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# Phytosociological studies of *Malus sylvestris* in North Hesse and Upper Franconia, Germany

## Geobotanische Analyse nordhessischer und oberfränkischer Wildapfel-Vorkommen

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### Abstract

*Malus sylvestris* the European crabapple, a rare and threatened small tree species, has attracted increasing interest since it was awarded tree of the year 2013 in Germany. In this study, we used the wide range of different habitats in Upper Franconia and North Hesse to reveal a more complete picture about its phytosociology and ecological behavior in these regions and to examine the main environmental factors which affect its distribution. We collected a data set of 31 relevés and used ordination techniques and comparisons with respect to well-established syntaxonomic classifications to analyze the phytosociology of *M. sylvestris*. It occurred in 7 communities, indicating its high adaptability and broad ecological amplitude. The *Aceri-Tilietum platyphylli* and the *Carici-Fagetum* (in North Hesse) are forest habitats on shallow soils on calcareous rocks and screes exposed to the sun for most of the day, which favor xerothermophilous and heliophilous species of dealpine and sub-Mediterranean origin. This is in stark contrast to its occurrences in the *Stellario nemorum-Alnetum glutinosae* on a nutrient-rich alluvial soil in the floodplain of the Red Main River in Upper Franconia. Crabapple abundances in the *Stellario-Carpinetum* (both early successional stages with *Pinus sylvestris*, *Betula pendula*, *Populus tremula* and intermediate to late successional stages with *Quercus robur*), residuals of secondary (semi-natural) mesoxerophytic grasslands of *Bromion erecti* overgrown with encroaching bushes and trees, mixed pine-hardwood stands ex *Hordelymo-Fagetum*, and a *Molinia caerulea-Oxalis acetosella*-Scots pine forest represent mesohemerobic ocurrences in secondary successional stages / managed forests. The *Aceri-Tilietum platyphylli* in North Hesse and the *Molinia caerulea-Oxalis acetosella* Scots pine forest were so far undescribed assemblages with *M. sylvestris*. Our findings confirm the low capacity of *M. sylvestris* to dominate its habitats, but also show that its ecological plasticity is even greater than previously thought. We conclude that crabapple occurs in diverse landscapes and across ecological gradients. It frequently co-occurs with rare and threatened species and species-rich communities linked to high light and high stress conditions.

**Keywords:** geobotany, forest ecology, nature conservation, phytodiversity, plant communities, rare tree species

**Erweiterte deutsche Zusammenfassung am Ende des Artikels**

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## 1. Introduction

The European crabapple *Malus sylvestris* has attracted increasing interest after it was awarded tree of the year in 2013 in Germany. Subsequently, it was the subject of a wide range of studies, among them a genetic survey of the species throughout Germany (BLE 2013). Recently, morphological and genetic features of *M. sylvestris* were investigated in detail in the Ore Mts. (Erzgebirge) (REIM et al. 2012, 2013).

In Upper Franconia, the species was suggested extinct and being replaced by its hybrid with *M.* × *domestica*, the domesticated apple (GATTERER & NEZADAL 2003). Since 2013 the species was rediscovered in Upper Franconia in the area surrounding Bayreuth and its morphology and species integrity was studied in detail using also genetic data (FUSSI 2015). Twigs, buds and leaves of *M. sylvestris* are glabrous when young; this is true also for the pedicels, the outside of calyx and the receptacle, the fruits are small, usually less than 4 cm in diameter, sour in taste and adstringent (REIM et al. 2012, AAS 2013). Most upper Franconian crabapples that we could find were fully glabrous but, in close proximity to these genuinely wild crab apples, slightly hairy forms occur that are putative hybrids with the domesticated apple (*M. domestica*). Also in Hesse the genetic and morphological integrity of the European crabapple has been proven (HÖLTKEN et al. 2014).

*Malus sylvestris* is known as being very light demanding and occurring typically in riparian forests as described for the Rhine River valley (SCHNITZLER et al. 2014), in hedgerows and thickets or at the edges of forests (ELLENBERG 1988). According to TÜRK (1999) it occurs mostly in *Prunetalia spinosae* Tx. 1952 communities (mostly in the *Berberidion vulgaris* Br.-Bl. 1950 alliance) followed by phytocoenoeses with a tendency towards the communities of the order *Quercetalia pubescentis* Klika 1933, i.e., not only thermophilous oak-forests per se, but also smooth transitions and overlaps to *Erico-Pinion sylvestris* Br.-Bl. 1939, *Carici-Fagetum* Moor 1952, *Galio-Carpinetum* Oberd. 1957 and *Querco-Ulmetum* Issler 1924. The phytosociological context implicates that, on the one hand, *M. sylvestris* tolerates drought, flooding, and other abiotic stress factors but, on the other hand, is a light- and warmth-demanding species.

