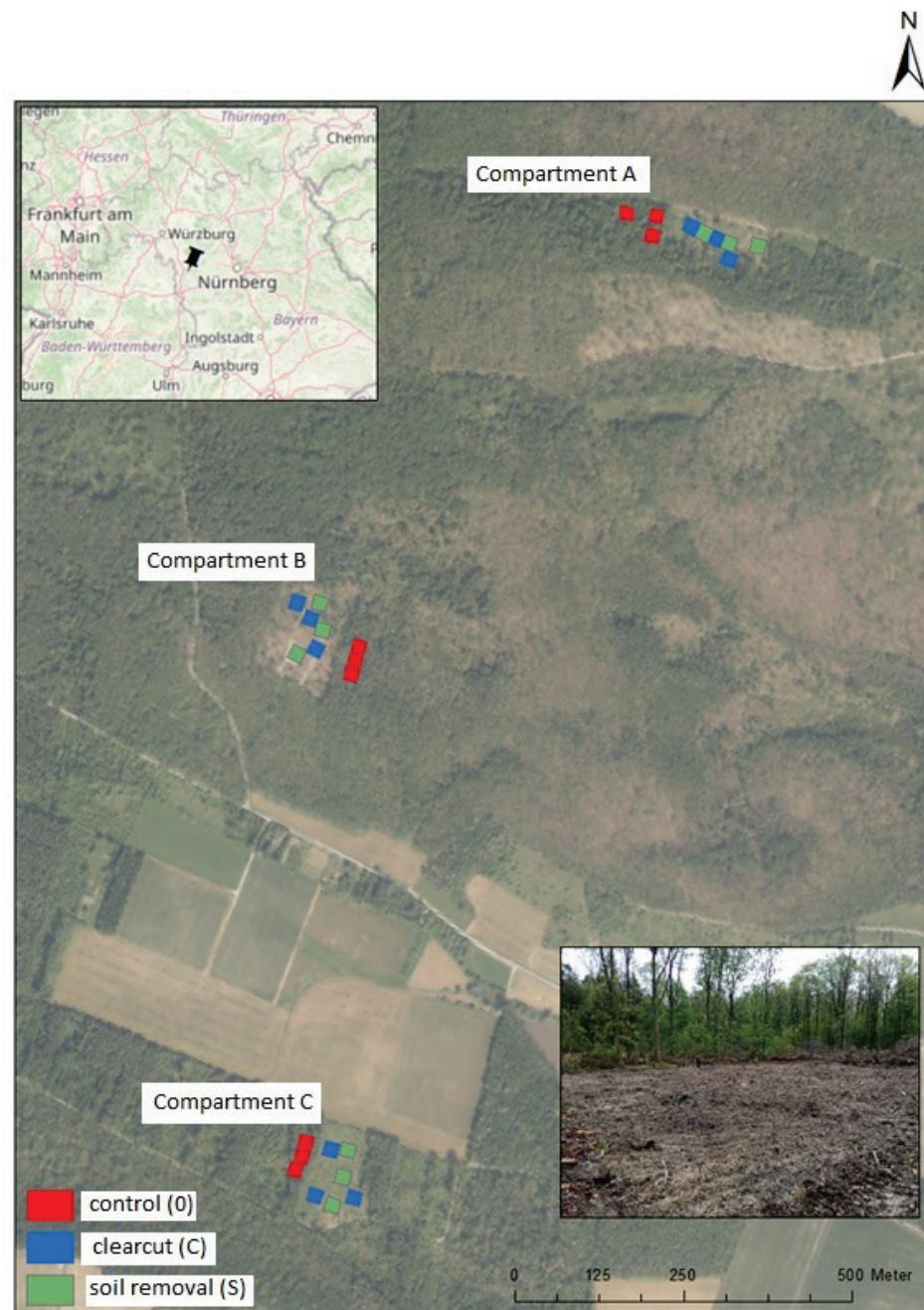


Fig. 1. Aerial photo map of the study sites; inset photo: soil removal plot. Map background: Open Street Map, Bayerische Vermessungsverwaltung.

Abb. 1. Luftbildkarte der Aufnahmeorte; Foto: Fläche nach Oberbodenabtrag. Kartenhintergrund: Open Street Map, Bayerische Vermessungsverwaltung.

2.2 Forest composition

The potential natural vegetation is formed by oak-hornbeam forests (*Galio-Carpinetum*, OBERDORFER 1992) with thermo-xerophytic and basiphytic species such as *Melica nutans* and *Carex montana* (TÜRK 1996). Heavy clays and dry cracks hinder the expansion of European beech and favour one of the most diverse forest communities in Bavaria (WALENTOWSKI et al. 2020). In a matrix of *Quercus petraea*, *Tilia cordata* and *Carpinus betulus*, rare tree species such as *Acer platanoides*, *Sorbus torminalis*, *Pyrus pyraster*, *Sorbus domestica* and *Ulmus laevis* are admixed. While seminatural mixed deciduous forests prevail, sandy acid soils derived from sandstones and fallow agricultural land have been locally converted to coniferous plantations with *Picea abies* and *Pinus sylvestris*.

2.3 Land use history

The southern Steigerwald is characterized by historical coppice-with-standards forests (BÄRNTHOL 2003). In conjunction with closely interlinked grasslands and orchards they form a biodiversity hotspot of national significance (WERKING-RADTKE & KÖNIG 2015, GROßMANN & PYTEL 2016).

3. Methods

3.1 Experimental design

The research design comprised the treatments control (0), clearcutting (C) and clearcutting with topsoil removal (S) in three forest compartments A, B and C (Fig. 1). A and B were previously coppiced deciduous stands, C was a conifer plantation. Triple replication of each variant resulted in 27 areas which are identified by a three-digit code (e.g. “AC1”) (Supplement S1). The clearcut (C, complete harvest of tree stand, RITTERSHOFER 2014) took place in 2018 on 18 randomly arranged areas. In 2019, within half of the clearcuts 10 cm topsoil was removed from nine 20 × 20 m parcels (“S”). Nine areas of equal size in the adjacent forest that had not been logged for 20 years served as control areas (“0”).

3.2 Vegetation plots

In the centre of each parcel, 10 × 10 m vegetation plots were staked out and surveyed twice for plant species composition (vascular plants, ground-dwelling mosses) and cover on a 13-part scale (LONDO 1976). Spring geophytes were recorded from the end of March to the end of April 2020, and all other plants from May to mid-July 2020 after full leaf emergence. Total cover of the various layers (moss, herb, shrub, 2nd tree, 1st tree layer, DIERSCHKE 1994) was estimated to the nearest 5% interval in the summer period. Vegetation plots were processed with TURBOVEG software (HENNEKENS & SCHAMINÉE 2001).

3.3 Environmental variables

The relief parameters slope, aspect and elevation a.s.l. were recorded with inclinometer, compass and GPS device (Garmin, model Astro 320).

The Global Site Factor (GSF, as a proxy for global **solar radiation** expressed as a relative proportion of full lighting) was determined on the basis of five hemispherical photos (corners, centre) taken with a wide-angle lens (Sigma EX DC 4.5 mm) on days with uniform sky lighting and subsequent processing with the HemiView software (Version 2.1, Delta-T Devices; VIEGLAIS & RICH 1998).

Hourly measurements of **temperature** at the soil surface and at 1.3 m height were carried out on each plot from 6 April to 29 August 2020 with temperature loggers (model EL-USB-1, Easylog)

attached to wooden pegs. Temperature amplitude was quantified as the distance between the first and third quartile of the observed distribution of values (IQR: interquartile range).

The **pH-value** of the topsoil (uppermost 5 cm of mineral soil) was measured in fresh samples after addition of distilled water (soil: solution ratio = 1: 2.5; WUNDRAM 2006, ARBEITSGEMEINSCHAFT FORSTEINRICHTUNG 2016).

3.4 Data processing and analysis

Vegetation relevés were arranged in a differentiated table according to treatments and compartments. Significant diagnostic species ($p < 0.05$) for compartments and treatments were determined by indicator species analysis according to DUFRÈNE & LEGENDRE (1997) in PCOrd (MCCUNE & MEFFORD 1999).

Mean unweighted Ellenberg indicator values for light, moisture, reaction and nutrients (ELLENBERG 2001) were calculated in TURBOVEG. Based on the species classification by GRIME (2006), the following ruderality index was computed for each plot:

$$Ri_n = \frac{r + sr + cr}{sr + r + csr + cs + cr} * 100$$

where lower case letters denote the number of observed species types per strategy type. Late frosts were defined as temperatures below freezing point occurring after leaf emergence (as of 25 April 2020) and quantified as duration in hours.

