

Legacy of historical litter raking in temperate forest plant communities

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Funding information

Grantová Agentura České Republiky, Grant/Award Number: 17-09283S; European Research Council under the European Union's Seventh Framework Programme, Grant/Award Number: FP7/2007-2013 and 278065; Long-term Research Development Project, Grant/Award Number: RVO 67985939

Co-ordinating Editor: Sara Cousins

Abstract

Question: European temperate forests have been managed for millennia, and this management has left a long-lasting legacy in soil chemistry and plant species composition and diversity. One of the most common practices was the raking of leaf litter, which was used as bedding for farm animals. We asked, what is the legacy of historical litter raking for contemporary forest plant communities?

Location: Czech Republic.

Methods: We explored the effect of historical litter raking on species richness and diversity of the forest herbaceous layer. We also tested whether long-term soil acidification and nutrient depletion caused by litter raking were reflected in Ellenberg indicator values for nutrients and soil reaction and in the higher abundance of specialists of acidophilous forest types. We used written historical evidence to identify areas where litter raking was practised in the 19th century. We analysed the differences between vegetation plots located in areas affected and unaffected by the past litter raking. Our analysis included almost 2,500 vegetation plots recorded between 1980 and 2015.

Results: Litter raking was historically practised in a striking 85% of forested townships. Although litter raking had no significant effect on overall species richness, we found significant differences of diversity patterns among forest types. Historically raked plots were taxonomically more similar. We found no difference in the mean Ellenberg indicator values for soil reaction and nutrients between the affected and unaffected plots, and only a weak positive response of selected herb species of acidophilous forests.

Conclusions: We provide the first empirical evidence of the historical litter-raking legacy in forest communities on a large scale. Despite its historical frequency, we found only a weak legacy of historical litter raking in present-day plant communities. Future studies could potentially use other, finer-scale methods in smaller territories to complement our results.

KEYWORDS

biotic homogenization, forest management, herbaceous layer, historical ecology, human impact, management legacy, plant species diversity, temperate forest

1 | INTRODUCTION

Past human management has left a legacy in present ecosystems (Foster et al., 2003). This knowledge is particularly obvious in Europe where evidence that ecosystems have co-evolved with humans since prehistory is plentiful (Birks, Birks, Kaland, & Moe, 1988). Soils can bear traces of past agricultural use for millennia (Dambrine et al., 2007; Plue et al., 2008). Altered soil chemistry is subsequently reflected in vegetation composition and diversity. Examples include sites of Roman villas abandoned 2,000 years ago (Dupouey, Dambrine, Laffite, & Moares, 2002), late medieval villages (Hejcman, Karlík, Ondráček, & Klír, 2013) and high medieval mottes (Closset-Kopp & Decocq, 2015).

Knowledge of land-use legacies is important for the assessments of driving factors behind recent vegetation patterns and processes. In their review, Perring et al. (2016) argue that it is necessary to understand the interactions of past management with recent environmental changes, such as increased atmospheric N deposition or climate change. However, studies addressing management usually considered the most obvious factors, such as tree cutting intensity and game density, while other historically important management forms remain little researched (e.g., Bernhardt-Römermann et al., 2015; Verheyen et al., 2012; but see Den Ouden, 2000). One such management form was litter raking, which was widely practised in European forests for centuries (Glatzel, 1991; Leuschner & Ellenberg, 2017). However, its legacy for current forest biodiversity and composition is largely unknown, leaving a gap in both basic research and its applications in nature management.

Forest litter was historically collected as bedding for domestic animals. Afterwards, bound with animal excrement, it was used as manure for fertilizing crops (Glatzel, 1991). The practice was probably very common in the past few centuries (Bürgi, Gimmi, & Stuber, 2013). By integrating historical data into a geochemical model, Gimmi et al. (2013) demonstrated that litter raking in the past caused a reduction in soil C pools, from which recovery is still on-going. McGrath et al. (2015) showed that litter raking resulted in the export of large quantities of N from forests to agricultural land. Regarding tree species preference, pine, spruce and birch litter were the most popular (Gimmi & Bürgi, 2007; Pfeffer, 1948), but litter from other trees was also used (Ebermayer, 1876). Forest accessibility was an important factor regarding the presence and regularity of litter raking (Gimmi & Bürgi, 2007).

Tree litter plays a significant role in forest ecosystems. It protects soil against erosion and compaction, and buffers microclimatic fluctuations in the soil. It is also an important part of an ecosystem's nutrient cycle and buffering capacity (Facelli & Pickett, 1991; Glatzel, 1991). The export of large amounts of base cations from forest ecosystems probably caused soil acidification (Bürgi et al., 2013; Glatzel, 1991) and changed C cycling, soil physical properties and soil microclimate (Sayer, 2005). Field experiments simulating litter raking in forest ecosystems corroborated these findings. Hofmeister, Oulehle, Krám, and Hruška (2008) showed that cation pools in the soil and spruce needles significantly decreased already

in the first years of experimental litter raking in a mountain forest. In a 7-year litter raking experiment in a Scots pine forest in southern Germany, Prietzel and Kaiser (2005) demonstrated that N concentration decreased more in sites subject to higher N deposition levels. As a result, litter raking affected the performance of woody species, including seedling germination and growth (Prietzel & Kaiser, 2005; Sayer, 2005). Due to its adverse effects on soil fertility and timber production, litter raking was banned in many European countries in the second half of the 19th century (Ebermayer, 1876). Despite the ban, litter raking was occasionally practised, particularly in remote areas, well into the 20th century (Bürgi et al., 2013).