*Malus sylvestris* is threatened according to the Bavarian and Hessian Red Lists of plants (SCHEUERER & AHLMER 2003, BARTH et al. 2008). SCHNITZLER et al. (2014) identified habitat homogenization by river regulation and change in forest management towards shady high forests as major causes of population decline in the floodplains of the Rhine valley. Even HÖLTKEN et al. (2014) considered conversion of coppice forest into high forest an important cause of the species' decline. In Hesse, WINTERHOFF (1965) and HÖLTKEN et al. (2014) identified exposed, dry habitats on calcareous rocks and pine tree forests with high light levels as suitable refuges of wild crabapple. We found that the habitats of the genuinely wild crabapples in Upper Franconia were clearly different from those of North Hesse. We therefore compared the phytosociology of *M. sylvestris* between the two regions in detail, addressing the following questions: (1) In which plant communities or habitats does the European crabapple occur and are there assemblages in which it has not been described yet? (2) How broad is the range of tolerance to environmental factors, summarized in the term ecological amplitude (PATTON 2011), and (3) what are the most important ecological maxima and minima?

## 2. Study area

The study area in North Hesse (NH) is part of the so called Hessische Schweiz near the city of Eschwege and is characterized by Triassic limestone outcrops (Muschelkalk). The ridges and slopes bear striking vegetation complexes of xerothermophilous forests, scrub and non-forest vegetation, which appear to be natural or semi-natural.

The case study area in the wider surroundings of Bayreuth in Upper Franconia (UF) is divided into three spatially adjacent but geologically different subareas: first, the Red Main River valley, second, a part of the Trossingen Formation (`Feuerletten´ in Bavaria), which marks the end of the sandstone Keuper (DOPPLER et al. 2004) near Bayreuth. Feuerletten substrates are well-known for dry-mesic to wet-mesic and superficially acidic two-layer soils of loose sand on hardened clay and are mostly stocked with pine forests. The third subarea is located at the western border of the upper Franconian Jura near Hollfeld and is characterized by formations of the Upper Jurassic. The underlying marls and limestones result in soil chronosequences with Rendzic Leptosol and Vertic Cambisol, hence the karstic limestone plateau was also influenced by veils of Loess.

The climate data of both case study areas indicate a moderately warm (annual mean temperature between 7.7 °C in Hitzelrode [NH] and 8.3 °C in Bayreuth [UF]) and moderately rainy climate (average annual precipitation between 638 mm in Bayreuth [UF] and 727 mm

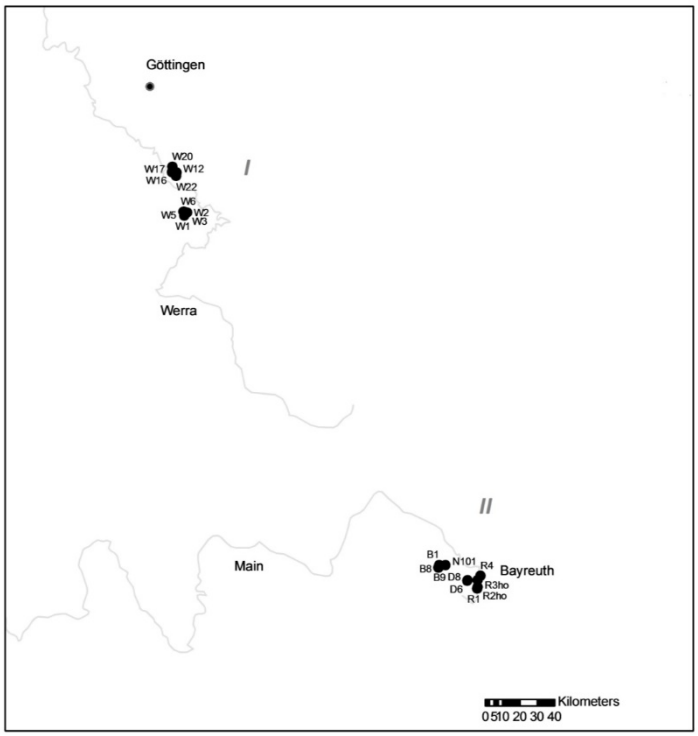


**Fig. 1.** Map of the study area. I - North Hesse (surroundings of Eschwege / lower Werra valley); II - Upper Franconia (surroundings of Bayreuth) (Made with Natural Earth).

**Abb. 1.** Karte der Untersuchungsgebiete. I - Nordhessen (Umgebung von Eschwege / Unteres Werratal); II – Oberfranken (Umgebung von Bayreuth).

**Table 1.** Biologically meaningful climate characterization of the study area.

**Tabelle 1.** Vegetationswirksame Klimakennwerte der Untersuchungsgebiete.

| | NORTHERN BAVARIA (surroundings of Bayreuth) | NORTH HESSE (surroundings of Eschwege) |
|---|---|---|
| Gd - growth district (codes and names of National Forest ecological regions according to GAUER & ALDINGER 2005) | 52.6 - Upper Main Hills<br>60.1 - Northern Franconian Jura and northern Upper Palatine Jura | 37.12 - *Ringgau* and adjoining Werra-region |
| alt. zone | 300–450 | 300–450 |
| *climate data 1982–2012 temperature* | | |
| T [°C] - annual mean temperature | 8.0↔8.3 | 7.7↔7.9 |
| $T_{May\text{-}Sep}$ [°C] - mean temperature of the growing season (May-September) | 14.9↔15.3 | 14.2↔14.5 |
| $T_{\Delta}$ [K°] - temperature difference between the coldest and the warmest month [K°] | 18.4↔18.5 | 17.3↔17.5 |
| $T_{jan}$ [°C] - mean temperature of the coldest month | -1.3↔0.8 | -1.2↔1.0 |
| $T_{jul}$[°C] - mean temperature of the warmest month | 17.2↔17.6 | 16.1↔16.5 |
| *precipitation* | | |
| Prec [mm year-1] - mean annual precipitation | 638↔672 | 666↔727 |
| $Prec_{May\text{-}Sep}$ [mm] - mean precipitation of the growing season (May-September) | 320↔334 | 324↔350 |
| *climate indices* | | |
| $IDM_{May\text{-}Sep}$ - De Martonne aridity index for the growing season (May-September) | 12.6↔13.4 | 13.2↔14.5 |
| EQ - Ellenberg-Quotient mean temperature of the warmest month (July, $T_{Jul}$) divided by mean annual precipitation (Prec): EQ = 1000 ($T_{jul}$/Prec) | 25.↔ 27.6 | 22.1↔ 24.8 |