The effects of the treatment (fixed factor) and compartment (random factor) on the measured variables were analysed using a mixed linear model (GLM) in R (R CORE TEAM 2013). Model significance was calculated and interpreted according to BARTON (2015), differences between treatments were examined using a post hoc test (HOTHORN et al. 2008, BARTON 2015). The main gradients of species composition were extracted by detrended correspondence analysis (DCA; LEYER & WESCHE 2008) of the root-transformed species matrix with PC-ORD (MCCUNE & MEFFORD 1999) and were interpreted through vector projections of environmental variables.

4. Results and discussion

The section explores the multivariate patterns of species composition regarding experimental treatments and proceeds to the testing of the underlying research questions. The studied vegetation is characterised as belonging to the *Carpinion* alliance by absence of *Fagus sylvatica* and high constancy of *Dactylis polygama*, *Stellaria holostea* and many other basiphytic species of the order *Fagetalia*.

4.1 Gradients of species composition

As expected, DCA-axis 1 (eigenvalue 0.41834, gradient length of 3.573) was closely related to treatments (Fig. 2), whereas axis 2 (eigenvalue 0.34299) revealed different species composition in the studied compartments (Fig. 3).

4.1.1 Comparison of compartments

With high cover of *Dactylis polygama* and *Poa nemoralis*, canopy dominance of *Fraxinus excelsior* and *Tilia platyphyllos* and diagnostic nitro- and basiphytes like *Alliaria petiolata*, *Mercurialis perennis*, *Carex guestphalica* and *Arum maculatum* (Supplement S1), compartment A shows affinities to the *Galio-Carpinetum tilietosum* subassociation (OBERDORFER 1992).

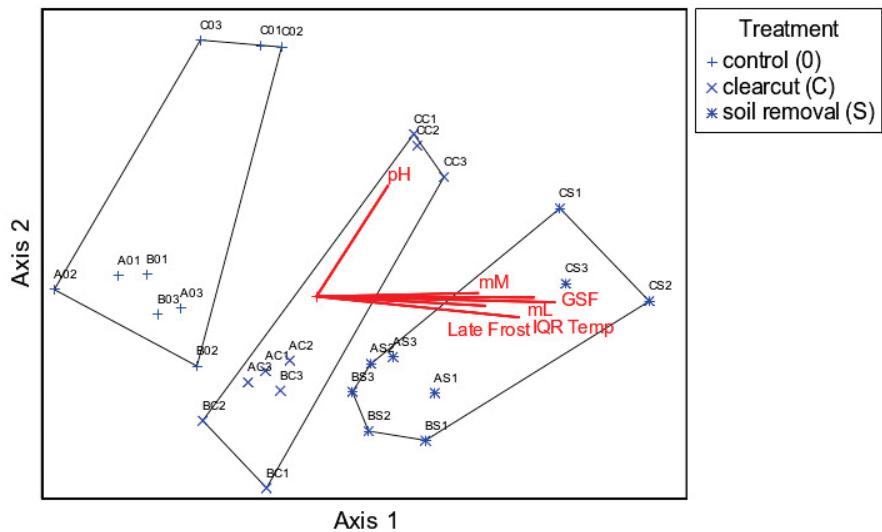


Fig. 2. DCA-ordination of species composition with plots grouped by treatment; vectors display correlation of axes with important environmental variables (GSF: global site factor, IQR Temp: interquartile range of temperature at 1.3 m, Late Frost: number of hours with late frost at 1.3 m) and Ellenberg indicator values (mM: moisture, mL: light).

Abb. 2. DCA-Ordination der Artenzusammensetzung, Gruppierung der Plots nach Behandlung; Pfeile geben die Korrelation der Achsen mit wichtigen Umweltvariablen wider (GSF: Global Site Factor, IQR Temp: Interquartils-Abstand der Temperatur in 1,3 m, Late Frost: Anzahl der Stunden mit Spätfrost in 1,3 m) und Ellenberg-Zeigerwerte (mM: Feuchte, mL: Licht).

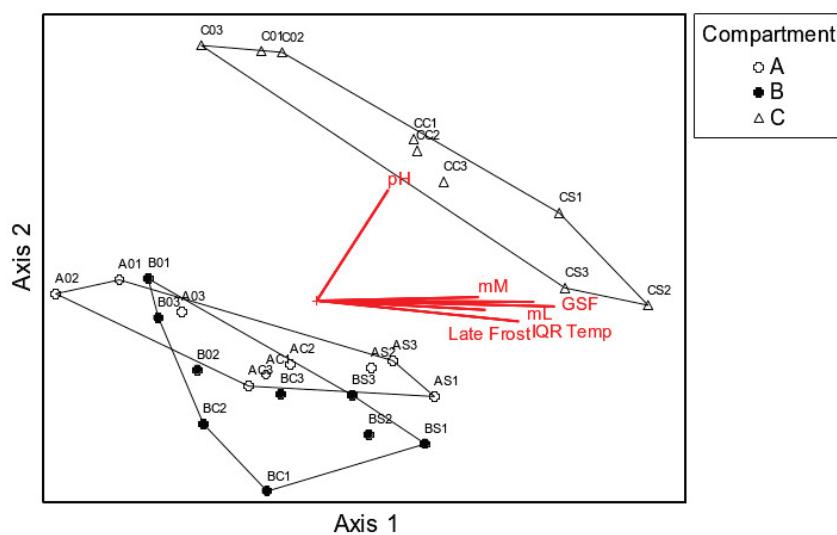


Fig. 3. DCA-ordination of species composition with plots grouped by compartments A–C; explanation of vectors in Figure 2.

Abb. 3. DCA-Ordination der Artenzusammensetzung, Gruppierung der Plots nach Versuchsbeständen A–C; Legende der Pfeilbeschriftungen siehe Abbildung 1.

Compartment B represents a rather typical *Galio-Carpinetum asaretosum* (OBERDORFER 1992) characterized by xerophytes like *Carex flacca*, *C. montana*, *Melica picta* and *Convalaria majalis* (Supplement S1). Occurrence of acidophytes (*Calamagrostis arundinacea*, *Festuca heterophylla*) in compartment B coincides with lower soil pH (Fig. 5), sandy topsoil and admixture of the conifers *Pinus sylvestris*, *Picea abies* and *Pseudotsuga menziesii* in the canopy.

The coniferous plantation in compartment C was differentiated by *Geum urbanum*, *Rubus fruticosus* and the seral shrubs *Crataegus monogyna*, *Prunus spinosa*, *Rosa canina* et *arvensis* (*Prunetalia* species; UEBELER 2012), indicating xeric (low water storage capacity, 90 mm), calcareous sites (base saturation type 1+) and recent afforestation on agricultural land. The moss *Scleropodium purum* in control plots can be attributed to the canopy of conifers (*Pinus sylvestris*, *Picea abies*).

4.1.2 Comparison of treatments

Control plots are characterized by intact tree layers, regeneration of *Acer campestre*, *Quercus petraea* and *Prunus avium*, and by the forest species *Dryopteris carthusiana*, *Rhytidadelphus triquetrus*, *Calamagrostis arundinacea* and *Scleropodium purum*. *Thuidium tamariscinum* and *Asarum europaeum* tolerate clearcutting, but not soil removal.

Milium effusum was most frequent on clearcuts. Otherwise, clearcuts shared a large group of diagnostic disturbance indicators and mostly nitrophytic ruderals like *Cirsium palustre*, *Rubus caesius* and *Lactuca serriola* with soil removal plots.

The diagnostic species of soil removal plots comprised ruderals like *Cirsium arvense* and meadow plants like *Daucus carota*, *Silene flos-cuculi*, *Leucanthemum vulgare* and *Campanula patula* with intermediate or low Ellenberg nutrient values.

Removing the tree stand resulted in drastic changes of light (GSF, mL) and soil moisture (mF) as well as temperature amplitudes and opened niches for ruderal vegetation (MUCINA 1993) germinating from seedbank (KARPOV 1960) or seed rain, such as *Epilobium* spp. and *Rubus* spp. as well as pioneer trees such as *Betula pendula* and *Pinus sylvestris*.