Only a handful of experimental studies documented the impact of litter raking on plant community diversity and composition (cf. Sayer, 2005). In temperate forests, the herbaceous layer is especially important, because most plant diversity is concentrated there (Gilliam, 2007). Changes induced by litter raking can be driven by four mechanisms: (a) removing litter causes higher humidity and temperature fluctuations between the outer environment and the soil, affecting decomposition and mineralization of dead organic matter (Xu, Liu, & Sayer, 2013); (b) soil nutrient pool impoverishment (Kreutzer, 1972; Prietzel & Kaiser, 2005; Tyrol Soil Survey 1988); (c) changes in tree layer composition mediating light conditions in the understorey and soil chemistry (Gimmi, Wohlgemuth, Rigling, Hoffmann, & Bürgi, 2010); and (d) regular mechanical disturbances in the herbaceous layer (no specific focus in published literature). The few existing field experiments with litter raking demonstrated that the forest herbaceous layer responded in the expected manner. For example, a 16-year long field experiment by Dzwonko and Gawroński (2002) showed that litter raking prevented change from acidophilous to neutrophilous vegetation. Similar results were observed in a 5-year experiment in a thermophilous oak forest (Douda, Boublík, Doudová, & Kyncl, 2017). In a 7-year experiment in *Pinus sylvestris* stands on dune sand, Beer and Ewald (2005) observed a decrease in Ellenberg indicator values for nutrients. Soil disturbances can lead to the exclusion of sensitive plant species in favour of stress-tolerant and ruderal species (cf. Lindholm & Nummelin, 1983; Wiegmann & Waller, 2006). Regarding the effect on plot species richness, most field studies documented a positive effect (Douda et al., 2017; Dzwonko & Gawroński, 2002; Lindholm & Nummelin, 1983; Vild, Kalwij, & Hédl, 2015). The impact on taxonomic heterogeneity is still unknown. Beer and Ewald (2005) reported increased within-plot compositional heterogeneity, but it is unclear whether the same applies to heterogeneity among plots. At the landscape scale, litter raking, as a relatively uniform type of regular disturbance, will likely have a homogenizing effect on plant communities in the forest herbaceous layer.

Some herbaceous layer changes, such as the above-mentioned increased richness of ruderal species, are likely to be transitional because most ruderal species are not able to survive without regular disturbances (Baskin & Baskin, 2014). On the other hand, changes induced by soil impoverishment and acidification may last much longer, because the recovery of soil chemistry after management abandonment can be rather slow (Hüttel & Schaaf, 1995;

Kreutzer, 1972; Tyrol Soil Survey 1988). Jandl, Starlinger, Englisch, Herzberger, and Johann (2002) mentioned that the transformation of oak forests into pine forests in southern Austria was claimed to have been the result of site "degradation" (meaning probably soil nutrient impoverishment) induced by litter raking as early as the 16th century.

But is there any scientific evidence of the persisting long-term effects of past litter raking on the herbaceous layer? To the best of our knowledge, this topic has not been evaluated so far (cf. Sayer, 2005). Furthermore, most studies focusing on legacies of other management forms were conducted on small scales (Den Ouden, 2000). In the present study, we used 19th-century litter raking data from the eastern part of the Czech Republic (ca. 27,000 km²) and evaluated its net effect on forest herbaceous layer communities recorded in thousands of recent plots. By comparing understorey vascular plant communities between sites where litter raking was historically practised and sites where it was not, we focused on the following hypotheses. Plots with historical litter raking have (a) higher species richness, (b) lower compositional heterogeneity, (c) higher richness of selected specialists of acidophilous forest types, (d) lower average Ellenberg indicator values for nutrients and soil reaction, and (e)

different responses according to the five main forest vegetation types occurring in the study region.

2 | METHODS

2.1 | Study area

The study area covers the historical regions of Moravia and Czech Silesia (Figure 1) in the eastern part of the Czech Republic. The area comprises 26,808 km². Land forms range from flat lowlands in the southern and central parts to mountains up to 1,491 m a.s.l. in the north and northeast. Climate is temperate with mean annual temperatures ranging from about 1–10°C and precipitation from about 500–1,500 mm (Tolász, Míková, Valeriánová, & Voženílek, 2007). Geologically, the region lies between the Bohemian Massif on the west and the Western Carpathians on the east. These two units are built mostly of crystalline and sedimentary bedrock, respectively. Land cover has been co-determined by human management at least since the Neolithic, ca. 7,500 years ago. Forests constitute about 34% of the land cover and increasingly dominate with altitude. The currently prevailing Norway spruce is a native species but its proportion has increased through planting in the past two centuries.

