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Litter quality and microtopography as key drivers to topsoil properties and understorey plant diversity in ancient broadleaved forests on decalcified marl

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HIGHLIGHTS

- Litter quality and microtopography were more important than elevation or subsoil properties.
- Litter quality and microtopography showed separate effects, but also reinforced each other.
- Hornbeam litter led to high pH, soil moisture and understorey diversity, especially in depressions.
- Beech litter led to low pH, soil moisture and understorey diversity, especially on local mounds.
- Tree species thus acted as local ecosystem engineer, but together increased habitat diversity.

GRAPHICAL ABSTRACT

Mass of the organic layer just before leaf fall, pH and moisture content of the mineral topsoil (0–5 cm), and understorey cover in 200 7 × 7 m plots in natural deciduous forests on decalcified marl in Luxembourg. Hornbeam = plots dominated by *Carpinus betulus* L.; beech = plots dominated by *Fagus sylvatica* L.; mixed = plots with intermediate amounts of hornbeam and beech. Depressions = local height below average values; low mounds = local height 0–2 cm above average values; high mounds = local height >2 cm above average values. ¹ = significant effect of tree type in a two-factor analysis ($p < 0.05$); ² = significant effect of microtopography; ³ = significant interaction between tree type and microtopography.

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ABSTRACT

In forest ecosystems, litter quality is a major driver for soil and understorey characteristics, but elevation, microtopography and subsoil properties may also be important. We tested the importance of each factor in two ancient mixed forests on decalcified marl, dominated by trees with different litter quality such as European hornbeam, with high-palatable litter, and beech, with low-palatable litter. We mapped elevation, differences in local height (microtopography), tree distribution and understorey cover on slopes ranging from crest to bottom, and sampled 200 7 × 7 m grid cells for characteristics of litter input, understorey, topsoil and subsoil. In both forests, elevation decreased gradually, but microtopography showed irregular patterns of depressions and mounds of a few cm below or above average local height. Tree distribution was not affected by elevation or subsoil properties, but clearly by microtopography. Adult beech was abundant on local mounds, while hornbeam was more common in local depressions. Topsoil and understorey characteristics were mainly affected by litter quality (tree species dominance) and microtopography. Litter quality had separate effects from

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Plant diversity

microtopography, but could reinforce this. High litter quality (hornbeam) and low local height both led to high earthworm activity, low litter mass, high erosion, impermeable clay layers close to the surface, high pH, high soil moisture and high diversity of the understorey. Low litter quality (beech) and high local height both led to low earthworm activity, high litter mass, low erosion, low pH, low soil moisture and low plant diversity. Beech and hornbeam may act as ecosystem engineers, which change habitat conditions and local hydrology, and make habitats more suitable to themselves, and/or unsuitable to the other. However, they also increased spatial complexity of the forest and length of the habitat gradient. This may increase forest biodiversity as a whole, but also resilience to prolonged wet or dry periods.

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1. Introduction

Litter quality is an important driver in forest ecosystems, which affects accumulation of organic matter on the forest floor (e.g., Swift et al., 1979; Aubert et al., 2004), often through activity of soil animals such as earthworms (Pop, 1997; Hättenschwiler and Gasser, 2005; Yang and Chen, 2009). Low-degradable litter generally leads to dense litter layers with distinct organic horizons, while more palatable litter types produce only thin, undifferentiated litter layers (Ponge, 2003). Litter quality may also affect habitat factors such as pH and soil moisture, which are important to plant diversity (Ellenberg et al., 1974).

In tree plantations and common garden experiments, pH values of the topsoil usually decrease under trees with low-degradable litter, due to retarded decomposition and production of organic acids (e.g., Binkley and Valentine, 1991; Neirynek et al., 2000; Aubert et al., 2004; Mueller et al., 2012). Under trees with high-degradable litter, however, pH values may be relatively high, possibly because the trees retrieve base cations from deeper soil layers by the roots (Duvigneaud and Denayer-De, 1970; Mohr and Topp, 2005). Also, earthworms are generally more common under trees with high-palatable litter, and bring base-rich soil material from lower depth to the topsoil (Jongmans et al., 2003). Acidification of the topsoil under trees with low-degradable litter was supported by Kooijman and Cammeraat (2010), who found lower pH values under European beech (*Fagus sylvaticus* L.) than under hornbeam (*Carpinus betulus* L.), which clearly differ in litter quality (e.g., Swift et al., 1979; Laskowski et al., 1995; Aubert et al., 2003, 2004).

Litter quality may also affect habitat factors such as soil moisture. Under trees with low-degradable litter, moisture content of the mineral soil may be relatively low, due to high water storage in dense litter layers (Rode, 1999). Under trees with high-degradable litter, however, water storage in the litter layer is low, and water holding capacity in the mineral soil may further increase due to high earthworm activity and excrements enriched in clay and organic matter (Pulleman et al., 2005). Litter quality effects on soil moisture may be particularly clear in loamy soils on decalcified marl and loess, which are common in NW-Europe and sensitive to clay-eluviation (Blume et al., 2016). In such soils, topsoils are usually relatively porous due to eluviation of clay particles, while the subsoil is clay-rich and water-stagnant or impermeable (Blume et al., 2016). Under trees with high-degradable litter, high earthworm activity may increase the amount of bare soil at the soil surface, which increases erosion of soil particles (van Zon, 1980; Cammeraat, 2002). This brings the water-stagnant subsoil closer to the surface, and increases moisture content of the topsoil (Kooijman and Cammeraat, 2010). In contrast, the topsoil is relatively dry under trees with low-degradable litter, because dense litter layers prevent erosion, and the water-stagnant layers are usually found much deeper in the soil (Kooijman and Cammeraat, 2010).