Increasing treatment intensity favoured heliophytes like *Cirsium palustre*, *Ranunculus repens*, *Campanula patula* und *Juncus effusus*. Diagnostic species of the genera *Bromus* und *Arctium* as well as the companions *Cirsium arvense*, *Hypericum perforatum* und *Taraxacum Sect. Ruderalia* suggest classification of disturbed plots as *Arctietum nemorosi* (OBERDORFER et al. 1978, MUCINA 1993). *Silene flos-cuculi*, *Myosotis scorpioides* and *Galium palustre* indicate hygric conditions after soil removal. The weak positive correlation of mN to axis 1 ($r = -0,21$) speaks against de-eutrophication effects of the treatments.

4.2 Study Questions

The relevant variables were tested in the GLM according to questions H1–5 (Tab. 1 and 2) and are interpreted below.

Q1: Do radiation (GSF) and heliophytic species increase with intensity of intervention?

According to the GLM, clearcutting and topsoil removal had a significant influence on radiation (Tab. 1 and 2) and there was a linear relationship between the intensity of the intervention and GSF ($R^2 = 0.69$).

Table 1. Output of the mixed linear model with treatment as fixed and compartment as random factor; significance levels *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.
Tabelle 1. Output des Gemischten Linearen Modells mit Behandlung als fixiertem und Untersuchungsbestand als Zufallsfaktor.

Variable	Treatment	Estimate	Std. Error	z Value	p^*	R^2 Treatment	R^2 Treatment + Compartment
Global Site Factor	Intercept	0.25598	0.08157	3.138	0.0017 **	0.6961093	0.8689917
	Clearcut	0.40011	0.0518	7.724	1.13E-14 ***		
	Soil Removal	0.59753	0.0518	11.535	<2E-16 ***		
Light value (mL)	Intercept	5.0478	0.1858	27.171	<2E-16 ***	0.476241	0.6010669
	Clearcut	0.3611	0.1887	1.914	0.0556		
	Soil Removal	1.0356	0.1887	5.488	4.06E-08 ***		
IQR T Soil Surface	Intercept	42.278	1.893	22.331	<2E-16 ***	0.6127052	0.6863704
	Clearcut	11.111	2.051	5.418	6.02E-08 ***		
	Soil Removal	13.778	2.051	6.719	1.83E-11 ***		
IQR T 1.3m	Intercept	41.667	1.225	34.015	<2E-16 ***	0.7900103	0.8229367
	Clearcut	13.056	1.388	9.407	<2E-16 ***		
	Soil Removal	12.833	1.388	9.247	<2E-16 ***		
pH value	Intercept	5.4448	0.517	10.531	<2E-16 ***	0.02388296	0.8382121
	Clearcut	0.262	0.1822	1.438	0.1505		
	Soil Removal	0.341	0.1822	1.871	0.0613		
Nutrient value (mN)	Intercept	5.8256	0.3764	15.477	<2E-16 ***	0.06863721	0.4137716
	Clearcut	-0.3833	0.3201	-1.198	0.231		
	Soil Removal	-0.5433	0.3201	-1.698	0.0896		
Ruderality (Ri)	Intercept	8.611	2.955	2.914	0.00357 **	0.2546763	0.4631567
	Clearcut	6.911	2.841	2.433	0.01497 *		
	Soil Removal	9.686	2.841	3.41	0.00065 ***		

Table 2. Post hoc test for pairwise comparison of the test variants.**Table 2.** Post hoc-Test zum paarweisen Vergleich der Testvarianten.

Variable	Treatment	Estimate	Std. Error	z Value	p *
Global Site Factor	C-0	0.4001	0.0518	7.724	<1E-04 ***
	S-0	0.5975	0.0518	11.535	<1E-04 ***
	S-C	0.1974	0.0518	3.811	0.00038 ***
Light value (mL)	C-0	0.3611	0.1887	1.914	0.13475
	S-0	1.0356	0.1887	5.488	<0.001 ***
	S-C	0.6744	0.1887	3.574	0.00106 **
IQR T Soil Surface	C-0	11.111	2.051	5.418	<1E-04 ***
	S-0	13.778	2.051	6.719	<1E-04 ***
	S-C	2.667	2.051	1.3	0.395
IQR T 1.3 m	C-0	13.0556	1.3879	9.407	<1E-06 ***
	S-0	12.8333	1.3879	9.247	<1E-06 ***
	S-C	-0.2222	1.3879	-0.16	0.986
pH value	C-0	0.262	0.1822	1.438	0.321
	S-0	0.341	0.1822	1.871	0.147
	S-C	0.079	0.1822	0.434	0.902
Nitrogen value (mN)	C-0	-0.3833	0.3201	-1.198	0.455
	S-0	-0.5433	0.3201	-1.698	0.206
	S-C	-0.16	0.3201	-0.5	0.871
Ruderality (Ri)	C-0	6.911	2.841	2.433	0.0397 *
	S-0	9.686	2.841	3.41	0.00194 **
	S-C	2.774	2.841	0.977	0.59161

In all three compartments, radiation increased with the intensity of the intervention. The different starting levels in the compartments could be explained by land use history and tree stock: The pure deciduous forest (A) was darker than the deciduous-coniferous mixed forest (B) and the pure coniferous forest (C). After clearcutting, up to 70% of the canopy remained in compartment A, and up to 40% in compartment B was shaded by remaining trees and deadwood. The cleared coniferous forest in compartment C reached similar levels of shading as the soil removal variants in compartments A and B.

Ellenberg light values correlated positively with GSF at $r = 0.76$ and showed a dichotomy: All control variants and the clearing variants of compartments A and B scored light numbers between 4.4 and 5.5, whereas the cleared coniferous forest of compartment C and all soil removal parcels scored values between 5.5 and 6.6. Due to the different behaviour of the cutting variants in the compartments, the GLM was not significant for the treatment.

Q2: Does an open-land microclimate with larger temperature amplitudes arise with increasing intensity of intervention?

The influence of radiation attributable to the degree of forestry intervention on temperature (MITSCHERLICH 1981) is confirmed by a tight linear relationship between GSF and temperature amplitude measured at 1.3 m height ($R^2 = 0.74$). Air temperatures after clearcutting with (S) and without topsoil removal (C) differed only slightly in the observation period.

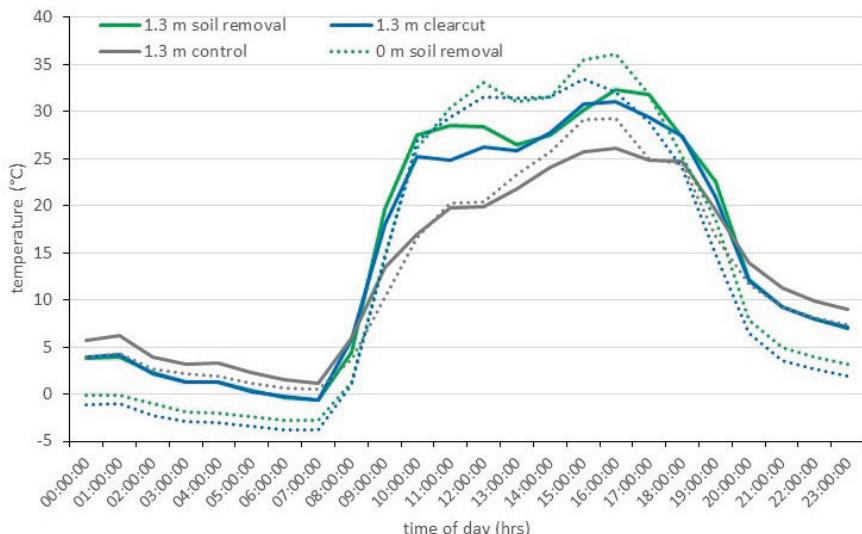


Fig. 4. Average temperature profile of the air (1.3 m) and near-ground temperature on control, clearcut and topsoil removed surfaces in the observation period.

Abb. 4. Mittlerer Tagesgang von Luft- (1,3 m) und bodennaher Temperatur auf Kontroll-, Kahlschlag- und Bodenabtragsplots während des Beobachtungszeitraums.

Medians of CC and SR plots were identical at 15.5 °C, and mean temperatures after clearcutting (16.9 °C) and topsoil removal (17.5 °C) differed by only 0.6°C. Measured maximum and minimum temperatures were comparable, whereas temperature amplitudes (IQR) were considerably (2.5 °C) larger on topsoil removal than on clearcuts and much smaller on control plots (Fig. 4), which were characterized by a lower median, less extreme maxima and a significantly narrower amplitude. Closed canopies damped mean temperatures by 1.9 °C compared to clearcuts and by 2.5 °C compared to bare soil. In all plots, temperatures at soil surface showed higher maxima and lower minima than at 1.3 m. On the SR and CC plots mean ground temperatures were slightly lower than at 1.3 m, whereas in control plots measurement series close to the ground had slightly lower (-0.4 °C) mean temperatures. The measurements confirm a more balanced climate in the forest due to a narrower amplitude. Temperatures close to the ground reached higher max/min values, leading to outliers in the measurement series.