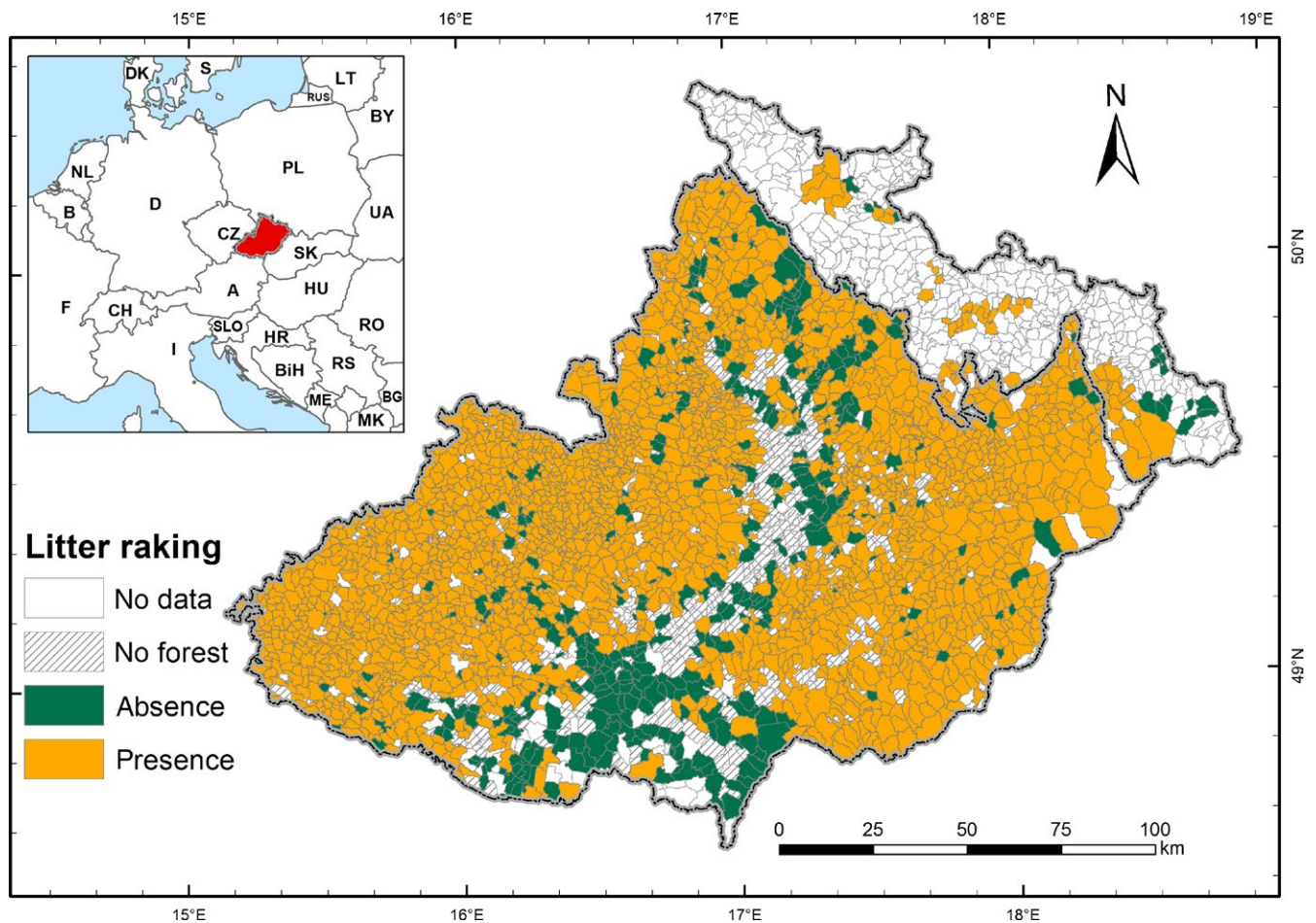


FIGURE 1 Map of the study area with indication of the 19th century litter raking. Spatial units (townships) are delimited by thin grey lines, and historical regions by thick lines: the northeast part is Silesia and the southwest part is Moravia [Colour figure can be viewed at wileyonlinelibrary.com]

2.2 | Vegetation data

Vegetation-plot data were retrieved from two resources: the Czech National Phytosociological Database (Chytrý & Michalcová, 2012) and a database of forest vegetation plots maintained at the Institute of Botany of the Czech Academy of Sciences (<http://ekol-brno.ibot.cas.cz/en/database>). Vegetation was recorded by means of the Braun-Blanquet approach (Dengler, Chytrý, & Ewald, 2008), i.e., all species were recorded within vertical layers and their cover was estimated. The sampling period was limited to dates after 1980 so that the data reflect forest vegetation in the past three decades (1980–2015) and plot sizes were restricted to the range between 100 and 500 m². We further used only plots located in townships with a known litter raking history (see Historical data below) and plots with reasonably accurate geographic coordinates (we excluded plots with duplicated coordinates and plots with coordinates outside forested areas). The resulting data set consisted of 2,494 plots.