in Hitzelrode [NH]) of the colline-submontane zone (WALENTOWSKI et al. 2013; data were taken from www.climate-data.org). The study area in UF exhibits a more continental climate than NH. This is indicated by warmer summers, a more marked contrast between summer and winter, and increased hygric continentality, expressed by lower values of $IDM_{May\text{-}Sep}$ and higher values of *EQ* (Table 1).

The floodplain of the Red Main is typically inundated once or several times a year, and its nutrient-rich alluvial soil supports a potential natural vegetation (PNV) of the *Stellario nemorum-Alnetum glutinosae* Lohmeyer 1957. The PNV of the two-layer soils derived from the Feuerletten (Sandstonekeuper) is supposed to be an acidophilous oak forest, according to HAERDTLE et al. (1997), most probably the *Calamagrostio arundinaceae-Quercetum petraeae* (Hartmann 1934) Scamoni et Pass. 1959 *convallarietosum*, variant of *Molinia arundinacea*. This type indicates a sub-continental climate, a tendency to nutrient-poor raw-humus (*Vaccinium vitis-idaea*, *V. myrtillus*, *Calluna vulgaris*), a sandy topsoil (further acidophytes), and a clayey subsoil, colloid-rich (*Convallaria majalis*, *Brachypodium pinnatum*, *B. sylvaticum*), and swelling and shrinking of the substrate (*Molinia arundinacea*, *Potentilla erecta*). The PNV of calcareous soils at the plateau of the Northern Franconian Jura is the *Hordelymo-Fagetum* Kuhn 1937.

The PNV of the outcropping limestone of the Middle Triassic (Muschelkalk) in North Hesse near Eschwege is particularly characterized by xerothermophilous forests, specifically by mosaic-complexes of the *Carici-Fagetum* on exposed scarps and ridges and the *Aceri-Tilietum platyphylli* Faber 1936 on coarse-grained soils of landslide deposits. The limestone karst scenery of the lower Werra valley is well known for exclaves of dealpine relict species (e.g., *Carduus defloratus*, *Laserpitium latifolium*) and leading-edge occurrences of subcontinental and sub-Mediterranean elements such as *Arabis pauciflora*, *Bupleurum longifolium* or *Scorzonera hispanica* (SCHMIDT & MAST 1996, GAUER & ALDINGER 2005).

## 3. Methods

### 3.1 Vegetation sampling

The size of the plots was fixed at 100 m², with a *M. sylvestris* tree as the center point of each plot. The shape of the plots was generally square, but in some cases was modified to obtain a representative portrayal of homogeneous vegetation, e.g., elongated in shape for sample plots in riverine forests along watercourses.

Cover values of vascular plants and bryophytes refer to the vertical projection of the aboveground living parts only (aerial cover), overhanging the surface of the sampling unit. The vertical stratification (arrangement of vegetation in layers) followed the rules of TURBOVEG classification (HENNEKENS & SCHAMINEE 2001): Tree layer (high) = t1, tree layer (middle) = t2, shrub layer (high) = s1, shrub layer (low) = s2, herb layer = hl, Juvenile = jl, moss layer = ml. Species occurrences in discrete special habitats like epixylic bryophytes were not recorded. To minimize biases of subjective judgment and errors related to that we ensured that all relevés in both areas were recorded by the same person. However, this also meant that the data collection lasted several months and later records may suffer from low recognisability of spring forest geophytes.

Data such as sampling location, recording date, Gauss-Krueger coordinates, altitude above sea level, aspect, slope and percent cover of vegetation layers were documented in the sampling protocol (table header of Supplements S1, S2 und E1).

The nomenclature of vascular plants and bryophytes follows the checklist for Germany (JANSEN & DENGLER 2008) and the nomenclature of plant communities follows RENNWALD (2000).

### 3.2 Data analysis

The plant communities were identified using the methods described in DIERSCHKE (1994) and FISCHER (2003). The classification of the syntaxa (associations) was based on the classifications given in HAERDTLE et al. (1997) and PREISING et al. (2003). The classifications were additionally compared with those given in OBERDORFER (1992).