Litter quality and the associated changes in habitat conditions may also affect diversity of the understorey. Plant species richness is generally higher under trees with high-degradable litter than with low-degradable litter types (van Oijen et al., 2005; van Calster et al., 2008; Wulf and Naaf, 2009; Kooijman, 2010). Trees with high-degradable

litter are even planted to ameliorate understorey diversity in forests affected by high atmospheric deposition. However, while litter quality effects are clear in forest plantations and common garden studies, they may be obscured in more natural forests, in which trees with high or low litter quality may occur in mixed patches. Also, site factors such as subsoil properties and position on the slope play a role, independent of litter quality. Soil pH may be affected by litter quality, but also by depth of soil formation and decalcification (Blume et al., 2016). Also, topslopes are usually better drained than lower slopes, which may lead to different moisture conditions irrespective of litter quality. Microtopography, i.e. variations in local height between local depressions and mounds, may also be an important site factor. Studies on microtopography are rare (Samonil et al., 2016), and local height is largely ignored as factor in relation to understorey diversity. However, in soils with water-stagnant layers in the subsoil, local height may determine whether forest patches are relatively wet or dry (Cammeraat, 2002), which may affect plant species richness (Kooijman and Cammeraat, 2010).

Site factors such as subsoil properties, elevation and microtopography may even influence the type of litter, if trees have different habitat preferences. Beech trees are characterized by low-degradable litter (Swift et al., 1979; Aubert et al., 2004), but are also sensitive to wet conditions (Bolte et al., 2007; Leuschner and Ellenberg, 2017), and may thus be more common in topslope positions and local mounds. Hornbeam trees possess high-degradable litter, but are also more wet-tolerant than beech trees, and may thus be more common lower down the slope or in local depressions. Differences in pH may then be due to differences in litter quality between the tree species, but also to the site factors which determined establishment of the trees.

The objective of this study was to test whether litter quality effects on topsoil and understorey characteristics could be separated from potential effects of site factors such as subsoil properties, elevation and microtopography. This has never been done before, as many studies address litter quality (e.g., Binkley and Valentine, 1991; Neirynek et al., 2000; Aubert et al., 2004; Marechal et al., 2010; Mueller et al., 2012), but no other factors. We selected two ancient forests in Luxembourg, dominated by European hornbeam (*Carpinus betulus* L.) and beech (*Fagus sylvatica* L.), which are common species in western Europe, but clearly differ in litter quality (e.g., Swift et al., 1979; Laskowski et al., 1995; Aubert et al., 2003, 2004). The two forests were located on decalcified marl, which is characteristic of large parts of western Europe, sensitive to clay-eluviation and thus very suitable to detect changes in habitat conditions other than pH (Blume et al., 2016). We mapped tree distribution, elevation, microtopography and understorey cover. We also installed two measurement grids on forest slopes along a local brook from crest to bottom, each consisting of 100 cells of 7x7m, to measure variables related to tree cover and litter input, depth of soil formation and decalcification, as well as topsoil and understorey characteristics. We first tested hypothesis 1 that beech and hornbeam did not differ in distribution patterns, which may confound potential effects of litter quality. We then tested hypothesis 2 that litter quality was more important for topsoil and understorey characteristics than elevation, microtopography and subsoil properties. We then grouped the 200

Fig. 1. Location of the study area Schrondweilerbësch near Diekirch, Luxembourg, indicated by the white area inside the circle. In the figure on the right, the locations of the grids within the Schrondweilerbësch area, north and south of the main road, are indicated. Both grids are positioned along a brook, and show a diagonal elevation gradient of 6.3 and 5.8 m for north and south respectively.

Base map source: map.geoportail.lu.

grid cells in different classes of litter quality and local height, and tested hypothesis 3 that litter quality and microtopography, which were clearly correlated, also had separate effects.

2. Methods

2.1. Study area

The study was carried out in ancient forest, situated in the Keuper area of the Gutland region in Luxembourg (Fig. 1). The region has a temperate humid climate, with average precipitation of 788 mm per year, and rainfall in all months. The forests are dominated by European hornbeam (*Carpinus betulus* L.) or European beech (*Fagus sylvatica* L.), intermixed with common oak (*Quercus robur* L.). Hornbeam has generally higher initial N-content, lower lignin:N ratios, is preferentially eaten

by earthworms and often disappears from the forest floor in a few months (Kooijman and Cammeraat, 2010). Beech litter, in contrast, is less palatable, and in most cases accumulates in dense organic layers. The forests show a patchy structure, ranging from shallow, relatively wet depressions dominated by hornbeam with high understorey cover, to relatively dry mounds of a few cm height, dominated by beech with dense litter layers (Fig. 2). The forests were already indicated on the topographic map of 1777 (le Ferraris, 1777), and, except for some harvesting of oak trees, mainly undisturbed by man (Cammeraat, 2002). Vegetation types ranged from Galio-Carpinetum under Hornbeam to Galium odorati-Fagetum under Beech (Niemeyer et al., 2010).

Bedrock consists of nearly horizontal strata of dolomitic marls of the Triassic Steinmergelkeuper formation. Humus forms ranged from Vermimull under hornbeam to Mullmoder under beech (Green et al.,

Fig. 2. Different forest patches in Luxembourg Keuper forests, with a shallow depression with hornbeam and high understorey cover in the front, and a slightly higher and drier local mound with beech and a dense litter layer in the back of the picture. Photograph taken by Jan van Arkel.

1993). Soils generally have a AhE-Bg-Bw-C profile, and a clear to abrupt textural change between the topsoil (AhE) and the subsoil (Bg-Bw-C). Soil type ranged from stagnic Luvisol to luvic Planosol (FAO, 2014), also classified as Aquic Distric Eutrochrept (Soil Survey Staff, 2014). The topsoil has a siltloam texture, due to lateral eluviation of clay, but the subsoil is clay-rich (van den Broek, 1989). This leads to a strong decrease in hydraulic conductivity with increasing depth, and perched water tables after heavy rain. In the topsoil, macropores, derived from earthworm and mole activity, serve as preferential flow paths of water, and their spatial distribution plays an important role in the hydrological response of the area (Cammeraat, 2002).