There was an exponential relationship between the variables late frost and GSF ($y = 0.0857e^{6.1264x}$, $R^2 = 0.55$), which is typical for intact canopies (MITSCHERLICH 1981). However, remaining slash and resprouting deciduous stumps had a mitigating influence on temperature extremes after leaf emergence on clearcut plots. Despite similar canopy and radiation, visible late frost damage was only detected on soil removal, not on clearcut plots, indicating a significant treatment effect.

The GLM confirmed research question 2. However, heterogeneous radiation on clearcut plots blurred the distinction between clearcutting and topsoil removal. Regardless of intervention intensity, open space climate prevailed above a certain GSF threshold, above which the two treatments differed only in terms of late frost events.

Q3: Does the pH-value of the topsoil increase with increasing intervention strength?

There was no consistent relationship between intervention intensity and pH value of the topsoil across the three study compartments, which largely differed between controls (87% variance explained by random factor), probably due to differences in soil substrates (Fig. 5).

The main soil type in compartment A was a two-layered brown earth with negligible hydromorphic features, and mild clay overlying heavy clay in the subsoil. The soils had high base saturation (type 2) with ample calcium, magnesium and potassium reserves, only slight acidification in the topsoil and AWSC of 145 mm. In compartment B, the main soil type was strongly hydromorphic pseudogley with high base saturation (type 2), but more acidified topsoil and an AWSC of 137 mm. The main soil type in compartment C was a slightly pseudo-gleyed Pararendzina with mild clay overlying loam, high base saturation (type 1+) and AWSC of 90 mm.

Q4: Do soil disturbance and ruderal plants increase with intervention intensity?

Topsoil removal favoured ruderal species, which is in contrast to the objective of favouring stress strategists. While controls and topsoil removal areas differed significantly (Tab. 1), there was only a weak linear relationship with ruderal cover and intensity (Supplement S1).

Intermediate strategists (CSR) were dominant in all plot groups, ruderality index reached maximum values of 30% in topsoil removal plots of compartment C. As expected, clear-cutting and soil removal treatments exhibited higher ruderality mostly due to *Cirsium* spp., *Urtica dioica* and *Galium aparine* (cf. BRANDES 1978). Differences in ruderality between the treatments were only prominent in compartment C, resulting in a linear dependence with intensity ($R^2 = 0.81$) due to increasing cover of non-forest species such as *Myosotis arvensis*, *Rosa arvensis*, *Daucus carota* and *Cirsium arvense*. The situation in compartment C may be explained by the relative proximity of agricultural land (as a source of diaspores and atmospheric nutrient input) and land use history. Historical maps and photos confirm,

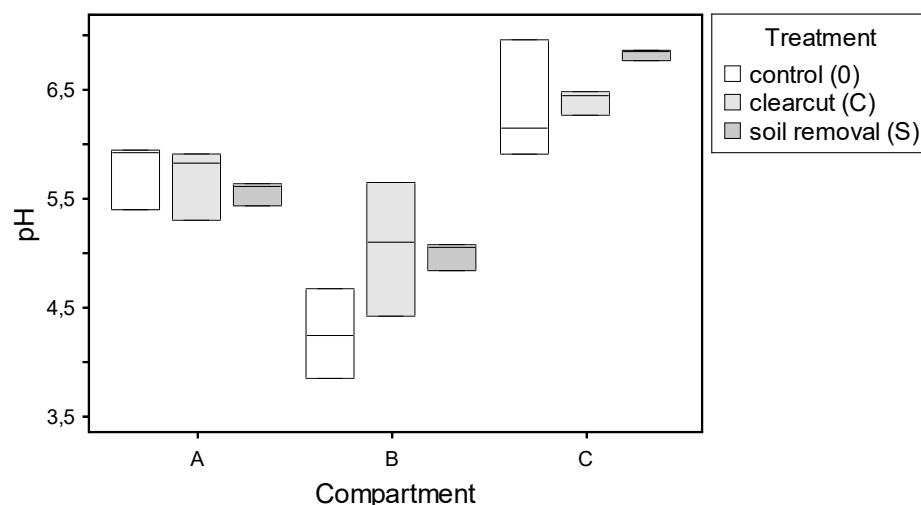


Fig. 5. pH value as box plots across compartments and treatments.

Abb. 5. pH-Werte als Boxplots gegliedert nach Untersuchungsbeständen und Behandlungen.

that the coniferous forest stand was established on former agricultural land around 1945. Thus, ruderal and other non-forest species may have emerged from the seed bank. At old forest sites (compartments A and B) soil removal favours a mixture of ruderal species with forest species.

Q5: Does occurrence of nitrophytic species peak at intermediate intervention level (clearcutting) and does soil removal favour oligotraphent, stress-tolerant plants?

The hypothesis combines the expectation that clearcutting favours nutrient release from biomass residues and humus stocks, but that removing topsoils counteracts mineralisation and favours oligotraphent stress strategists. Observed patterns in mN do not confirm Q5 at the level of the whole dataset nor within any of the three compartments (Fig. 6).

Nutrient values in compartment A showed a strong reduction in nitrophytes with increasing intervention. Control plots in this compartment were classified as highly eutrophic, clear-cut plots as eutrophic, and soil removal plots as mesotrophic according to EWALD & ZICHE (2017). However, eutrophic mN-values of control plots in compartment A stand out (random factor compartment explains 41% of variance), which can be attributed to the absence of conifers and higher pH/absence of sandy topsoil (A vs. B). Canopy dominance of *Fraxinus excelsior* and *Tilia platyphyllos* with easily decomposable litter and narrow C/N-ratio favour fast nutrient turnover (CHUDOMELOVÁ et al. 2017), which can apparently be reduced by removing the canopy and humus-rich topsoil. The treatments tend to remove the a priori differences between compartments and homogenize nutrient values at intermediate, meso- to eutrophic levels. Thus, reducing mN-values through topsoil removal remained the exception.

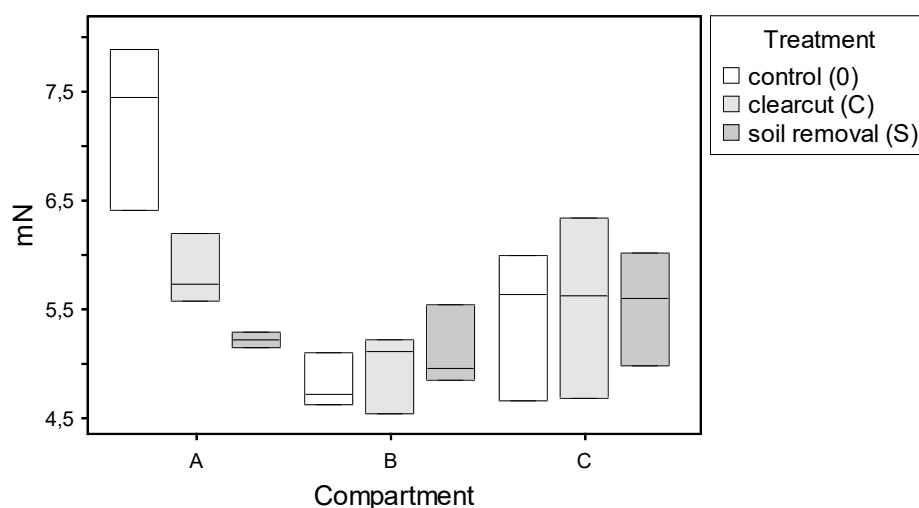


Fig. 6. Mean nutrient values shown as box plots across compartments and treatments.

Abb. 6. Mittlere Nährstoffzahl als Boxplots gegliedert nach Untersuchungsbeständen und Behandlungen.