2.3 | Environmental data

We used plot header data for altitude, aspect and slope when available. If missing, we used values extracted from the fourth generation Digital Terrain Model of the Czech Republic (Czech Office for Surveying, Mapping and Cadastre, <http://geoportal.cuzk.cz/>). We calculated the *Heat Load Index* based on aspect, slope and spatial coordinates using Equation 3 in McCune and Keon (2002). The SRTM digital elevation model with 90-m resolution (v 4.1; <http://srtm.csi.cgiar.org>) was used to calculate three topographic variables capturing different aspects of land-surface topography. As a proxy for local soil moisture, we calculated the *Topographic Wetness Index* using FD8Q flow-routing recommended by Kopecký and Čížková (2010). To characterize plot position at the watershed scale, we calculated the *Convergence Index* expressing terrain convexity up to 900 m from the plot. To give higher importance to local topography, we used inverse distance-weighted cell values in the calculation. Finally, to express the topographic position of plots at the landscape scale, we calculated plot *Vertical Distance to Channel Network* defined as cells having catchment area above 10e⁶ (FD8Q flow-routing). We used SAGA GIS (Conrad et al., 2015) for all calculations.

Soil group according to the soil classification system for the Czech Republic (Němeček, Macků, Vokoun, Vavříček, & Novák, 2001) was extracted from a digital soil map (Czech Geological Survey, Soil map 1:50,000; <http://mapy.geology.cz>). Additionally, the categories of the Czech Forest Ecosystem Classification based on the Typological System of Forest Management Planning Institute (Viewegh, Kusbach, & Mikeska, 2003) were used. Forest types were defined by two environmental factors: climate and soil conditions. These categories formed the *Forest Site Complex* as a synthetic variable of abiotic site conditions.

The *Phytogeographic Division* of the Czech Republic (Skalický, 1988) was used to categorize areas along a floristic altitudinal and geographic gradient, which is also related to the intensity of historical

human impact. Each plot was associated with a corresponding phytogeographic district.

We used monthly maximum and minimum temperatures and monthly precipitation to calculate 19 bioclimatic variables often used in species distribution modelling (so-called core bioclim variables (Kriticos et al., 2012). The mean (1986–2010) monthly climatic values were extracted from interpolated grids with 0.5-km resolution provided by the Czech Hydrometeorological Institute. To calculate 19 bioclimatic variables from monthly climatic values for each vegetation plot, we used the *biovars* function from the *dismo* R package (R Foundation for Statistical Computing, Vienna, AT).

To assess the impact of historical litter raking following *Forest type*, the data set was classified into five groups of plots according to the dominant tree species: (a) oak forests, dominated by oak (*Quercus petraea*, *Q. robur* and *Q. pubescens*), (b) oak–hornbeam forests, with lime (*Tilia cordata*, *T. platyphyllos*) or hornbeam (*Carpinus betulus*) mixed with oak (as above), (c) beech forests, dominated by beech (*Fagus sylvatica*), (d) eutrophic forests, dominated by lime (as above), maple (*Acer platanoides*, *A. pseudoplatanus*), ash (*Fraxinus excelsior*) or alder (*Alnus glutinosa*), (e) coniferous forests, dominated by pine (*Pinus sylvestris*), fir (*Abies alba*) or spruce (*Picea abies*).

We also calculated the proportion of forested area in a 500-m buffer around each vegetation plot (*Distance to Forest Edge*) using Corine Land Cover 2006, v 18_4 (European Environment Agency under the framework of the Copernicus programme).

2.4 | Historical data

The most important source used in this paper was the so-called Stable Cadastre. Cadastral surveys were prepared in the Czech Lands since the 17th century. Their main aim was to survey the entire country and describe the use of each piece of land, based on which tax was established (Bumba, 2007). The first reasonably accurate survey to include all land was the Josephian Cadastres at the end of the 18th century. However, this cadastre lacked accurate maps. In contrast, the Stable Cadastre was based on a dense network of triangulation points resulting in high-quality maps (Bičík et al., 2015). Moravia and Silesia were mapped between 1824 and 1836. This was followed by office work to establish the land use, value and tax of each parcel, which included many terrain visits to settle contested issues. For Moravia, the results of this long process were put on paper between the years 1841 and 1850 (the material is kept in the Moravian Provincial Archives under shelfmark MZA D 8). Many types of detailed and summary documents were produced. For our purposes, the most important are the protocols of the forest commission. Among other things, these protocols contained information on the presence of *Nebennutzungen* ('side uses' meaning non-timber uses) in each township (*Katastralgemeinde* in the original, meaning a village and its lands). Litter raking was one of these uses. The protocols were explicitly meant to contain complete information; therefore the lack of information on litter raking meant the actual absence of this practice. For most townships, only presence/absence was recorded.



	Presence	Absence	No forest	No data
Thermophyticum (%)	34.3	24.5	33.2	8
Mesophyticum (%)	70.3	7.2	4.4	18.1
Oreophyticum (%)	72.5	10	0.6	16.9
Whole study region (%)	62.6	11	10.4	15.9

TABLE 1 Percentage of townships with data on litter raking (*litter raking present/absent, no forest, no data*) according to the altitudinal zones of the phytogeographic division of the Czech Republic