Two forested slopes were selected, which were both considered to be representative for ancient mixed forest on decalcified marl (Duijsings, 1985; van den Broek, 1989; Cammeraat, 1992, 2002; Kooijman and Cammeraat, 2010). They were located north and south of the road that separates the forest areas. In each forest, a measurement grid was installed on a gently undulating slope, from crest to bottom, located along a local brook. Each grid consisted of 10×10 cells of 7×7 m. The size of the grid cells was found to be representative for hornbeam or beech patches in mixed forests in earlier studies (Kooijman and Cammeraat, 2010). In each grid, the main slope was running from crest to bottom, but also from the top at the upstream side of the brook to the bottom near the downstream part, and had a general inclination of 6%. In each grid, many parameters were measured in the centre of each grid cell (Appendix 1; supplementary materials). However, tree distribution, elevation, local height and understorey cover were mapped in each grid in more detail.

2.2. Tree and undergrowth mapping

In each grid, the locations, species and circumferences at breast height of all trees were recorded in October 2009. Both grids showed a mixture of beech and hornbeam, with 69 beech and 120 hornbeam trees in the north forest (North), and 126 beech and 114 hornbeam trees in the south forest (South). Approximately one third of the trees had diameter <15 cm and were considered as young trees, while two third had diameter >15 cm, and were considered as adult trees. Oak trees were less common with 45 and 37 trees in North and South respectively, and did not affect habitat factors and undergrowth diversity in our previous study (Kooijman and Cammeraat, 2010).

Tree dominance index (TDI) is a proxy for litter quality, based on dominance by beech or hornbeam. Tree dominance index was calculated for all 200 grid cells, to test relationships between litter quality and subsoil properties or soil and understorey characteristics. For each hornbeam and beech tree in the grid, its relative importance was calculated based on the circumference at breast height, with the formula: (species factor * circumference)/average circumference. The species factor was -1 for hornbeam and 1 for beech, to discern the two species, while allowing for a continuous scale to test relationships with other continuous variables. For each tree, the relative importance values were interpolated in ESRI ArcGIS 10 using inverse distance weighted interpolation from the Geostatistical Analyst extension, and exported to a raster with standard grid cell size. This raster was sampled at the centre points of the grid cells with the Spatial Analyst toolbox, to obtain a TDI value for each grid cell. The TDI was treated as a continuous variable in statistical analyses, but was also used to distinguish between hornbeam-dominated, mixed and beech-dominated plot types. Hornbeam plots had TDI values of -0.40 or lower, beech plots values of 0.40 or higher, and mixed plots values in between.

To test the assumption that stem circumference was indeed representative for the relative influence of a tree, TDI was compared to field estimates of cover values and actual litter input of each species in each grid cell. Cover values were visually estimated in October 2010, before leaf fall. Fresh litter input was collected in 25×25 cm plots in the centre of each grid cell in December 2010, right after leaf fall, and separated into different species. Beech:hornbeam ratios were calculated as

beech/(beech + hornbeam) cover or litter. Beech:hornbeam ratios highly correlated with TDI, with $R^2 = 0.54$ for cover values and 0.46 for litter input, which further supported that TDI could be used as proxy for litter quality.

In each grid, understorey cover was manually mapped in May 2010, in two different classes: dense litter layers ($<15\%$ plant cover) and high undergrowth cover ($>15\%$ plant cover). The maps were scanned, digitized for spatial analysis and imported in ESRI ArcGIS. Understorey cover and plant species composition were also recorded in each separate grid cell. Each vascular plant species present was listed, and cover values were estimated as percentage. Nomenclature was according to van der Meijden (2005). Bryophytes were rare on the forest floor, and mainly consisted of *Rhytidiadelphus triquetrus* (Hedw.) Warnst. In each plot, presence of tree seedlings with more than just cotyledons, which had actually established, was also noted.

2.3. Elevation and microtopography

Elevation, as proxy for the position on the slope, and microtopography were measured in May 2011, in and around each grid, on a more detailed scale than the 7×7 m grid cells. Point based elevation data were collected with a total station, a laser-operated theodolite. In the North forest, 929 points were measured with an average spacing of 3.4 m, and in the South forest 773 points with an average spacing of 3.9 m. In both areas, 75% of the point-based measurements were used to create a Digital Elevation Model (DEM) with 1×1 m grid cells using linear interpolation. The remaining 25% of the points were used to estimate average interpolation accuracy, which was found to be approximately 4 and 3 cm for North and South respectively. With this DEM, elevation could be calculated, which in both grids gradually decreased from the crest at the upstream side of the brook, to the bottom near the downstream part. Differences in elevation between upper and lower corners of the grid were 6.3 m for North and 5.8 m for South.

Microtopography, i.e. small differences in local height, was estimated by calculating relative height (in cm) above a mean surface. This mean surface was calculated by subtracting the elevation value of a centre grid cell in a moving window in the DEM from the mean elevation of this moving window. The window size varied between 9×9 , 11×11 and 13×13 cells, which resembled microtopography at a scale of 9 , 11 , and 13 m respectively. We continued with the intermediate model at a scale of 11 m, which was large enough to calculate a mean surface elevation, and small enough to distinguish patterns of small scale relief. The output was a map with high and low areas with respect to the surrounding area. In North, local height varied between -2.2 and 4.4 cm, and in South between -3.0 and 5.8 cm. The microtopographical map was subdivided in four classes: deep depressions with local height values >2 cm below average, shallow depressions with local height $0-2$ cm below average, low mounds with local height $0-2$ cm above average, and high mounds with local height >2 cm above average.

Apart from the more detailed maps, elevation and local height were also calculated for each of the $200 \times 7 \times 7$ m grid cells, as the mean from the nine central 1×1 m subcells. Elevation and local height were treated as continuous variable for the 200 grid cells, but local height was also used to distinguish between different microtopographical classes: deep depressions, shallow depressions, low mounds and high mounds, with local height values as above. However, the deep depression grid cells consisted of three hornbeam plots, one mixed and one beech plot, which was too low for a separate class. Deep and shallow depressions were thus combined in one class.