4.3 Caveats in interpreting indicator values

As Ellenberg nutrient values are a widely-used proxy for the eutrophication of forests (ROTH et al. 2020), one would expect that they are suited to test for successful de-eutrophication. However, their performance may be compromised when comparing different vegetation formations (WAMELINK et al. 2002, 2003). Nutrient values of plant species and vegetation may also be biased by correlation with other factors like soil reaction (SZYMURA et al. 2014), which showed comparable variation in our study and were highly correlated across and within the studied compartments. In forests, both nutrient and reaction values strongly depend on chemical and biological properties of forest floors such as litter quality, humus content, C/N-ratio and release of organic acids. In fact, correlations between pH, mR and mN were strongest in the subsets of undisturbed control plots and in control and clearcut plots regarded together (Tab. 3). Weak relationships in soil removal plots indicated an uncoupling of chemical soil properties and community composition. We hypothesize, that the latter is strongly governed by dispersal and seed bank dynamics. In contrast, the relationship between radiation (GSF) and light values held well across treatments.

4.4 Efficiency of topsoil removal in deciduous forest

While topsoil removal seems to be well-established as a restoration measure in heaths (GEISSEN et al. 2013), fens (EMSENS et al. 2015), wet (KLIMKOWSKA et al. 2007) and dry grasslands (TÖRÖK et al. 2011), the few scientific studies on topsoil removal in temperate forests of Europe are from *Pinus sylvestris* on sand (e.g. BEER & EWALD 2005, PRIETZEL & KAISER 2005, ZANIEWSKI et al. 2015, FISCHER et al. 2016), where litter raking and sod plugging had a long tradition. As in heath ecosystems, removal of organic forest floors takes out the bulk of stored mineral nutrients leaving bare sand as a habitat for stress tolerant target species like lichens, *Lycopodium* spp. and *Pulsatilla* spp. (HEINKEN 2008).

In temperate deciduous forests, topsoil removal has so far been employed to remove encroaching or invasive understorey vegetation and facilitate tree regeneration (RESCO DE DIOS et al. 2005, LÖF et al. 2012). Likewise, our experiment aimed at creating temporary clearings for heliophilous species: Young *Euphydryas maturna* caterpillars feed on *Fraxinus excelsior* leaves occurring under precisely defined thermal and hygric conditions, while older larvae extend their diet to *Ligustrum vulgare*, *Plantago* spp. (occurring on one soil removal plot in compartment C) and *Pulmonaria* spp. (FREESE et al. 2006); larvae of *Eriogaster catax* feed on *Prunus spinosa* and *Crataegus* spp. (occurring in clearcut and

Table 3. Coefficient of determination between measured variables and Ellenberg indicator values within different groups of the treatments control (0), clearcutting (C) and soil removal (S).

Tabelle 3. Bestimmtheitsmaß zwischen Messgrößen und Ellenberg-Zeigerwerten innerhalb verschiedener Gruppen der Behandlungen Kontrolle (0), Kahlschlag (C) und Bodenentfernung (S).

R ²	0	0+C	C	C+S	S	0+C+S
pH-mR	0.405	0.308	0.079	0.049	0.090	0.186
mR-mN	0.780	0.650	0.514	0.432	0.497	0.637
GSF-mL	0.147	0.577	0.604	0.735	0.666	0.758

topsoil removal plots of compartment C) (SITAR et al. 2019). Clearing and soil removal in the young forest and close to margins (compartment C) was most efficient in providing specific food plants. AMBROŽOVÁ et al. (2021) demonstrated positive effects of coppicing and soil removal on the diversity of detritivorous dung and rove beetles reacting to temperature and humidity imposed by the dominant vegetation layers.

While creating openings, microclimate and favouring food plants, treatments have so far not been efficient in creating oligotraphent microhabitats, but have rather favoured eu- to mesotraphent ruderal vegetation. These findings are in line with a review of coppicing effects on nutrient status (EWALD et al. 2017). Soil removal reduced nutrient status only in the highly eutrophic deciduous forest of compartment A, but led to complex responses under low pH and in the presence of conifers, where oligotraphent forest species were replaced by meso- to eutrophic ruderal species.

Studying effects of topsoil removal on soil nutrient concentrations and stocks were beyond the scope of our project. Beyond a few pedological studies, that quantified nutrient removal by litter raking in *Pinus sylvestris* (PRIETZEL & KAISER 2005) and *Picea abies* stands (HOFMEISTER et al. 2008), direct measurements of nutrients after topsoil removal in temperate deciduous forests are lacking.

5. Conclusions and outlook

Topsoil removal does not warrant rapid de-eutropication, but rather leads to the establishment of meso- to eutrophic and subhygic ruderal vegetation in *Galio-Carpinetum* forests. Effects of clearcutting and soil removal on vegetation are highly contingent on the initial status of forest stands in terms of tree species composition, topsoil pH and land use legacies. The experiment should be re-surveyed for long-term effects after several years, when short-term ruderal dynamics have calmed down. It remains to be discovered whether oligotrophic vegetation, specific food plants and the *Lepidopteran* target species will benefit in the long run.

Erweiterte deutsche Zusammenfassung

Hintergrund, Untersuchungsgebiet & Methoden – Lichte Wälder oligotropher Standorte sind von besonderem Interesse für den Arten- und Biotopschutz, bedürfen jedoch unter den heutigen Stoffeinträgen und Bewirtschaftungsregimes ähnlich wie Heiden und Kalkmagerrasen eines gezielten Naturschutzmanagements.

Im Stadtwald Bad Windsheim (Mittelfranken, Bayern) wurden in einem Praxisversuch an drei Waldorten (pnV *Galio-Carpinetum*, zwei naturnahe Laubwälder, ein Nadelholzforst) mit den Varianten Kontrolle, Kahlschlag und Oberbodenabtrag geprüft, wie sich die Eingriffsintensität auf die Standortbedingungen und Vegetation auswirken, insbesondere ob (1) Strahlungsgenuss und lichtbedürftige Pflanzarten gefördert, (2) ein Offenland-Mikroklima mit größeren Temperaturamplituden geschaffen, (3) der pH-Wert des Oberbodens erhöht und (4) durch Bodenverwundung das Auftreten von Ruderalarten gefördert werden. (5) Schließlich wurde ein maximales Auftreten nitrophytischer Pflanzarten nach Kahlschlag (mittlerer Störungsintensität) sowie eine Förderung von stresstoleranten, oligotraphenten Arten nach Bodenabtrag erwartet.

Dazu wurden auf 27 100 m² großen Plots die Vegetation auf der Londo-Skala erfasst sowie relativer Strahlungsgenuss (GSF) mittels Hemisphärenfotos, Temperaturen in stündlicher Auflösung am Boden und in 1,3 m Höhe und pH-Werte des Oberbodens gemessen. Die Vegetationsaufnahmen wurden durch Berechnung ungewichteter Ellenberg-Zeigerwerte für Licht, Feuchte, Reaktion und Stickstoff, eines Ruderalitätsindex auf Basis der CSR-Klassifikation nach GRIME (2006) sowie mittels Entzerrter

Korrespondenzanalyse (DCA) ausgewertet. Die Behandlungsvarianten wurden an Hand von Joint Plots der DCA-Achsen mit Zeigerwerten und Umweltvariablen sowie durch Boxplots verglichen. Der Einfluss der Behandlungen auf Vegetation und Standortvariablen wurde durch gemischte lineare Modelle (GLM) statistisch getestet.

Ergebnisse und Diskussion – Die Erhöhung der Einstrahlung (Forschungsfrage 1) wurde durch ein hochsignifikantes GLM (Behandlungseffekt $R^2 = 0,70^{***}$) bestätigt, obwohl die Einstrahlung auf den Kontrollparzellen unterschiedliche Ausgangsniveaus gehabt hatte. Einstrahlung und mittlere Ellenberg-Lichtzahlen der Parzellen waren zwar positiv korreliert ($r = 0,76$) und die Bodenabtrags-Plots (5,5–6,6) lagen durchweg ca. eine Stufe über den Kontrollen (4,4–5,5). Jedoch unterschied sich der Effekt des Kahlschlags auf die Lichtzahl zwischen den Versuchsbeständen: In den beiden Laubwäldern waren ähnliche Werte wie in den Kontrollen, im Fichtenbestand dagegen ähnliche wie nach Bodenabtrag zu verzeichnen.

Die Behandlungen führten auch, wie gemäß Frage 2 erwartet, zu einer deutlichen Erhöhung der täglichen Temperaturamplituden, welche ihrerseits eng mit der Strahlung korreliert waren. Die Störungsvarianten unterschieden sich hinsichtlich Mitteltemperaturen und Extremwerten wenig, jedoch traten nach Bodenabtrag wesentliche größere Temperaturamplituden auf. Mit zunehmender Einstrahlung nahm die Spätfrostdauer exponentiell zu, wobei Bestandesreste und Stockausschläge auf den Kahlschlägen den Frost abmilderten und die nach Bodenabtrag eintretenden sichtbaren Schäden verhinderten.