Processing the Stable Cadastre is very time-consuming and poses considerable challenges in document access. Therefore we could not include in the database data from Silesia, for which documents are kept at the Provincial Archives in Opava. To compensate for this, we processed the so-called *Forststatistik von Mähren und Schlesien*. This survey was initiated by local forest statistician Heinrich C. Weeber. Published in the journal of Moravian and Silesian foresters (*Verhandlungen der Forst-Section für Mähren und Schlesien*) in the years 1853–1857, the survey was based on information gathered from local forest managers in a form compatible to cadastral surveys. Non-timber uses were recorded as qualitative information (present/absent) only. Furthermore, recording was not comprehensive; therefore we interpreted the lack of litter raking as actual absence only if other uses were mentioned. As described in detail in the next paragraph, this restriction meant that data were available for very few townships in Silesia, rendering the possible differences in data quality between the Stable Cadastre and the *Forststatistik* of minor importance as far as the overall results were concerned. To obtain a proxy for human pressure on forests for each township, we used data on human populations (*Number of houses*) from the first comprehensive population survey in 1869 (Růžková & Škrabal, 2006). We obtained a digital version of these data from the Land Use Cover Changes (LUCC) Czechia Database (<http://web.natur.cuni.cz/ksgrrsek/lucc/index.php?scn=2>). Lastly, we used *forest area* (in ha) in the 19th century in each township.

Results of the archival work are displayed in the Figure 1. We found written evidence of litter raking in 63% of all townships in the study region – i.e., 85% of forested townships with known litter raking history. In 11% of all townships litter raking was absent; 10% of townships had no forests and no data were available for 16% of townships (mostly due to the lack of sources in Czech Silesia). Despite our efforts with the *Forststatistik*, we managed to find data for only 77 townships in Silesia, i.e., less than 3% of all townships with data on litter raking in this region. The proportion of forested townships with litter raking was the lowest in the lowlands (Thermophyticum), whereas it was much higher in the uplands (Mesophyticum) and in the mountains (Oreophyticum) (Table 1).

Using historical data for analysing species diversity in vegetation plots suffers from the relatively coarse, although the best available, resolution of archival data. As a result, we cannot be sure whether each single plot in townships with documented historical management was indeed subjected to litter raking because there were usually several forests in a single township, which may have differed in dominant forest type. Also, we cannot assume that litter raking was never practised in regions where our data showed its absence. Even

if litter raking was not practised in 19th century, it may have been practised earlier or later. Therefore, the townships analysed in this study may differ only in the time since litter raking abandonment.

2.5 | Data analyses

2.5.1 | Permutation tests of multivariate regression

Multiple relationships between species richness and environmental variables were analysed using regression modelling. We tested the hypothesis that the explanatory variable *litter raking* influences species diversity. Our data did not distinguish for raking intensity; therefore we created two data sets with and without raking. Due to the unequal number of plots, we randomly selected the same number of samples without replacement from each data set. Environmental conditions for each vegetation plot were used as covariates represented by topographic factors (*Altitude, Convergence Index, Heat Load Index, Topographic Wetness Index, Vertical Distance to Channel Network*), climatic factors (*PCA axis1, PCA axis2*), edaphic factors (*Czech Forest Ecosystem Classification, Soil group*), anthropogenic factors (*Number of houses in 1869*), biotic factors (*Forest Type, Forest Area, Phytogeographic Division*) and methodological factors (*Year of sampling, Plot area* and spatial coordinates). Comparison of raked and non-raked plots for selected variables is shown in supporting information Appendix S1. The model was adjusted for spatial and temporal correlations. It included sampling year and 2-D smooth of longitude and latitude as covariates. To assess the significance of the partial effect of the explanatory variable (litter raking), the frequency distribution of the *F*-statistic was estimated from multiple regression models calculated on 500 bootstrapped samples with replacement from the data set. The *p*-value was calculated as the proportion of 500 iterations where the *F*-statistic from the randomized data equalled or exceeded the *F*-statistic from the non-randomized data. This approach was applied to the whole data set and also separately for each forest type except coniferous forests (due to the small number of plots).

2.5.2 | Beta diversity calculation

To assess whether litter raking caused taxonomic homogenization, we calculated β -diversity among plots through the multiple site dissimilarity approach (Baselga, 2010) implemented in the *betapart* package (Baselga & Orme, 2012) in the R software (v 3.2.3). To gain deeper insights into β -diversity patterns, we decomposed the overall β -diversity into two components – nestedness and spatial

turnover. We calculated spatial turnover to assess the measure of replacement of certain species by other species.

Because of the unbalanced number of plots with litter raking and without litter raking, we adjusted the number of plots by randomly selecting the same number of samples from litter raking and the control data set. This selection was repeated 500 times with replacement. The mean values of β -diversity components and species numbers were calculated for each iteration. To assess the differences in species number and β -diversity between plots with and without raking, the frequency distribution of the mean was calculated and graphically displayed. Finally, the significance of differences between plots with and without raking was determined by bootstrap analysis. At first, we calculated randomized sampling distribution of the difference between means. Following this approach we tested the hypothesis that the difference between mean species diversity in the plots with and without raking equals zero. The proportion of the 500 iterations for which the randomized mean difference equals or exceeds the non-randomized mean difference was used for p -value estimation. This approach was applied on the whole data set and also separately for each specific forest type except coniferous forests (due to the small number of plots).