2.4. Soil sampling and laboratory analysis

The entire organic layer was manually sampled in 25×25 cm plots in the centre of each of the 200 grid cells, at the end of October 2009, just before leaf fall, to obtain a minimum estimate of the mass of the organic

layer. Fresh litter was still rare in October, but excluded if present. As already mentioned, litter input was sampled in December 2010, right after leaf fall. Fresh litter was collected in 25×25 cm plots in the centre of each grid cell, and separated into different species.

The mineral topsoil was sampled inside the 200×25 cm plots in the centre of each grid cell in October 2009. We concentrated on the upper 5 cm, because litter quality effects were expected especially in the topsoil. The mineral topsoil was sampled in three subsamples in metal rings of 100 cm^3 , which were combined to one composite sample. Organic layer and topsoil samples were collected within three days, to restrict variability in soil moisture as much as possible. Rainfall in the area had been relatively low with 11.8 mm in the three weeks before sampling, while the average for the whole month is 75.8 mm. During the sampling period, some rain fell at night, but in very low amounts (0.2 mm).

Subsoil parameters such as depth of the C-horizon (soil depth), which is an indicator of the depth of soil formation, and decalcification depth (lime depth) were determined in the centre of each of the 200 grid cells with an auger and 10% HCl solution in autumn 2009 and spring 2010. Depth of the clay-rich B-horizon, which acts as an impermeable layer to rain water, was determined with a small auger. Depth of the B-horizon was measured 3–4 times in the centre of each grid cell, with mean values used as input value for statistical analysis.

Perched water tables, which are important to hydrology and soil erosion, only occur after heavy rain (Cammeraat, 2002; Kooijman and Cammeraat, 2010). Depth of the perched water table was measured after heavy rain of 28 mm in the night in December 2010. In the morning, a hole was made with an auger in the central part of each grid cell until water was visible. Perched water tables were measured the same morning. Water tables were also measured the day after, in the opposite order. Water tables had then generally dropped 6–8 cm, but distribution patterns were similar to the day before. In two plots in the north forest, and four plots in south, perched water tables were absent, and not taken into further account. Plots without perched water mostly consisted of beech plots on high mounds near the crest of the slope.

The pH of the mineral topsoil samples was determined in demineralized water with 1:2.5 weight:volume ratio. Samples of organic layer and mineral topsoil were dried for 48 h at 70°C and weighed. For the mineral samples, dry bulk density and volumetric moisture content were calculated. With bulk density, porosity was calculated, based on rock particle density of 2.65 g cm^{-3} (Scheffer, 1982). Air-filled pore space was calculated by subtracting volumetric moisture content from porosity. Corrections for soil organic matter, which did not consistently differ between hornbeam and beech and ranged between 4 and 5%, were not applied. Soil organic C and N content were measured with a CNS analyzer (Westerman, 1990). Distribution of dry macro-aggregates in the topsoil was measured by sieving over 16, 8, 4.8, 4, 2, 1, 0.5, 0.25, 0.125 and 0.106 mm sieves (Cammeraat and Imeson, 1988). Because we focused on the general pattern, rather than detailed aggregate distribution, fractions smaller and larger than 4.8 mm were combined as small and large macro-aggregates respectively.

2.5. Statistical analysis

To test whether hornbeam and beech trees had a preference for particular microtopographical positions, or were preferentially located in areas with high understorey cover or dense litter layers, the tree maps were combined with the microtopographical and understorey maps in ESRI ArcGIS 10. Distribution patterns were calculated for young and adult trees separately. We tested whether the distribution of microtopographical classes differed from an equal distribution with chi-square tests (Mason et al., 1994). The critical χ^2 value for three degrees of freedom was 7.815. We also tested whether the distribution of individual trees over microtopographical classes differed from the distribution of microtopographical classes themselves or from the

distribution of other tree species. We did this for the entire dataset, but also for the areas with high undergrowth cover or dense litter layers separately.

The $200 \times 7 \times 7$ m grid cells formed the basis for the statistical analysis of subsoil, topsoil and understorey characteristics, as they were sampled on that scale. For some parameters, the two forests slightly differed. In North, average pH was 4.9, average C:N ratio was 14.4 g g^{-1} and average understorey cover was 20%; in South, average values were 5.1, 13.8 g g^{-1} and 26% respectively. However, the two forests showed similar response patterns to abiotic site factors and TDI (Tree dominance index), and data were combined in one dataset, and tested for normality. The relative importance of different site factors to litter input, topsoil and understorey characteristics was tested with stepwise multiple linear regression (Cody and Smith, 1987). The site factors were (1) north or south forest, (2) elevation, (3) depth of the C-horizon, (4) lime depth, (5) TDI and (6) local height. Correlations between individual site factors were tested with Pearson correlation tests (Cody and Smith, 1987), and were significant if $p < 0.05$.

The potential effects of TDI and local height, which were most important to topsoil and understorey characteristics, were analyzed in more detail. Differences in distribution of TDI types (hornbeam-dominated, mixed forest and beech-dominated plots) over different microtopographical classes (depressions, low mounds and high mounds) were tested with chi-square tests, with expected frequencies based on the total amounts of plots in each TDI and microtopographical class (Mason et al., 1994). The critical χ^2 value for two degrees of freedom was 5.991. The effects of TDI and microtopography on topsoil and understorey characteristics were tested with two-way general linear models (Cody and Smith, 1987). Effects were significant if $p < 0.05$. When significant effects were present, differences between individual mean values were post-hoc tested with Lsmeans tests.

3. Results

3.1. Tree distribution in relation to microtopography and understorey cover

The Tree dominance index (TDI) map showed a patchy distribution of areas dominated by hornbeam or beech (Fig. 3). Tree dominance index was not affected by elevation ($R = -0.02$), as this gradually decreased from the upper left to the lower right corner of the grids (data not shown). Tree dominance index was also not affected by subsoil properties such as depth of the C-horizon ($R = -0.00$) or decalcification ($R = 0.10$). However, TDI significantly correlated with local height ($R = 0.27$).