The detrended correspondence analysis (DCA) was carried out using PC-ORD (MC CUNE & MEFFORD 2011). In the second matrix, we provided seven quantitative variables including the species number and the ordinal scaled Ellenberg indicator values (EIVs; ELLENBERG et al. 2001) and designated the vegetation type as a coding variable. In combination with Pearson correlation analyses, presumed influences of environmental factors on species combinations were visualized. As proposed by ZELENÝ & SCHAFFERS (2012), we refrained from testing the significance of these correlations, since variables deduced from species compositions are dependent variables. The collected data was also used for statistics of vertical structures of the vegetation stands at the 31 plot sites and for the calculation of the importance value index (IVI) of *M. sylvestris* in the vegetation stands of the relevé plots. The IVI is calculated as the sum from (i) the relative frequency (calculated from number of plots); (ii) the relative density (calculated from number of individuals); and (iii) the relative dominance (calculated from cover). The importance value ranges between 0 and 300 (cf. NGUYEN et al. 2014).

# 4. Results

## 4.1 Phytocoenological differentiation and communities

The DCA of the 31 plots with 205 species revealed 7 groups of relevés which we assigned to 7 communities (for relevés see Supplements S1–S2): in North Hesse, the *Carici-Fagetum* and *Aceri-Tilietum platyphylli* were detected on limestone rocks and slopes. In Upper Franconia we identified the following communities: the *Stellario-Carpinetum* (both early successional stages with *Pinus sylvestris*, *Betula pendula*, *Populus tremula* and intermediate to late successional stages with *Quercus robur*), residuals of secondary mesoxerophytic grasslands of *Bromion erecti* overgrown with encroaching bushes and trees, mixed pine-hardwood stands ex *Hordelymo-Fagetum*, a *Molinia caerulea-Oxalis acetosella*-Scots pine forest ex *Calamagrostio arundinaceae-Quercetum petraeae* and the *Stellario nemorum-Alnetum glutinosae*.

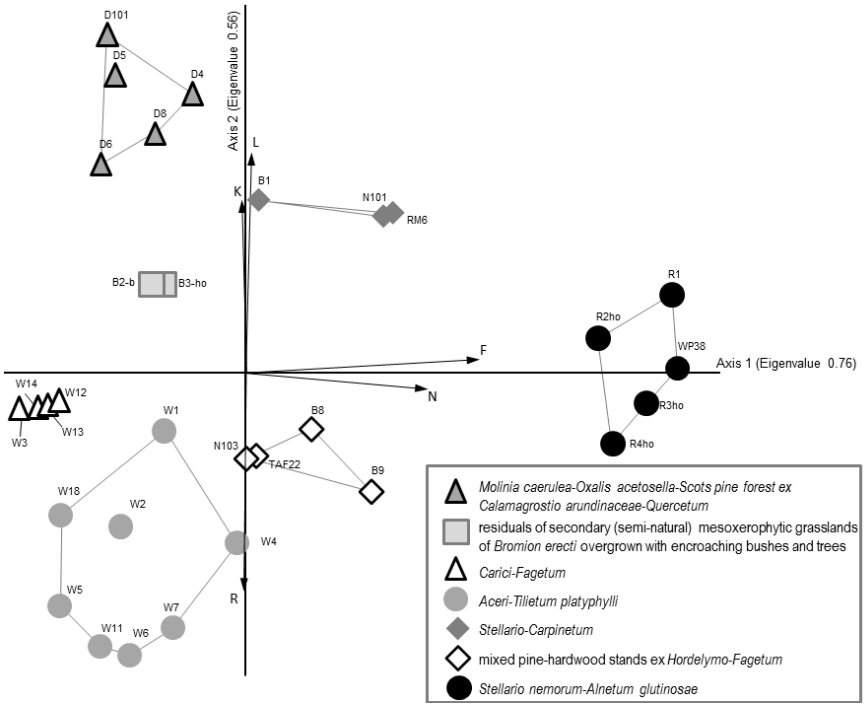


**Fig. 2**. DCA diagram of 31 wild apple plots recorded in 2017; for plot-ID´s see Supplement S1 and S2. Ordination of the plots is based on cover values of in total 205 species. Mean Ellenberg values for temperature, soil moisture, soil reaction and nutrients used as passive variables not affecting plot scores (cutoff $r^2$ value: 0.400); length of gradients axis 1: 4.65 SD, axis 2: 4.29 SD.

**Abb. 2**. DCA-Diagramm der 2017 aufgenommen 31 Wildapfel-Plots; Aufnahme-ID´s gem. Beilage S1 und S2. Die Ordination der Aufnahmeflächen beruht auf den Deckungswerten von insgesamt 205 Gefäßpflanzen- und Moosarten. Zeigerwerte für Temperatur (T), Feuchte (F), Reaktion (R) und Stickstoff (N) wurden als passive Größen ohne Einfluss auf die Berechnung verwendet (cutoff $r^2$ value: 0,400). Gradientenlänge Achse 1: 4,65 SD; Achse 2: 4,29 SD.

Axis 1 of the DCA has an Eigenvalue of 0.76 (Fig. 2). This axis explains 29% of the variation and correlated positively to EIV-N and EIV-F (Table 2 and 3). High N and F values separate relevés representing the *Stellario nemorum-Alnetum glutinosae* from the borders of the floodplain of the Red Main from all others. The mixed pine-hardwood stands ex *Hordelymo-Fagetum* and relevés of the *Stellario-Carpinetum* have intermediate values for nutrient availability and moisture. The *Carici-Fagetum* and *Aceri-Tilietum platyphylli* of North Hesse on karstic limestone form the other extreme, i.e., low water and nutrient supply.