2.5.3 | Effects through soil acidity and fertility

To evaluate the hypothesis that litter raking supports species of oligotrophic and acidophilous substrates due to the effect on soil chemistry, we evaluated the performance of diagnostic species of acidophilous oak forests (*Genisto germanicae-Quercion*) and beech forests (*Luzulo-Fagion*) based on vegetation classification in the Czech Republic (Chytrý & Tichý, 2003).

To specify the relationship between each diagnostic species and the presence of litter raking, we used species response curves based on detrended canonical correspondence analysis (DCCA). To adjust the model for potential correlations, explanatory variables *Year*, *Forest type*, *Altitude* and *Geographic coordinates* were used as covariates. Species-response curves were fitted by GLM with Poisson error distribution, log link function and control for over-dispersion.

Finally, we evaluated the hypothesis that raked plots have lower Ellenberg indicator values (EIVs) for soil reaction and nutrients by comparing plot averages (Diekmann, 2003; Ellenberg, Weber, Düll, Wirth, & Werner, 1992). We tested the differences among two groups of samples with and without litter raking using a modified permutation test (MoPeT) with mean of species weighted by species abundances (Zelený & Schaffers, 2012). The testing procedure is based on the permutation of the mean randomized EIVs calculated from species EIVs randomized among species.

3 | RESULTS

3.1 | Effects on diversity and compositional heterogeneity

Results from multivariate regression analysis showed no independent effect of litter raking on species richness for the

whole data set ($pseudoF_{4,1949} = 0.89$, $p = 0.282$). On the other hand, we found a significant partial effect of interaction terms between litter raking and forest type on species richness ($pseudoF_{4,1945} = 4.71$, $p = 0.042$). This means that the assumed legacy of litter raking in present species richness has been structured according to forest type. There was significantly lower species richness in raked oak forests (raked mean = 27.38, non-raked mean = 30.55, $p = 0.004$), while species richness was higher in raked eutrophic forests (raked mean = 30.87, non-raked mean = 26.63, $p = 0.001$; Figure 2). No significant difference was found in other forest types.

Testing for the potential effects of litter raking on compositional heterogeneity among plots showed that in the plots with litter raking the mean value of turnover was lower (raked mean = 0.9915, non-raked mean = 0.9921, $p = 0.011$; Figure 2).

3.2 | Effects through soil acidity and fertility

Only four out of 15 selected species diagnostic for acidophilous forest types had significantly higher predicted abundance in plots with litter raking (Table 2). Contrary to the hypothesis, there was no difference in either average EIVs for nutrients ($F = 13.680$, $p = 0.331$) or soil reaction ($F = 3.328$, $p = 0.645$) between the plots in historically raked and non-raked sites.

4 | DISCUSSION

4.1 | Ecological legacy of historical litter raking

Our results showed that the legacy of past litter raking on the current herb layer is weaker than expected from experimental inference and studies on soil chemistry legacies. Contrary to our expectations, only four out of 15 species selected as the most sensitive to historical litter removal showed a significant positive response (see Appendix S2 for all species). Specifically, we indirectly corroborated the observation of Lindholm and Nummelin (1983) that *Avenella flexuosa* responds well to litter raking. A potential explanation for the lack of change is that the effect of historical litter raking is relatively short term. If litter raking was abandoned shortly after the period recorded in the historical sources we used, its legacy may no longer be detectable. Other considerations include the recovery of chemistry conditions in the upper soil layer after disturbances (Leuschner, Wulf, Bäuchler, & Hertel, 2014). Soil recovery is probably facilitated by litter accumulation and subsequent decomposition, which in turn replenish basic cations and P pools (Facelli & Pickett, 1991). As the first 10 cm of a soil profile are the most important for herb layer species, the recovery of soil can quickly drive compositional changes. Besides, there are indications that this recovery can be hastened by N addition into the soil, because, as Jandl et al. (2002) showed, planting N-fixing plants improved soil chemistry conditions in forest sites degraded by historical litter raking in Austria. Current atmospheric N deposition probably acts in a similar way. A weak relationship between litter raking and current