Depressions accounted for 46% of the combined surface area of North and South, and local mounds for 54% (Fig. 4). The distribution of the microtopographical classes did not significantly differ from an equal distribution ($\chi^2 = 6.78$; $p > 0.05$; Fig. 5). For young hornbeam and beech trees, distribution patterns did also not differ and young trees and adult hornbeam could apparently grow anywhere. This was also the case for adult hornbeam. However, adult beech showed clear habitat preferences. Distribution of adult beech significantly differed between microtopographical classes ($\chi^2 = 25.97$; $p < 0.01$), and >40% of adult beech was found on high mounds, but <30% in depressions. Adult beech also differed from adult hornbeam ($\chi^2 = 44.18$; $p < 0.01$), which was more common than beech on low mounds and in depressions. Adult beech also differed from young beech ($\chi^2 = 30.29$; $p < 0.01$), which was occurring everywhere.

Areas with high or low understorey cover were not equally distributed over the microtopographical classes ($\chi^2 = 12.95$; $p < 0.01$). High understorey cover was especially found in depressions, while dense litter layers predominated on high mounds. For most tree types, distribution patterns in relation to understorey cover did not differ from expected frequencies. However, adult beech was more common in areas with dense litter layers ($\chi^2 = 79.78$; $p < 0.01$), especially on high mounds.

Fig. 3. Tree dominance index (TDI), the relative tree dominance of hornbeam and beech in two Luxembourg Keuper forests North and South of the main road. The TDI is based on an inverse distance weighted interpolation of the tree location data of hornbeam and beech, taking into account the circumference at breast height.

3.2. Potential effects of site factors on topsoil and understorey characteristics

For topsoil characteristics, the factor forest was important to some extent for pH and C:N ratio of the mineral topsoil, and the amount of small aggregates (Table 1). Subsoil properties such as soil depth and lime depth were not relevant to topsoil characteristics, and explained 2% of the additional variance at most. Average depth of the C-horizon was $45 (\pm 12)$ cm, and lime depth around $51 (\pm 15)$ cm below the surface. Elevation was also not relevant. Elevation only correlated with perched water table after heavy rain, indicating that water tables were

higher at the lower elevations near the brooks. For most topsoil characteristics, TDI and local height were the most important explanatory variables, except for soil C content. Tree dominance index especially affected mass of the organic layer, air-filled pores, small aggregates and depth of the clay-rich subsoil, and local height C:N ratio, pH and moisture content of the topsoil.

Understorey cover was to some extent affected by the factor forest. However, this parameter was mostly affected by local height. For plant species number, TDI was more important. Hornbeam and beech juveniles were only slightly affected by TDI, and even less by other site factors.

Fig. 4. Tree distribution, microtopography and understorey characteristics in two Luxembourg Keuper forests, North and South of the main road. The position of each individual beech ($\blacktriangle$) and hornbeam ($+$) tree is indicated. Microtopography is given in cm below or above average local height. Shaded areas have dense litter layers (<15% understorey cover); unshaded areas have high understorey cover (>15%).

Fig. 5. Distribution patterns for different microtopographical classes and hornbeam and beech trees. A = total area; B = areas with high undergrowth cover only; C = areas with dense litter layers only. Microtopographical classes are given in cm below or above average local height; young trees have diameter <15 cm, and adult trees >15 cm.

3.3. Effects of tree dominance and microtopography on topsoil and understorey characteristics

In the more detailed analysis of TDI and local height, the distribution of plot types over microtopographical classes again showed significant differences, with χ^2 values of 6.43 ($p < 0.05$) for hornbeam plots, and 6.64 ($p < 0.05$) for beech plots. In the depression plots, which included shallow depressions with local height <2 cm below average, 44% was dominated by hornbeam, but only 21% by beech. In the high mound plots, however, 22% was dominated by hornbeam, but 56% by beech. Hornbeam plots were thus more abundant than expected in depressions, and beech plots on high mounds.

Topsoil and understorey characteristics were generally affected by both TDI and microtopography, which had separate effects, but could also reinforce each other (Figs. 6–8). High litter quality had generally similar effects as low local height, while low litter quality and high local height were also comparable. The largest differences were thus found between depressions with hornbeam and high mounds with beech, with intermediate values for other combinations of microtopographical position and tree type.

In hornbeam-dominated plots, mass of the litter layer was generally low and ranged around $0.4\text{--}0.5\text{ kg m}^{-2}$ in all microtopographical classes (Fig. 6). In beech plots, litter mass was much higher, and increased from 0.8 kg m^{-2} in depressions to 1.3 kg m^{-2} on high mounds. Carbon stocks in the mineral topsoil were not affected by TDI or local height, but C:N ratios were significantly lower in depressions with hornbeam than in high mounds with beech. Topsoil pH values showed similar patterns, and pH was significantly higher in depressions with hornbeam than on high mounds with beech.

Topsoil characteristics related to soil water regime were also affected by TDI and local height (Fig. 7). Bulk density was higher in hornbeam than in beech plots, albeit mainly in depressions. Soil moisture was also higher in depressions with hornbeam than on high mounds with beech, while air-filled pore space and the amount of small aggregates showed the opposite pattern. The impermeable clay-rich subsoil was close to the surface in hornbeam plots, but found much deeper in the soil in beech plots, especially on high mounds. Perched water tables after heavy rain, which stagnated on the impermeable clay-rich subsoil, were also affected by TDI, and were close to the surface under hornbeam, and deeper in the soil under beech. In 14 plots, mostly dominated by hornbeam, perched water tables even reached the surface, which could lead to overland flow. However, perched water tables were also affected by microtopography, with water tables close to the surface in depressions and on low mounds, but deeper in the soil on high mounds.

Understorey cover was significantly higher in depressions with hornbeam than on high mounds with beech (Fig. 8), in accord with the mapping patterns. Understorey cover was 31% on average in depressions with hornbeam, but only 12% in high mounds with beech. Plant species diversity was also higher in hornbeam depressions than on beech mounds. Plant diversity was especially low on high mounds, due to lower presence of wet-tolerant spring ephemerals such as *Circaea lutetiana* and *Galium odoratum* (Appendix 2; supplementary materials). The spring ephemeral *Anemone nemorosa* occurred in all plots, but with much higher cover values in depressions than on high mounds. Juvenile hornbeam and beech plants were to some extent affected by TDI or local height, and were less common or absent in high mounds with beech. However, hornbeam juveniles were found in approximately 22% of the plots, while beech juveniles were present almost everywhere.