Die Behandlungen zeigten in den drei Versuchsbeständen inkonsistente Effekte auf die pH-Werte der Oberböden: In dem einen Laubwaldbestand mit hohem Ausgangs-pH (5,9) blieb der Effekt aus, im zweiten Laubwald erhöhte die Störung den pH von 4,2 auf 5, im Nadelwald von 6,1 auf 6,4 nach Kahlschlag und 6,8 nach Bodenabtrag. Die Frage 3 zu Grunde liegende Annahme wurde durch das GLM nicht bestätigt.

Die Störungsvarianten zeigten die gemäß Frage 4 erwartete Zunahme von Ruderalfpflanzen, ihre Intensität war jedoch hochgradig abhängig vom Ausgangsbestand. Sie war in alten Laubwaldbeständen viel geringer als im Nadelholzbestand, der sich in Recherchen als Erstaufforstung auf Ackerland erwies.

Der erwartete unimodale Behandlungseffekt auf die mittlere Nährstoffzahl (Frage 5: Steigerung bei Kahlschlag, Absinken nach Bodenabtrag) konnte nicht belegt werden. Die angestrebte Ausmagerung der Vegetation fand nur in einem der drei Versuchsbestände (Laubwald auf basenreichem Substrat mit hohen Ausgangswerten in der Kontrolle) statt.

Während der Projektaufzeit gelang es zwar in den künstlichen Lichtungen ein Offenland-Mikroklima mit entsprechender Schlagflurvegetation zu schaffen, die durch Bodenabtrag angestrebte Veränderung der Bodeneigenschaften (Erhöhung des pH-Wert, Ausmagerung) war dagegen nicht durchgehend nachweisbar, weil sich die untersuchten Waldökosysteme hinsichtlich Substrat, Bestockung und Nutzungsgeschichte deutlich unterschieden.

Acknowledgement

We thank Sven Finnberg, Forester of the Stadtwald Bad Windsheim, Hans Seitz for help with plant identification and Christina Hartung for editorial assistance.

Author contribution statement

HP carried out field work and data analysis, prepared graphs and tables, wrote the Methods and Results sections and drafted Introduction and Discussion; ST designed the experiment and reviewed the manuscript; JE reviewed the manuscript and wrote Introduction and Discussion.

ORCID iDs

Jörg Ewald  <https://orcid.org/0000-0002-2758-9324>
Simon Thorn  <https://orcid.org/0000-0002-3062-3060>

Supplements

Supplement S1. Vegetation table differentiated by treatments.

Beilage S1. Differenzierte Vegetationstabelle gegliedert nach Behandlungen.

References

- AMBROŽOVÁ, L., FINNBERG, S., FELDMANN, B., BUSE, J., PREUSS, H., EWALD, J. & THORN, S. (2021): Coppicing and topsoil removal promote diversity of dung-inhabiting beetles (*Coleoptera: Scarabaeidae, Geotrupidae, Staphylinidae*) in forests. – Agric. For. Entomol. 24: 104–113. <https://doi.org/10.1111/afe.12472>
- AELF AN (AMT FÜR ERNÄHRUNG, LANDWIRTSCHAFT UND FORSTEN ANSBACH) (2016): SPA 6327-471 Südlicher Steigerwald Managementplan Fachgrundlagen. – Ansbach.
- ARBEITSGEMEINSCHAFT FORSTEINRICHTUNG (2016): Forstliche Standortsaufnahme. Begriffe, Definitionen, Einteilungen, Kennzeichnungen, Erläuterungen. 7. Aufl. – IHW-Verlag, Eching bei München: 400 pp.
- BÄRNTHOL, R. (2003): Nieder- und Mittelwald in Franken. – Fränkisches Freilandmuseum, Bad Windsheim: 152 pp.
- BARTON, K. (2015): Package ‘MuMin’ – Version 1, 18 pp.
- BAYER. LFL (BAYERISCHE LANDESANSTALT FÜR LANDWIRTSCHAFT) (2023): Wetterstation Kaubenheim. – URL: <https://www.landentwicklung.rlp.de/Internet/AM/NotesBAM.nsf/0a1c4fe9e45b5fb6c12579c000526e5e/e6f1a50a61d005dec1257392004f2fd5?OpenDocument&TableRow=3.10#3>. [accessed 2023-10-23].
- BEER, A. & EWALD, J. (2005): Vegetationskundliche Untersuchungen rezent streugenutzter Kiefernwälder auf Binnendünen des niederbayerischen Tertiärhügellandes – *Tuxenia* 25: 93–109.
- BOND, W.J. (2005): Large parts of the world are brown or black: A different view on the ‘Green World’ hypothesis. – *J. Veg. Sci.* 16: 261–66. <https://doi.org/10.1111/j.1654-1103.2005.tb02364.x>
- BRANDES, D. (1978): Zur Verbreitung von Ruderalpflanzen im östlichen Südniedersachsen. – *Gött. Flor. Rundbr.* 12(4): 106–112.
- BUNZEL-DRÜKE, M., BÖHM, C., FINCK, C., KÄMMER, G., LUICK, R. & REISINGER, E. (2008): Praxisleitfaden für Ganzjahresbeweidung in Naturschutz und Landschaftsentwicklung – „Wilde Weiden“. – In: Arb.gem. Biol. Umweltschutz Kreis Soest e.V., Bad Sassendorf-Lohne. – URL: https://www.wsl.ch/fileadmin/user_upload/WSL/Mitarbeitende/wohlgemu/buergi_wo2002.pdf [accessed 2023-03-26].
- BÜRGI, M. & WOHLGEMUTH, T. (2002): Natur aus Bauernhand – auch im Wald? – *Informationsbl. Forschungsbereich Landsch.* (WSL) 55: 1–3.
- CHUDOMELOVÁ, M., HÉDL, R., ZOUHAR, V. & SZABÓ, P. (2017): Open oakwoods facing modern threats: Will they survive the next fifty years? – *Biol. Conserv.* 210: 163–73. <https://doi.org/10.1016/j.biocon.2017.04.017>
- DIERSCHKE, H. (1994): Pflanzensoziologie – Grundlagen und Methoden. – Ulmer, Stuttgart: 683 pp.
- DUFRÈNE, M. & LEGENDRE, P. (1997): Species assemblages and indicator species definition. the need of an asymmetrical and flexible approach. – *Ecol. Monogr.* 67: 345–366. [https://doi.org/10.1890/0012-9615\(1997\)067\[0345:SAAIST\]2.0.CO;2](https://doi.org/10.1890/0012-9615(1997)067[0345:SAAIST]2.0.CO;2)
- ELLENBERG, H., WEBER, H.E., DÜLL, R., WIRTH, V., WERNER, W. & PAULIBEN, D. (2001): Zeigerwerte von Pflanzen in Mitteleuropa. 3. Aufl. – *Scr. Geobot.* 18: 1–262.
- EMMERT, U. (1969): Erläuterungen zur Geologischen Karte von Bayern 1: 25000 Blatt Nr. 6428 Bad Windsheim. – Bayerisches Geologisches Landesamt, München: 166 pp.