The second DCA axis was positively correlated to EIV-K and EIV-L and negatively correlated to EIV-R (Table 3). The sequence of communities along DCA axis 2 was (from left to right): *Aceri-Tilietum platyphylli*, *Carici-Fagetum*, mixed pine-hardwood stands ex *Hordelymo-Fagetum* (on calcareous substrates), *Molinia caerulea-Oxalis acetosella* pine forest (on acidic substrate). In addition, the latter community seems to be correlated with the highest indices of continentality and light availability.

All in all, *M. sylvestris* was found in communities at very different levels of soil reaction, soil moisture, nutrient availability, continentality and even light availability. However, regarding light availability we should note that even the relevés of *Aceri-Tilietum platyphylli* with lowest indicator values are anything but shady, closed forests.

Even if the low statured crabapples were mostly overtopped by higher trees, the canopies of the vegetation stands at the plot sites were rather sparse (average of 58% canopy cover) (Table 4). However, the spectrum of the canopy cover ranged from semi-open (20% cover) to closed (100%). The light requirements of *M. sylvestris* and many other light demanding species were always fulfilled, probably due to patches of higher than normal light influx or edge light effects in case of adjacent open spaces.

**Table 2.** Coefficient of determination ($r^2$) of the regression between distance in ordination space and Sørensen-distance in the original floristic space (McCune & Grace 2002).

**Tabelle 2.** Bestimmtheitsmaß ($r^2$) der Regression zwischen der Distanz im Ordinationsraum und der Sørensen-Distanz im ursprünglichen floristischen Datensatz (McCune & Grace 2002).

| Axis | $r^2$ | cumulative $r^2$ |
|---|---|---|
| 1 | 0.293 | 0.293 |
| 2 | 0.303 | 0.596 |
| 3 | 0.025 | 0.620 |

**Table 3.** Pearson-Correlation ($r$) of Ellenberg Indicator values of the relevé samples with DCA axis 1 and 2.

**Tabelle 3.** Pearson-Korrelation ($r$) der mittleren Ellenberg-Zeigerwerte der Aufnahmen mit der ersten und zweiten Achse der DCA.

| | DCA axis 1 | DCA axis 2 |
|---|---|---|
| Ellenberg-light availability [L] | 0.136 | 0.811 |
| Ellenberg-temperature [T] | -0.126 | 0.357 |
| Ellenberg-continentality [K] | -0.109 | 0.717 |
| Ellenberg-soil moisture [F] | 0.844 | 0.200 |
| Ellenberg-soil reaction or pH [R] | -0.066 | -0.806 |
| Ellenberg-nutrients [N] | 0.744 | -0.215 |

**Table 4.** Statistics of vertical structures of the vegetation stands at the 31 plot sites.

**Tabelle 4.** Kennwerte der Vertikalstrukturen der Bestände der 31 Vegetationsaufnahmeflächen.

| | minimum | maximum | average | Stand. dev. |
|---|---|---|---|---|
| Cover Tree layer | 20% | 100% | 58% | 19 |
| Cover Shrub layer | 0% | 80% | 28% | 22 |
| Cover Herb layer | 0% | 100% | 68% | 25 |
| Cover Moss layer | 0% | 90% | 11% | 24 |
| Height (highest) trees | 6 m | 30 m | 20 m | 7 |
| Height *Malus sylvestris* trees | 2 m | 18 m | 8.5m | 4 |

We found the crabapple only rarely as a juvenile tree (juv) or as an adult tree individual in the canopy of overwood (t1). Most occurrences were in the understorey (t2), and it was less common in the shrub layer (S) (Fig. 3). 65% of the crabapples were between > 4 and 10 m in height. The highest one was found in the riparian alluvial forest of the Red Main river and grew up to 18 m. However, the crabapple trees in the xerothermophilous forests in North Hesse never reached more than 8 m.

Though the plots been had selected for the presence of *M. sylvestris*, the importance value index of the crabapple in the vegetation was rather low (IVI of 19.2).

## 5. Discussion

The low importance value index indicated that the crabapple normally cannot dominate and thus outcompete other species. As a species that requires high light intensities for growth and survival of juveniles (LEUSCHNER & ELLENBERG 2017) and that remains a small tree or shrub of about 4 to 10 m high, *M. sylvestris* will always be rare in the forest vegetation, unless environmental stress, disturbance, or anthropogenic impact affect canopy openings in space and time. Our phytosociological results suggest that the crabapple trees included in this study grew under high light conditions in early successional stands. Even the survival of adult understorey trees, which barely exceeded 10 m height, relies on high availability of light (either light pine and oak forests, or forest margins alongside streams, cliffs, screes, forest glades etc.). Apart from its shade-avoidance, it is able to cope even with acid podsolic sandy soils poor in nitrogen and phosphorus (ROSSNER 1988/89), with either water surplus or water deficiency, and grows even on sunny slopes and screes and appears to be decidedly versatile and tenaciously stress tolerant. Our results show that *M. sylvestris* occurs in many different communities, supporting this interpretation of versatility.