4. Discussion

4.1. Slope position and subsoil characteristics unimportant

Position on the slope and subsoil characteristics often affect tree distribution and topsoil properties (Ellenberg et al., 1974; Blume et al., 2016). However, in our study, this was not the case. For most topsoil and understorey characteristics, elevation was not relevant. This may be due to the only gradually changing slope, and elevation differences of <7 m. Elevation was mainly relevant to the perched water table after heavy rain, which increased from crest to bottom due to the down-slope movement of water.

Decalcification depth, which may affect pH and tree distribution patterns in many soil types (Ellenberg et al., 1974; Blume et al., 2016), was also not relevant. Erosion of the topsoil was probably not high enough for substantial differences in depth to the lime-rich soil layers. Also, lime-rich conditions generally started around 51 cm below the surface.

Table 1

Stepwise linear regression with site factors as independent variables, and topsoil and understorey characteristics as response variables. Soil depth = depth of the C-horizon; lime depth = depth of decalcification; TDI = tree dominance index, a proxy for litter quality. For each response variable, site factors explaining >10% of the variance are given in bold.

	Forest	Soil depth	Lime depth	Elevation	TDI	Local height	Total model R ²	Model p value
Mass organic layer (g m ⁻²)	0.01	0.02	0.01	0.03	0.33	0.05	0.45	0.0001
C-content topsoil (kg m ⁻²)	–	0.01	–	0.05	0.01	–	0.07	0.008
C:N ratio topsoil	0.07	–	–	–	0.05	0.22	0.34	0.0001
pH _{H2O} topsoil	0.06	0.01	0.01	–	0.04	0.12	0.24	0.0001
Bulk density (g cm ⁻³)	0.03	–	–	–	0.06	0.04	0.13	0.0001
Volumetric soil moisture (%)	0.02	–	0.01	–	0.09	0.16	0.30	0.0001
Air filled pores (%)	0.03	–	–	0.03	0.20	0.09	0.35	0.0001
Small aggregates (%)	0.09	–	0.01	0.03	0.12	0.04	0.29	0.0001
Depth clay-rich B (cm)	0.02	–	–	–	0.44	0.02	0.48	0.0001
Depth perched water table (cm)	0.03	–	0.03	0.14	0.06	0.04	0.30	0.0001
Understorey cover (%)	0.07	–	0.01	–	0.07	0.15	0.31	0.0001
Understorey species number	–	0.01	0.01	0.01	0.12	0.03	0.19	0.0001
Hornbeam juveniles (presence)	–	–	0.02	0.01	0.03	–	0.06	0.027
Beech juveniles (presence)	0.02	0.01	0.02	0.02	0.05	0.03	0.15	0.0001

This is approximately 6 cm below the impermeable B-horizon, which prevents contact with the topsoil (Cammeraat, 2002).

4.2. Microtopography as key factor

Studies on microtopography are rare (Samonil et al., 2016), and local height is largely ignored as habitat factor. Nevertheless, microtopography was an important driver of tree distribution, topsoil and understorey characteristics. In depressions, soil moisture was relatively high, probably because the impermeable subsoil and perched water tables after heavy rain were close to the surface. This may lead to high earthworm activity, and low mass of the organic layer, in accord with Yang and Chen (2009). High earthworm activity may also increase

clay content (Pulleman et al., 2005; Kooijman and Cammeraat, 2010), which leads to higher water holding capacity and soil aggregation, lower amounts of air-filled pores, and further increased soil moisture. High earthworm activity may also counteract acidification, and increase pH (Jongmans et al., 2003).

High pH and soil moisture may in turn explain high understorey cover and diversity in depressions, and presence of wet-tolerant plant species such as *Circaea lutetiana* and *Ficaria verna* (Ellenberg et al., 1974). In NW-Europe, species richness is generally higher at high than at low pH, due to the higher regional species pool for soils with high pH (Pärtel, 2002). Also, high soil moisture is advantageous to understorey species when photosynthesis is hampered by low light, because stomata can remain open. However, the plants have to tolerate

Fig. 6. Mass of the organic layer and C-content, C:N ratio and pH of the topsoil (0–5 cm) in different combinations of tree type and microtopography in natural forests on decalcified marl in Luxembourg. Depression = local height below average; low mound = local height 0–2 cm above average; high mound = local height > 2 cm above average. Values are mean values ($n = 4–45$) and standard errors. ¹ = significant effect of tree type ($p < 0.05$); ² = significant effect of microtopography; ³ = significant interaction between tree type and microtopography; ^{ns} = not significant.

Fig. 7. Characteristics of the topsoil (0–5 cm) related to soil moisture regime in different combinations of tree type and microtopography in natural forests on decalcified marl in Luxembourg. Depression = local height below average; low mound = local height 0–2 cm above average; high mound = local height > 2 cm above average. Values are mean values (n = 4–45) and standard errors. ¹ = significant effect of tree type (p < 0.05); ² = significant effect of microtopography; ³ = significant interaction between tree type and microtopography.

oxygen-poor conditions from time to time. In depressions, soil moisture was relatively high even after low rainfall in the weeks before sampling, and may rise to 52% at field capacity (Kooijman and Cammeraat, 2010). At that point, air-filled pore space decreases to 17%, which is close to the aeration limit of 10%, when the amount of oxygen is clearly restricted (Zou et al., 2000).

Local mounds were however relatively dry, because impermeable subsoils and perched water tables after heavy rain were located deeper in the soil. Some of the high mound plots did not even show perched water tables after heavy rain. Understorey cover and diversity were lower than in depressions, possibly because photosynthesis was hampered by low light and drought stress. Also, high mounds had low pH because acidification of the topsoil was not counteracted by digging earthworms, which may further reduce plant diversity (Pärtel, 2002).