- EMSENS, W.J., AGGENBACH, C.J., SMOLDERS, A.J. & VAN DIGGELEN, R. (2015): Topsoil removal in degraded rich fens: Can we force an ecosystem reset? – Ecol. Eng. 77: 225–232. <https://doi.org/10.1016/j.ecoleng.2015.01.029>
- EWALD, J., HENNEKENS, S., CONRAD, S. ... GODEFROID, S. (2013): Spatial and temporal patterns of Ellenberg nutrient values in forests of Germany and adjacent regions – a survey based on phytosociological databases. – Tuxenia 33: 93–109.
- EWALD, J. & PYTEL, P. (2016): Leitbilder, Möglichkeiten und Grenzen der De-Eutrophierung von Wäldern in Mitteleuropa. – Nat. Landsch. 91: 210–217. <https://doi.org/10.17433/5.2016.50153392.210-217>
- EWALD, J., ROTHE, A., HANSBAUER, M., SCHUMANN, C., WILNHAMMER, M. & SCHÖNFELD, F. (2017): Energiewende und Waldbiodiversität. – BfN-Skripten 455: 1–128.
- EWALD, J. & ZICHE, D. (2017): Giving meaning to Ellenberg nutrient values: National forest soil inventory yields frequency-based scaling. – Appl. Veg. Sci. 20: 115–123. <https://doi.org/10.1111/avsc.12278>
- FISCHER, A. (1999): Floristical changes in Central European forest ecosystems during the past decades as an expression of changing site conditions. – EFI-Proceedings 27: 53–64.
- FISCHER, A., MICHLER, B. & FISCHER, H.S. (2016): Konzept eines Schutz- und Hilfsprogramms für Flechten-Kiefernwälder in Bayern. Handbuch. – Technische Universität München, Geobotanik, Freising: 26 pp.
- FISCHER, A., MICHLER, B., FISCHER, H.S., BRUNNER, G., HÖSCH, S., SCHULTES, A. & TITZE, P. (2015): Flechtenreiche Kiefernwälder in Bayern: Entwicklung und Zukunft. – Tuxenia 35: 9–29. <https://doi.org/10.14471/2015.35.012>
- FREESE, A., BENES, J., BOLZ, R., CIZEK, O., DOLEK, M. & GEYER, A. (2006): Habitat use of the endangered butterfly *Euphydryas maturna* and forestry in Central Europe. – Anim. Conserv. 9: 388–397. <https://doi.org/10.1111/j.1469-1795.2006.00045.x>
- GANN, G.D., McDONALD, T., WALDER, B. ... Dickson, K.W. (2019): International principles and standards for the practice of ecological restoration. 2nd ed. – Restor. Ecol. 27: S1–S46. <https://doi.org/10.1111/rec.13035>
- GEISSEN, V., WANG, S., OOSTINDIE, K., HUERTA, E., ZWART, K.B. & SMIT, A. (2013): Effects of topsoil removal as a nature management technique on soil functions. – Catena 101: 50–55. <https://doi.org/10.1016/j.catena.2012.10.002>
- GRIME, J.P. (2006): Plant strategies, vegetation processes, and ecosystem properties. 2nd ed. – John Wiley & Sons, Chichester: 417 pp.
- GROßMANN, J. & PYTEL, P. (2016): Ökologische Bewertung von Streuobstwiesen anhand von Mikrohabitaten - ein Fallbeispiel. – Mitt. Bad. Landesver. Naturkunde u. Naturschutz 22: 105–117.
- HÉDL, R., KOPECKÝ, M. & KOMÁREK, J. (2010): Half a century of succession in a temperate oakwood: from species-rich community to mesic forest. – Divers. Distrib. 16: 267–76. <https://doi.org/10.1111/j.1472-4642.2010.00637.x>
- HEINKEN, T. (2008): Die natürlichen Kiefernstandorte Deutschlands und ihre Gefährdung. – Beiträge aus der NW-FVA 2: 19–41.
- HENNEKENS, S.M. & SCHAMINÉE, J.H.J. (2001): TURBOVEG, a comprehensive data base management system for vegetation data. – J. Veg. Sci. 12: 589–591. <https://doi.org/10.2307/3237010>
- HOFMEISTER, J., OULEHLE, F., KRÁM, P. & HRUŠKA, J. (2008): Loss of nutrients due to litter raking compared to the effect of acidic deposition in two spruce stands, Czech Republic. – Biogeochemistry 88: 139–151. <https://doi.org/10.1007/s10533-008-9201-z>
- HÖLZEL, N. (2019): Wälder. – In: KOLLMANN, J., KIRMER, A., TISCHEW, S., HÖLZEL, N. & KIEHL, K. (Eds.): Renaturierungsökologie: 101–124. Springer, Berlin.
- HOTHORN, T., BRETZ, F. & WESTFALL, P. (2008): Simultaneous inference in general parametric models. – Biom. J. 50: 346–363. <https://doi.org/10.1002/bimj.200810425>
- JOTZ, S., KONOLD, W., SUCHOMEL, C. & RUPP, M. (2017): Lichte Wälder und biotische Vielfalt. – Ber. Naturforsch. Ges. Freiburg i. Br, 107: 13–153.
- KARPOV, V.G. (1960): On the quantity and the species compositions the viable seeds in the soil of spruce forests of *Piceetum myrtillosum* type [Russian with English summary]. – Trudy Moskov Obshch. Isp. Prirody 3: 131–140.

- KIRBY, K.J., BUCKLEY, G.P. & MILLS, J. (2017): Biodiversity implications of coppice decline, transformations to high forest and coppice restoration in British woodland. – *Folia Geobot.* 52: 5–13. <https://doi.org/10.1007/s12224-016-9252-1>
- KLIMKOWSKA, A., VAN DIGGELEN, R., BAKKER, J.P. & GROOTJANS, A.P. (2007): Wet meadow restoration in Western Europe: A quantitative assessment of the effectiveness of several techniques. – *Biol. Conserv.* 140: 318–328. <https://doi.org/10.1016/j.biocon.2007.08.024>
- LEYER, I. & WESCHE, K. (2008): Multivariate Statistik in der Ökologie. Eine Einführung. Korrigierter Nachdruck. – Springer, Berlin: 221 pp.
- LÖF, M., DEY, D.C., NAVARRO, R.M. & JACOBS, D.F. (2012): Mechanical site preparation for forest restoration. – *New For.* 43: 825–848. <https://doi.org/10.1007/s11056-012-9332-x>
- LONDO, G. (1976): The decimal scale for relevés of permanent quadrats. – *Vegetatio* 33: 61–64. <https://doi.org/10.1007/BF00055300>
- MCCUNE, B. & MEFFORD, M.J. (1999): PC-ORD. Multivariate analysis of ecological data: version 4 for Windows: [user's guide]. – MjM Software, Gleneden Beach, OR: 237 pp.
- MICHELS, H.G. (2021): Konzeption zur Erhaltung und Wiederherstellung lichter Wälder in Baden-Württemberg. Unter Mitarbeit von Mattias Rupp, Winter, Maria-Barbara, Magg, Nora und Jörg Kleinschmit. – Forstliche Versuchs- und Forschungsanstalt Baden-Württemberg. – URL: <https://www.fva-bw.de/projekte/projekt/1292-konzeption-zur-erhaltung-und-wiederherstellung-lichter-waelder-in-baden-wuerttemberg> [accessed 2023-03-26].
- MITSCHERLICH, G. (1981): Waldklima und Wasserhaushalt. 2., überarb. Aufl. – Sauerländer (Wald, Wachstum und Umwelt, eine Einführung in die ökologischen Grundlagen des Waldwachstums / von Gerhard Mitscherlich; Bd. 2), Frankfurt am Main: 265 pp.
- MÖLDER, A., MEYER, P. & NAGEL, R.-V. (2019): Integrative management to sustain biodiversity and ecological continuity in Central European temperate oak (*Quercus robur*, *Q. petraea*) forests: An overview. – *For. Ecol. Manage.* 437: 324–39. <https://doi.org/10.1016/j.foreco.2019.01.006>
- MUCINA, L. (Ed.) (1993): Die Pflanzengesellschaften Österreichs. – Fischer, Jena: 353 pp.
- MÜLLER-KROEHLING, S. (2007): Laufkäfer unterschiedlich bewirtschafteter fränkischer Eichenwälder, unter besonderer Berücksichtigung der Bedeutung von Mittelwäldern für die Biodiversität. – *Angew. Carabidol.* 8: 51–68.
- OBERDORFER, E. (1992): Süddeutsche Pflanzengesellschaften, Teil IV. Wälder und Gebüsche, 2 Vol. – G. Fischer, Stuttgart: 862 pp.
- OBERDORFER, E., KORNECK, D. & MÜLLER, T. (1978): Süddeutsche Pflanzengesellschaften, Teil II., 2., stark bearb. Aufl. – Fischer, Jena: 355 pp.
- PERRING, M.P., DIEKMANN, M., MIDOLLO, G. ... VERHEYEN, K. (2018): Understanding context dependency in the response of forest understorey plant communities to nitrogen deposition. – *Envir. Poll.* 242: 1787–1799. <https://doi.org/10.1016/j.envpol.2018.07.089>
- PRIETZEL, J. & KAISER, K.O. (2005): De-eutrisification of a nitrogen-saturated Scots pine forest by prescribed litter-raking. – *J. Plant Nutr. Soil Sci.* 168: 461–471. <https://doi.org/10.1002/jpln.200421705>
- RESCO DE DIOS, V., YOSHIDA, T. & IGA, Y. (2005): Effects of topsoil removal by soil-scarification on regeneration dynamics of mixed forests in Hokkaido, Northern Japan. – *For. Ecol. Manage.* 215: 138–148. <https://doi.org/10.1016/j.foreco.2005.05.010>
- RITTERSHOFER, F. (2014): Waldflege und Waldbau für Studium und Praxis. Mit einem Abschnitt über Naturschutz im Wald. 3., überarb. Aufl. – Rittershofer, Freising: 492 pp.
- ROTH, M. (2022): Understanding signs of eutrophication in the ground vegetation of temperate forests: the role of nitrogen deposition and other environmental factors. – Dissertation, Albert-Ludwigs-Universität Freiburg. – URL: <https://katalog.ub.uni-freiburg.de/opac/RDSIndexrecord/1833811925> [accessed 2023-02-10].
- ROTH, M., MICHELS, H.G., PUHLMANN, H., SUCKER, C., WINTER, M.B. & HAUCK, M. (2020): Responses of temperate forests to nitrogen deposition: Testing the explanatory power of modeled deposition datasets for vegetation gradients. – *Ecosystems*: 1–17. <https://doi.org/10.1007/s10021-020-00579-4>
- RUPP, M. (2010): Lichte Wälder durch Beweidung: Genese, Bedeutung als Biotope, Stellenwert in der Landschaft und im Naturschutz in Baden-Württemberg. – Treffpunkt Biologische Vielfalt IX: 25–32. BfN-Schriften 265.