Our data from the Red Main validated the appearance of *M. sylvestris* as a riverside species of riparian forests (*Alno-Ulmion*), even if not as usually included in the *Querco-Ulmetum* (OBERDORFER 2001, SCHNITZLER et al. 2014), but in the *Stellario nemorum-Alnetum glutinosae*. Moreover, we encountered *M. sylvestris* also in early succession stages of former open cultural landscapes covered with bushes and trees. This finding fits with observations on occurrences in *Prunetalia* communities (TÜRK 1999, OBERDORFER 2001), consisting of shrubs and small trees and driven by human impacts.

Thirdly, *Quercetalia pubescentis* associations and smooth transitions and overlaps to *Erico-Pinion sylvestris* were reported to be the (or one of the) most important xerothermophilous habitats of *M. sylvestris* (WINTERHOFF 1965, OBERDORFER 2001). WINTERHOFF (1960,

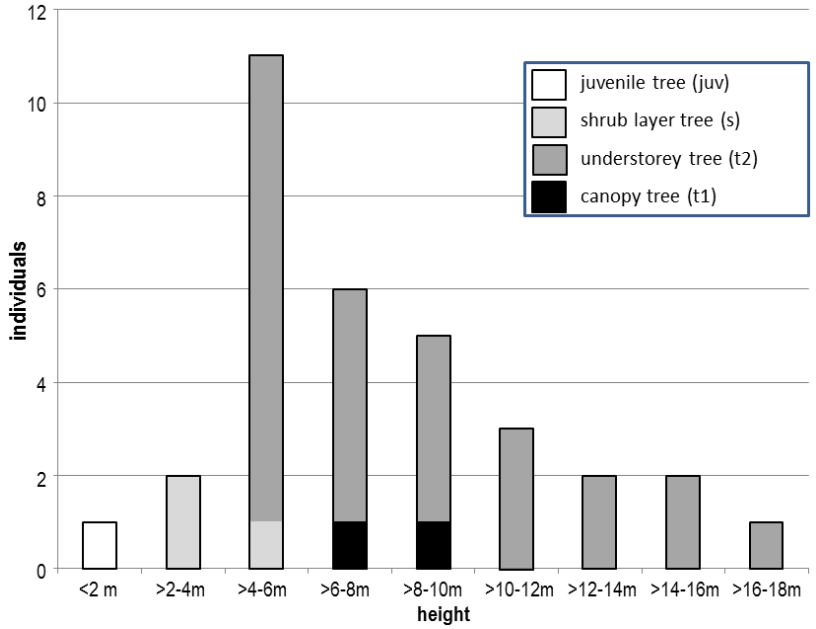


**Fig. 3**. Growth heights and layer affiliation of all recorded 33 crabapple individuals from the 31 relevé samples.

**Abb. 3**. Wuchshöhen und Schichtzugehörigkeit der 33 Wildapfel-Individuen in den 31 Vegetationsaufnahmeflächen.

1965), TÜRK (1999) and SCHMIDT (2000) also refer to its rare occurrences within the *Carici-Fagetum* with significantly reduced growth and competition power of beech. However, records with the species growing in the *Aceri-Tilietum platyphylli* have not yet been published to our knowledge. HEMP & HEMP (1996) point out that the *Aceri-Tilietum platyphylli* can be disproportionately enriched with *Carpinus betulus* along with several other deciduous trees, which are particularly capable of multiplication by stump shooting and thus promoted by centuries of coppicing and pollarding. We observed the same appearance for the *Aceri-Tilietum platyphylli* of North Hesse. However, our records of *M. sylvestris* in this community confirmed its known affinity to the *Quercetalia pubescentis* and thermophilous oak-hornbeam forests (*Galio-Carpinetum*).

Most of the relict species of the limestone karst landscapes of the lower Werra valley (WINTERHOFF 1965) are those with a sub-Mediterranean distribution such as *Arabis pauciflora*, *Bupleurum longifolium*, *Hieracium glaucinum*, *Sorbus aria*, *S. torminalis* and *Vincetoxicum hirundinaria*. *Arabis pauciflora* and *Bupleurum longifolium* (and also *Lithospermum purpurocaeruleum*) have a similar non-continuous distribution in Germany in the valleys of the Danube, the Altmühl, the Main, the Saale, the Werra and adjacent areas with a warmer climate such as the "Windsheimer Becken" or the "Grabfeld". Such a distribution pattern may hint at the main recolonization track of the European crabapple after the ice age from a south western refugium to North Hesse and Upper Franconia. According to CORNILLE et al. (2013) there are three subpopulations of *M. sylvestris* in Europe, a western, a south-eastern and a north eastern one. The authors have shown that the German populations genetically belong to the West European population of *M. sylvestris* originating from a refuge in

southern France or northern Italy. These results are confirmed by the geographic-genetic groups of the European crabapple presented by HÖLTKEN et al. (2014), since the most southwestern German populations are genetically similar to those of North Hesse and northern Bavaria.

Whereas *M. sylvestris* occurs on limestone outcrops in Hesse, it can rarely be found in such habitats in the Upper Franconian Jura. The exact causes for this are still unknown and should be the subject of further research. In contrast, we found crabapple habitats in Upper Franconia that are not documented in North Hesse. This especially concerns habitats in floodplains and in acidophilous woodlands. The occurrence of *M. sylvestris* in the *Oxalis-Molinia caerulea* pine forest community near Bayreuth is particularly noteworthy, since the crabapple is known as a basophilous species (TÜRK 1999). However, such a habitat is new for the European crabapple.