4.3. Litter quality effects

4.3.1. Hornbeam-dominated plots

Litter quality was important to topsoil and understorey characteristics as well. Moreover, litter quality effects were independent from microtopography. In accord with existing literature (e.g., Swift et al., 1979; Ponge, 2003; Aubert et al., 2004), hornbeam-dominated plots showed rapid litter decomposition in all microtopographical positions, due to its high palatability to earthworms (Pop, 1997; Aubert et al., 2003). We have no data on earthworm biomass, but in Kooch et al. (2011), earthworm abundance was more than two times higher under hornbeam than under (oriental) beech. Under hornbeam, pH values were relatively high, because acidification of the topsoil was counteracted by digging earthworms (Jongmans et al., 2003). Also, pH

Fig. 8. Understorey characteristics in different combinations of tree type and microtopography in natural forests on decalcified marl in Luxembourg. Depression = local height below average; low mound = local height 0–2 cm above average; high mound = local height >2 cm above average. Values are mean values ($n = 4–45$) and standard errors. ¹ = significant effect of tree type ($p < 0.05$); ² = significant effect of microtopography.

may further increase with retrieval of base cations by tree roots from deeper layers. This process was probably stronger under hornbeam than under beech, since cation uptake is higher (Duvigneaud and Denayer-De, 1970; Mohr and Topp, 2005).

Hornbeam plots were also relatively wet, even on local mounds, due to digging earthworms, which compensate for clay-eluviation from the topsoil with soil material from deeper layers (Pulleman et al., 2005). Higher clay content leads to higher water holding capacity, and lower amounts of air-filled pores (Kooijman and Cammeraat, 2010). Also, the impermeable subsoil was closer to the surface under hornbeam, probably due to erosion of soil particles from the topsoil. Under hornbeam, during part of the year, the soil is only partly covered with litter, and thus sensitive to splash erosion (van Zon, 1980; van Hooft, 1983). Erosion of soil particles is further increased by pipe flow through mole channels, which is common under hornbeam, as moles are attracted by the high amounts of earthworms (Cammeraat, 2002). Shallow topsoils in turn lead to higher perched water tables after heavy rain, which could lead to local overland flow and even more erosion, especially when hornbeam is growing in depressions (Cammeraat, 1992). In our study, perched water tables reached the surface of 14 mostly hornbeam-dominated plots.

The relatively wet and base-rich soils under hornbeam lead to high understory cover and diversity, due to higher species pools for high pH soils (Pärtel, 2002), tolerance to wet conditions and higher photosynthesis when the soil is moist. Also, dense organic layers were absent, which may hamper growth of spring ephemeral species (van Oijen et al., 2005; van Calster et al., 2008).

4.3.2. Beech-dominated plots

Beech-dominated plots also behaved according to existing literature (e.g., Swift et al., 1979; Ponge, 2003; Aubert et al., 2003, 2004). Under

beech, decomposition was low, and the organic layer consisted of several generations of litter. In the topsoil, pH values were also lower under beech than under hornbeam, in accord with e.g., Norden (1994), Neirynck et al. (2000); Aubert et al. (2004), Hagen-Thorn et al. (2004) and Kooch et al. (2011). Under beech, leaching of base cations was probably relatively high, because flow of water through the soil matrix predominated over pipe flow, due to low earthworm and mole activity (Cammeraat, 2002). Also, acidification was not counteracted by digging earthworms.

Beech plots were also relatively dry, due to high water retention in the dense litter layers (Rode, 1999). Also, the impermeable subsoil was found much deeper in the soil than under hornbeam, because dense organic layers protect the soil against erosion of larger soil particles (Lee and Foster, 1991; Oades, 1993; Greene and Hairsine, 2004). In addition, the topsoil was more porous under beech than under hornbeam. As matrix flow predominates over pipe flow (Cammeraat, 2002), clay eluviation from the topsoil may be higher under beech than under hornbeam, and loss of clay is not compensated by digging earthworms. As a result, perched water tables after heavy rainfall were relatively low, which prevented overland flow, and led to drier conditions in general.

The dry and acidic beech soils in turn led to low understory cover and diversity. Photosynthesis may already be restricted by low light, and further hampered by dry conditions (Vincke and Celvaux, 2005). Also, the species pool for acidic soils is lower than for base-rich soils (Pärtel, 2002). In addition, high ammonium levels under beech could be a problem (Kooijman, 2010), as many species preferentially take up nitrate (Falkengren-Grerup, 1995). Ammonium or aluminium may even become toxic below pH 4.5 (van den Berg et al., 2005; Zvereva et al., 2007), which was the case in many beech plots. Also, growth of spring ephemerals may be hampered by the thick organic layers, and

allelopathic effects may play a role as well. For European beech, data are not available, but Hane et al. (2003) described the negative impact of beech leaf leachates on sugar maple seedlings for American beech.

4.4. Microtopography and litter quality combined

Microtopography and litter quality are thus both important drivers of habitat differentiation in mixed forests on decalcified marl. Each had separate effects, which may counteract or reinforce each other. Young hornbeam and beech trees established everywhere, irrespective of local height, which is in accord with their wide range in habitat factors and co-occurrence in forests (Ellenberg et al., 1974; Wolters and Stickan, 1991; Brunet et al., 1997; Kooijman and Martinez-Hernandez, 2009; Niemeyer et al., 2010). If hornbeam establishes on local mounds, high litter quality would increase earthworm activity and counteract the acidification and clay eluviation processes characteristic for higher local height. Similarly, if beech establishes in local depressions, earthworm activity and erosion may be reduced, and pre-existing differences wiped out. However, if hornbeam establishes in local depressions, or beech on local mounds, litter quality and microtopography reinforce each other.