- SCHMIDT, M., FISCHER, P., GÜNZL, B., HEINKEN, T., KELM, H.-J., MEYER, P., PRÜTER, J. & WAESCH, G. (2008): Flechten-Kiefernwälder – Artenvielfalt durch alte Nutzungsformen? – AFZ/DerWald 8/2008: 424–425.
- SITAR, C., DAVID, S.V., MUNTEAN, I. & IACOB, G.M. (2019): Ecological niche comparison of two cohabiting species, the threatened moth *Eriogaster catax* and *Eriogaster lanestris* (*Lepidoptera: Lasiocampidae*) – relevance for their conservation. – Entomol. Rom. 23: 13–22. <https://doi.org/10.24193/entomolrom.23.2>
- SZYMURA, T.H., SZYMURA, M. & MACIOŁ, A. (2014): Bioindication with Ellenberg's indicator values: A comparison with measured parameters in Central European oak forests. – Ecol. Indic. 46: 495–503. <https://doi.org/10.1016/j.ecolind.2014.07.013>
- R CORE TEAM (2013): R: A language and environment for statistical computing Version 3.0.1.
- TÖRÖK, P., VIDA, E., DEÁK, B., LENGYEL, S. & TÓTHMÉRÉSZ, B. (2011): Grassland restoration on former croplands in Europe: an assessment of applicability of techniques and costs. – Biodivers. Conserv. 20: 2311–2332. <https://doi.org/10.1007/s10531-011-9992-4>
- TÜRK, W. (1996): Die Hainbuche in der realen und der potentiellen natürlichen Vegetation Mittel-europas unter besonderer Berücksichtigung Bayerns. – LWF Wissen 12: 17–25.
- UEBELE, M. (2012): Flora und Vegetation von Schlehengebüschen (*Prunella spinosae*) des Meer-holzer Hügellandes (Main-Kinzig-Kreis). – Bot. Natursch. Hessen 24: 5–31.
- VIEGLAIS, D.A. & RICH, P.M. (1998): Hemiview. Analysis of hemispherical photography. – Software.
- WALENTOWSKI, H., FISCHER, A., KÖLLING, C., TÜRK, W., RUMPEL, A. & EWALD, J. (2020): Handbuch der natürlichen Waldgesellschaften Bayerns. Ein auf geobotanischer Grundlage entwickelter Leitfaden für die Praxis in Forstwirtschaft und Naturschutz. 4. überarbeitete Aufl. – Geobotanica, Freising: 464 pp.
- WAMELINK, G.W.W., JOOSTEN, V., VAN DOBBEN, H.F. & BERENDSE, F. (2002): Validity of Ellenberg indicator values judged from physico-chemical field measurements. – J. Veg. Sci. 13: 269–278. <https://doi.org/10.1111/j.1654-1103.2002.tb02047.x>
- WAMELINK, G.W.W., VAN DOBBEN, H.F. & BERENDSE, F. (2003): Apparently we do need phytosociological classes to calibrate Ellenberg indicator values! – J. Veg. Sci. 14: 619–620. <https://doi.org/10.1111/j.1654-1103.2003.tb02190.x>
- WERKING-RADTKE, J. & KÖNIG, H. (2015): Wirkungen von Agrarumwelt- und Vertragsnaturschutzmaßnahmen. – Natur in NRW (NiN) 2: 1–30.
- VERHEYEN, K., BAETEN, L., DE FRENNÉ, P. ... VERSTRAETEN, G. (2012): Driving factors behind the eutrophication signal in understorey plant communities of deciduous temperate forests. – J. Ecol. 100: 352–365. <https://doi.org/10.1111/j.1365-2745.2011.01928.x>
- WUNDRAM, A. (2006): Beziehungen von Bodenpflanzen und Vegetationseinheiten frühling-geophytenreicher Laubmischwälder der Region Hannover zum pH-Wert und zur Stickstoff-Nettomineralisation des Bodens (Situation nach Einwirkung des sauren Regens). – Universität Hannover, Hannover: 217 pp. – URL: <https://www.repo.uni-hannover.de/bitstream/handle/123456789/6878/509856594.pdf> [accessed 2023-01-01].
- ZANIEWSKI, P.T., BERNATOWICZ, A., KOZUB, Ł., TRUSZKOWSKA, E., DEMBICZ, I. & WIERZBICKA, M. (2015): Traditionally managed patch of *Cladonia*-Scots pine forest in the Biebrza valley – specificity of the protected forest community shaped by human activity. – Ecol. Questions 20: 45–52. <https://doi.org/10.12775/EQ.2014.015>
- ZERBE, S. (2023): Forests. – In ZERBE, S. (Ed.): Restoration of Ecosystems – Bridging Nature and Humans: 107–152. Berlin, Springer. https://doi.org/10.1007/978-3-662-65658-7_7

Supplement S1. Vegetation table differentiated by treatments (from left to right: soil removal S – clearcut C – control 0) and forest compartments (A, B, C); column Ly (layer): t1 – upper tree, t2 – lower tree, h – herb, s-shrub; column N: Ellenberg indicator value for nutrients; frames denote diagnostic species of treatments and compartments.

Beilage S1. Differenzierte Vegetationstabelle gegliedert nach Behandlungen (von links nach rechts: Bodenabtrag-Kahlschlag-Kontrolle) und Ausgangsbestand (A, B, C); Spalte N: Ellenberg-Nährstoffzahl.

Single occurrences: Plot 1: *Picris hieracioides* 1, *Potentilla thuringiaca* 1; plot 4: *Eurhynchium striatum* 2, *Luzula luzuloides* 4, *Prunus padus* s1 4, *Vicia pisiformis* 4; plot 5: *Melica nutans* 2, *Poa annua* 2, *Pyrus communis* 1, *Vicia tetrasperma* 2; plot 6: *Vicia pannonica* 2; plot 10: *Brachypodium pinnatum* 2, *Hypericum pulchrum* 2; plot 12: *Arctium lappa* 2, *Senecio vulgaris* 2; plot 14: *Dianthus superbus* 2, *Pyrus pyraster* 2, *Rosa gallica* 1; plot 16: *Polytrichum formosum* 4, *Sorbus torminalis* 1; plot 18: *Agrostis gigantea* 4, *Ulmus glabra* 1; plot 19: *Deschampsia cespitosa* 4; plot 20: *Artemisia vulgaris* 4, *Stachys palustris* 5; plot 21: *Anthemis arvensis* 4, *Cardamine hirsuta* 4, *Plantago major* 4, *Poa trivialis* 5, *Solanum dulcamara* 4; plot 22: *Cornus sanguinea* s1 6, *Euonymus europaea* 2; plot 23: *Agrimonia eupatoria* 2, *Corylus avellana* 5, *Galium spurium* 4, *Sonchus arvensis* 4; plot 24: *Valeriana officinalis* 4; plot 25: *Clematis vitalba* hl 4, *Picea abies* hl 1, *Ulmus laevis* s1 4; plot 26: *Equisetum sylvaticum* 8, *Frangula alnus* 2, *Stachys sylvatica* 2; plot 27: *Epilobium angustifolium* 2, *Hylocomium splendens* 4.