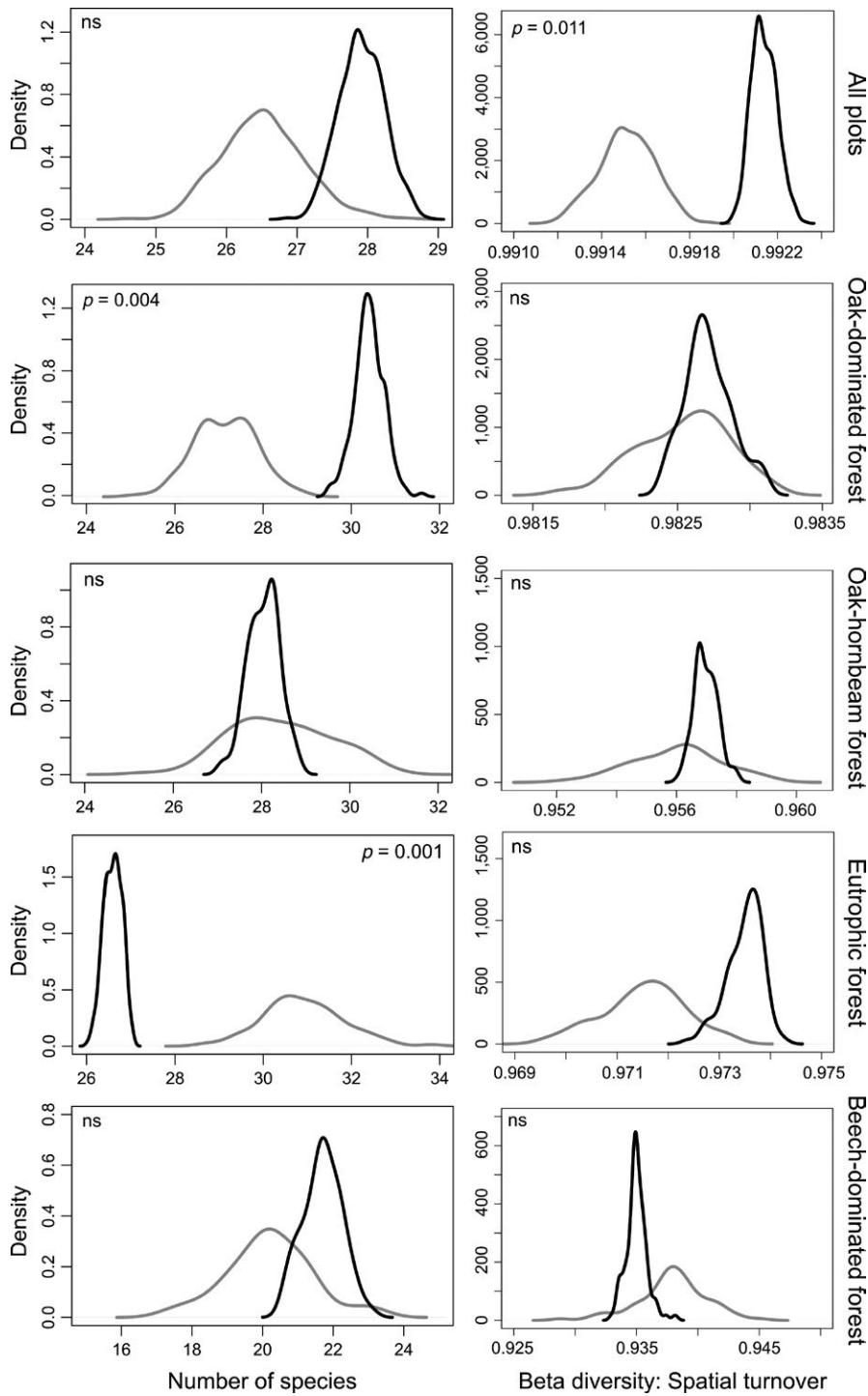


FIGURE 2 Comparison of the number of species per plot and β -diversity between plots with litter raking (grey lines) and without litter raking (black lines) for all plots and specific forest types. Density shows the distribution of 500 bootstrap replicates of the species number and β -diversity

vegetation can also be strongly affected due to high levels of noise stemming from the coarseness of the historical data (see Methods).

We did not detect increased species richness due to the legacy of historical litter raking, although most field experiments supported such a hypothesis. In experiments the increase was to a large extent constituted by annual species that were apparently not able to survive without regular disturbances. A partly connected and probably more plausible explanation lies in scale differences. Litter raking experiments are carried out on areas of a few square metres to a hectare while historical litter raking was a landscape-scale factor that

affected entire local to regional species pools. This may explain why the assumed impact of historical litter raking on herb layer diversity is more complex and differs among forest types. Another difference is the time scale, both regarding the duration of litter raking and the time period that elapsed between raking and vegetation survey.

4.2 | Different responses among forest types

There are several potential mechanisms that may contribute to differences among forest types. First, the intensity of litter raking

TABLE 2 List of selected species diagnostic for acidophilous forest types (following Chytrý & Tichý, 2003)

Species name	Regression coef.	F-value	p-value
<i>Vaccinium vitis-idaea</i>	80.91	12.3	<0.001
<i>Avenella flexuosa</i>	7.66	4.4	0.035
<i>Luzula luzuloides</i>	3.30	12.9	<0.001
<i>Hieracium murorum</i>	1.80	9.5	<0.010
<i>Vaccinium myrtillus</i>	1.74	1.1	0.295
<i>Oxalis acetosella</i>	1.20	1.4	0.243
<i>Dryopteris dilatata</i>	0.95	0.3	0.596
<i>Prenanthes purpurea</i>	0.28	0.1	0.812
<i>Maianthemum bifolium</i>	-0.30	0.1	0.747
<i>Hieracium sabaudum</i> agg.	-0.38	0.3	0.572
<i>Hieracium lachenalii</i>	-0.53	0.4	0.516
<i>Festuca ovina</i>	-0.74	0.4	0.518
<i>Melampyrum pratense</i>	-0.87	0.4	0.527
<i>Calamagrostis arundinacea</i>	-1.16	0.5	0.511
<i>Homogyne alpina</i>	-2.12	0.1	0.751

The statistic shows whether these species are more abundant in plots with historical litter raking (>0) or plots without litter raking (<0). Species are sorted according to the regression coefficient. Significant differences are marked in bold.