In hornbeam plots in depressions, erosion and lowering of the soil surface are stimulated by both litter quality and microtopography, and lead to development of relatively wet and base-rich habitats. Also, in beech plots on high mounds, both low litter quality and high local height lead to development of relatively dry and acidic soils. However, the most extreme wet and dry habitats did probably not develop within one tree generation. Slope denudation was estimated as 3.4 cm in thousand years for the entire slope (Duijsings, 1985, 1987), but could increase to 13 cm in thousand years in areas with regular overland and pipe flow (Cammeraat, 1992). This means that lowering of the soil surface with 8 cm, the difference between hornbeam depressions and beech mounds in depth of the impermeable subsoil, could take place within thousand years. However, more time is needed for formation of a typical soil profile under beech on high mounds. In such a profile, the impermeable subsoil was >15 cm below the surface, and the clay-impooverished topsoil >15 cm thick. For such a soil profile, several thousand years are needed, as development of a 20 cm thick clay-impooverished topsoil would require 3500–9400 years (van den Broek, 1989). This time span implies that more than one tree generation is needed. Also, the trees should mainly consist of beech, because establishment of hornbeam would counteract such soil development. As both beech and hornbeam have been around for 4000 years (Slotboom, 1963), prolonged persistence of beech is possible. However, this may also require some habitat preferences.

4.5. Habitat preferences of beech and hornbeam

Despite the wide range in habitat factors and co-occurrence of hornbeam and beech in many forests (Ellenberg et al., 1974; Wolters and Stickan, 1991; Brunet et al., 1997; Kooijman and Martinez-Hernandez, 2009; Niemeyer et al., 2010), distribution patterns over microtopographical positions differed between adult trees. Beech showed a clear preference for high mounds, probably because it generally avoids sites with stagnic soil types, flooding or high water levels (Bolte et al., 2007; Leuschner and Ellenberg, 2017). On sites with moderate soil moisture and acidity, however, beech is the most competitive tree species of Europe. Beech may thus have outcompeted hornbeam from the higher mounds, even though the latter species could grow anywhere. Beech may also have made the high mounds less suitable for hornbeam, because pH was below 4.5 in many beech plots. At this pH, aluminium may become toxic (van den Berg et al., 2005; Zvereva et al., 2007), especially because cation uptake is higher for hornbeam than for beech (Duvigneaud and Denayer-De, 1970).

In depressions, hornbeam was more common than beech. As already mentioned, beech generally avoids sites with stagnic soil types, flooding

or high water levels (Ellenberg et al., 1974; Bolte et al., 2007; Leuschner and Ellenberg, 2017). However, hornbeam could grow everywhere in the Keuper forest, and may be better adapted to wet conditions. In a pilot study, hornbeam fine roots were mainly horizontal and superficial, which may help with oxygen uptake under wet conditions (Kooijman et al., 2018). In contrast, beech roots were mainly vertical, and clearly decreased in wet soils with high perched water tables. Even though hornbeam may not specifically prefer depressions, it is doing better there than beech. Also, hornbeam may make depressions even more unsuitable for beech, with the cascade of processes starting with high litter quality, such as high earthworm activity, high erosion, impermeable subsoils closer to the surface, higher perched water tables and generally wetter conditions.

4.6. Habitat differences increase spatial complexity

Both hornbeam and beech may thus act as ecosystem engineers, which make their habitat more suitable for themselves, and/or less suitable for the other. However, while they create suitable patches in the forest for themselves, they also increase spatial complexity in habitat factors. Higher spatial complexity generally leads to higher diversity (MacArthur and MacArthur, 1961; Zellweger et al., 2015). The contribution of hornbeam and beech to the total length of the habitat gradient differed between particular topsoil characteristics, but was 38% and 62% on average (Fig. 9). This means that the length of the environmental gradient was much larger with the two species together, compared to each alone.

We did not study patterns in biodiversity other than for plant species, but hornbeam clearly increased pH of the topsoil, and may thus increase plant diversity in forests endangered by acidification (van Oijen et al., 2005). Hornbeam probably also increases earthworm biomass (Kooch et al., 2011), which is a food source for forest mammals such as mole and wild boar (Cammeraat, 2002). Also, both beech and hornbeam seeds are a food source for forest birds and mammals, but beech nuts are more nutritious and have higher protein and fat content even than acorns. Beech was less important for plant species and earthworms, but may increase mass and diversity of microarthropods and saprophytic fungi, especially in the litter layer (Tyler, 1992; Aubert et al., 2005).

Spatial complexity may also be important for adaptations to climate change (Braunisch et al., 2014). For forests on decalcified marl, the litter quality effects of beech and hornbeam on microtopography may reduce sensitivity of the forest to prolonged dry or wet periods. In prolonged dry periods, plants and soil animals may prefer depressions with relatively high soil moisture content, but in wet periods, they may move as much as they can to the higher mounds. This needs further study, but as both dry and wet periods are expected to be more common in NW Europe with future climate change (IPCC, 2014), litter quality effects on microtopography may increase resilience of the forest as a whole.

5. Conclusions

This study further supports that litter quality is an important driver in forest ecosystems, which changes topsoil and understorey characteristics. In contrast to hypothesis 1, beech and hornbeam did differ in distribution patterns, and were found in different microtopographical positions. However, this reinforced their litter quality effects on topsoil and understorey characteristics. According to hypothesis 2, litter quality was indeed more important than elevation and subsoil properties, but microtopography was also important. Although they had separate effects, litter quality and microtopography were clearly correlated, in accord with hypothesis 3, and basically reinforced each other. In ancient forests on decalcified marl, differences in litter quality may thus affect forest hydrology, and lead to intricate patterns of wet, intermediate and dry patches with different microtopography, habitat conditions and understorey. Hornbeam and beech may even act as ecosystem engineers, which create suitable habitats for themselves, or unsuitable for the other. However, on the slope scale, differences in litter quality and

Contribution of hornbeam and beech to habitat gradient (%)

Fig. 9. Contribution of hornbeam- and beech-dominated plots to the total length of the gradient in habitat factors.

microtopography increase spatial complexity of the entire ecosystem, which probably increases biodiversity and resilience to climate change of the forest as a whole.

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Author's contributions

AK, CC, LC and AC conceived the ideas and designed methodology; HW, AK and CC collected the data; AK, CC, NA and XM analyzed the data; AK and LC led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Declaration of competing interest

The authors declare that they have no conflict of interest.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2019.05.285>.

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