Crabapple abundances in the *Stellario-Carpinetum* (both early successional stages with *Betula pendula*, *Pinus sylvestris*, *Populus tremula* and intermediate to late successional stages with *Quercus robur*), residuals of secondary (semi-natural) mesoxerophytic grasslands of *Bromion erecti* overgrown with encroaching bushes and trees, mixed pine-hardwood stands ex *Hordelymo-Fagetum*, and even the *Molinia caerulea-Oxalis acetosella*-Scots pine forest represent mesohemerobic ocurrences in secondary successional stages / managed forests. They are examples of the positive impact of man's influence that might have favored the European crabapple and made it more common than it would have been under natural conditions (cf. HÖLTKEN et al. 2014).

## 6. Conclusions

The strongly different habitats of *M. sylvestris* in Hesse and in the Northern Franconian Jura show the high phytosociological amplitude of the crabapple and its high tolerance to extreme conditions, but also demonstrate the high light demand of the species. This means that forests with sparse canopies, forest margins and forest succession after disturbance, which facilitate spatial and temporal niches for light-demanding stress tolerators like crabapple, are crucial components of protection strategies of regionally rare and endangered tree species in sustainable forest management.

## Erweiterte deutsche Zusammenfassung

**Einleitung** – Der Europäische Wildapfel ist eine lichtliebende und konkurrenzschwache Baumart, die in Bayern und Hessen selten und gefährdet ist. Nach TÜRK (1999) kommt die Art am häufigsten in *Prunetalia*-Gesellschaften vor, hier schwerpunktmäßig im *Berberidion*. Seltener ist sie in *Quercetalia pubescentis*-Gesellschaften oder deren Übergängen zu *Erico-Pinion*-Gesellschaften sowie im *Carici-Fagetum*, *Galio-Carpinetum* und *Querco-Ulmetum* zu finden. Morphologisch lässt sich *Malus sylvestris* von *Malus domestica* und Hybriden durch seine kahlen Knospen, Sprossachsen und Laubblätter sowie der Kahlheit der Blütenstiele, des Blütenbodens und der Außenseiten des Blütenkelches unterscheiden; die Früchte sind klein (< 4 cm im Durchmesser), stark sauer und adstringierend (AAS 2013, REIM et al. 2013). In Nordhessen waren Vorkommen von *M. sylvestris* von felsigen Extremstandorten in der Gegend um Eschwege bekannt (HÖLTKEN et al. 2014). Im nordöstlichen Franken galt der Wildapfel dagegen als ausgestorben bzw. durch Hybriden mit dem Hausapfel ersetzt (vgl. GATTERER & NEZADAL 2003). Erfreulicherweise konnten wir im Raum Bayreuth seit 2013 an verschiedenen Wuchsorten *M. sylvestris* nachweisen. Ziel der Untersuchung war die Analyse der Vergesellschaftung und des ökologischen Verhaltens der Art in den beiden genannten Gebieten (Abb. 1).

**Untersuchungsgebiet** – In Nordhessen handelte es sich um steile Abbrüche des Muschelkalkes in der Umgebung von Eschwege. Die Kämme und Abbrüche dort weisen eine Xerothermvegetation mit dealpinen und submediterranen Reliktarten auf. In Oberfranken wurden Vorkommen des Wild-Apfels in drei Teilgebieten unterschiedlicher geologischer Ausgangsgesteine (Auelehme, Feuerletten, Malm) in der Umgebung von Bayreuth untersucht.

Kennzeichnend ist ein Hügellandsklima, das als mäßig warm (Jahresmitteltemperaturen zwischen 7,7 °C in Hitzelrode/Nordhessen und 8,3 °C in Bayreuth/Oberfranken) und mäßig niederschlagsreich (638 mm in Bayreuth und 727 mm in Hiztelrode) eingestuft werden kann (WALENTOWSKI et al. 2013, Klimadaten nach www.climate-data.org). Das Klima im Untersuchungsgebiet in Oberfranken ist mit wärmeren Sommern, höheren Temperaturspannen zwischen Sommer und Winter und einer stärkeren hygrischen Kontinentalität kontinentaler getönt als jenes in Nordhessen.