applied in various forest types may have differed because of human preference for the litter of some tree species over others (Gimmi & Bürgi, 2007; Pfeffer, 1948). Second, forest types may vary in their sensitivity to litter raking because of differing environmental (mainly soil) conditions. Differences in soil conditions in turn also determine dissimilar vegetation responses. Beer and Ewald (2005) attributed this inconsistency to greater depletion of N on N-rich soils compared to nutrient-poor soils. The change in soil pH can also depend on substrate acidity, because whereas the decomposition of leaf litter on basic substrates will result in pH decrease, the opposite will occur on acidic substrates. Third, forest types may differ in their ability to recover from disturbances, following the colonization credit hypothesis (Nave, Vance, Swanston, & Curtis, 2010). Finally, our data showed that the exploitation of upland vs lowland forests strongly differed (Figure 1; Table 1). To a large extent, such distribution coincides with the distribution of the main forest types. It is then a question of whether the forest types are independent from historical litter raking, i.e., to what extent were they formed by historical management. The legacy of raking on tree species composition was documented in the Swiss Rhone valley, where a significantly lower shift in species composition from pine to deciduous trees was found in stands which were formerly used for grazing and/or litter raking (Gimmi et al., 2010).

Gimmi et al. (2013) argued that no historical raking was practised in the lowland areas in the northwest part of Switzerland in the mid-19th century due to the availability of substitute products, such as straw. This may also explain the low occurrence of

historical litter raking in the lowland areas of Moravia, with the exception of the least forested (or completely deforested) areas and parts of river valleys (Figure 1). However, the Swiss authors did not come to their conclusions directly from archival data on litter raking but from proxy parameters. Specifically, they used the number of cattle per land unit as a proxy for litter demand, and grain production and the area of wet meadows as proxies for products.

The two forest types that responded significantly to litter raking by their species richness were oak forests (negatively) and eutrophic forests (positively). The species impoverishment in oak forests is relatively easy to explain, because this type of forest can be found mostly on nutrient-poor, acidic soils prone to further impoverishment due to litter removal. We argue that mainly species of acidophilous substrates, undemanding as regards soil nutrients, could survive the long-term effects of litter raking. The significant positive effect of historical litter raking in eutrophic forests is more difficult to explain. These forests are dominated by tree species such as lime and ash, producing litter rich in base cations, which results in fertile soils possessing a high buffering capacity (Lundström, Bain, Taylor, & van Hees, 2003). Therefore, high soil buffering capacity was assumed to ensure the resistance to acidification by litter removal. However, in the long run, the removal of noble hardwood litter may have intensified soil impoverishment. This could have suppressed the dominance of competitively strong species and created heterogeneous conditions suitable for plants with various demands on soil acidity and nutrients (Beer & Ewald, 2005). Quite paradoxically, the species enrichment in eutrophic forests historically subject to litter raking can be due to the arrival of species of mesotrophic and acidotrophic substrates normally not occurring there and co-existing with the original nutrient-demanding species.

4.3 | Biotic homogenization due to historical litter raking

Litter raking left a legacy of biotic homogenization in our study region. The mechanical disturbance by raking has most probably led to the local extinctions of sensitive species and the spread of less sensitive species, favouring decreased competition, which resulted in homogenized species assemblages (e.g., Wiegmann & Waller, 2006). The establishment of more similar species communities may have also resulted from consistent soil impoverishment across the environmental gradients.

A historical perspective of the role of traditional management sheds new light on biotic homogenization. Homogenization has been considered a modern threat to the Earth's biota in the context of biotic invasions and other global threats (e.g., McKinney & Lockwood, 1999). Biotic homogenization has been extended to forest vegetation due to game pressure or succession after the abandonment of coppicing (Kopecký, Hédli, & Szabó, 2013; Rooney, Wiegmann, Rogers, & Waller, 2004). Here we show that one specific form of historical management has left a long-lasting legacy in

regional forest β -diversity, rather than in species diversity on local scale (α -diversity).

5 | CONCLUSIONS

In spite of a number of sources of uncertainty in our data, we provide the first quantitative evidence that historical litter raking left a weak but persistent and recognizable legacy in the present forest herbaceous layer. However, our results failed to confirm that litter raking led to the expected ecological changes, namely an increase in acidophilous oligotrophic species and a decrease in Ellenberg indicator values for nutrients and soil reaction. Finer-scale data on past litter raking practices will probably be needed to complement our results.

ACKNOWLEDGEMENTS

The research leading to these results received funding from the European Research Council under the European Union's Seventh Framework Programme (FP7/2007-2013)/ERC Grant agreement no 278065, and the Grant Agency of the Czech Republic project No. 17-09283S. Additional funding was provided by the Long-term Research Development Project RVO 67985939. We thank M. Chytrý and D. Michalčová for providing the forest vegetation samples from the Czech National Phytosociological Database. We also thank I. Bičík for population data from the LUCC Czechia Database.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1 Comparison of raked and non-raked plots according to particular forest types for selected variables assessed in the analyses.

Appendix S2 Detrended Canonical Correspondence Analysis (DCCA) biplot of vegetation data, showing the first and second axes.

How to cite this article: Vild O, Šipoš J, Szabó P, et al. Legacy of historical litter raking in temperate forest plant communities. *J Veg Sci*. 2018;29:596–606. <https://doi.org/10.1111/jvs.12642>