**Methoden** – Die 31 erhobenen Vegetationsaufnahmen erfolgten durchgehend auf Flächen von 100 m² Größe. Auf Basis von pflanzensoziologischer Tabellenarbeit nach dem u. a. bei DIERSCHKE (1994) und FISCHER (2003) beschriebenen Verfahren wurden Differentialartenblöcke herausgearbeitet. Anschließend erfolgte eine Einordnung und Benennung der Syntaxa auf Grundlage der in PREISING et al. (2003) und HAERDTLE et al. (1997) veröffentlichten Übersichtstabellen. Darüber hinaus wurden die Syntaxa mit den bei OBERDORFER (1992) präsentierten Übersichtstabellen für Süddeutschland verglichen. Um Vegetationsgradienten zu beschreiben, wurde mit den wurzeltransformierten Deckungswerten von insgesamt 205 Arten eine Entzerrte Korrespondenzanalyse (DCA) berechnet. Die erste DCA-Achse hatte eine Gradientenlänge von 4,6. Um Anhaltspunkte zu erhalten, wie der Artenwechsel zwischen den Aufnahmen ökologisch interpretiert werden kann, wurden die Ordinationsachsen *post hoc* mit ungewichteten mittleren Ellenberg-Zeigerwerten (vgl. KOWARIK & SEIDLING 1989) korreliert. Alle statistischen Auswertungen erfolgten mit PC-ORD (MC CUNE & MEFFORD 2011). Um die Rolle des Wildapfels in den verschiedenen Vegetationsschichten zu verdeutlichen, wurden für die einzelnen Schichten die prozentualen Deckungen und der *Importance value index* (IV-Index) nach NGUYEN et al. (2014) berechnet.

**Ergebnisse** – In den Biplot-Diagrammen der DCA zeigten sich nach ihrer Artenverbindung 7 Aufnahmegruppen, die unterschiedlichen Pflanzengesellschaften entsprachen: In Nordhessen waren dies *Carici-Fagetum* und *Aceri-Tilietum platyphylli* und in Oberfranken *Stellario-Carpinetum* (Pionierstadien mit *Pinus sylvestris*, *Betula pendula* und *Populus tremula* sowie eichendominierte Bestände mit *Quercus robur*), verbuschte und z. T. aufgeforstete Restvorkommen ehemaliger Halbtrockenrasen des *Bromion erecti*, Föhren-Edellaubbaum-Mischbestände anstelle des *Hordelymo-Fagetum*, *Molinia caerulea-Oxalis acetosella*-Kiefernforst und *Stellario nemorum-Alnetum glutinosae* (Abb. 2). Die erste Achse der DCA hatte einen Eigenwert von 0,76 und erklärte 29 % der Variabilität im Ordinationsraum; sie war positiv mit der Zeigerwerten der Bodenfeuchte ($r$ = 0,84) und Stickstoffversorgung ($r$ = 0,74) korreliert. Die Anordnung des *Carici-Fagetum* und *Aceri-Tilietum platyphylli* auf der linken Seite der ersten Achse deuten somit auf flachgründig-durchlässige Standorte mit Wassermangel und eingeschränkter Stickstoffversorgung hin. Die Föhren-Edellaubbaum-Mischbestände anstelle des *Hordelymo-Fagetum* und das *Stellario-Carpinetum* zeigten eine gute bis sehr gute Stickversorgung und günstige Bodenfrische. Die feuchtesten und stickstoffreichsten Böden wurden vom *Stellario nemorum-Alnetum glutinosae* eingenommen. Die zweite DCA-Achse mit einem Eigenwert von 0,56 erklärte weitere 30 % der floristischen Variabilität. Der Achsenverlauf war positiv mit der Kontinentalitätszahl ($r$ = 0,72) und Lichtzahl ($r$ = 0,81), und negativ mit der Reaktionszahl ($r$ = -0,81) korreliert. Der Reaktionsgradient trennte die Waldgesellschaften auf Kalk (*Aceri-Tilietum platyphylli*, *Carici-Fagetum*, Föhren-Edellaubbaum-Mischbestände anstelle des *Hordelymo-Fagetum*) von dem *Molinia caerulea-Oxalis acetosella*-Kiefernforst mit einem sauren Wurzelraum. Letzterer Waldtyp war auch offenbar lichter und hatte ein stärkeres Offenlandklima, wie die höheren L- und K-Zeigerwerte zeigten. Die kleinwüchsigen Wildäpfel wurden in den Vegetationsaufnahmen meist von höheren Bäumen überschirmt. Das Kronendach war allerdings zumeist licht (durchschnittlich 58 % Deckung, Tab. 4). Bei dichterer Überschirmung wurden die Lichtansprüche offenbar dadurch erfüllt, dass Lichteinfall aus angrenzenden offenen Bereichen stattfand. Nur ausnahmsweise wurde der Wildapfel als Jungpflanze in

der Feldschicht oder als ausgewachsenes Individuum in der ersten Baumschicht angetroffen; fast alle Bäume wuchsen mit ihrer Krone in der zweiten Baumschicht. Zwei Drittel der Wildäpfel waren zwischen 4 und 10 m hoch. Der höchste erreichte 18 m und wuchs im Auwald (Abb. 3). Die Wildäpfel in den xerothermophilen Wäldern Nordhessens erreichten höchstens 8 m. Der IV-Index des Wildapfels in allen Beständen war mit 19,2 bemerkenswert niedrig.

**Diskussion** – Wie der niedrige IV-Index zeigt, ist *M. sylvestris* nicht in der Lage, seine Lebensräume zu dominieren. Mit seiner geringeren Wuchshöhe von zumeist 4–10 m muss er sich mit seiner Krone vielmehr in einen von anderen Gehölzarten aufgebauten Kronenraum einfügen. Da der Wildapfel zudem besonders in der Jugend hohe Lichtansprüche besitzt, muss die Art daher als ausgesprochen konkurrenzschwach bewertet werden.

Im Rahmen dieser Studie konnten erstmals Vorkommen des Wildapfels im *Aceri-Tilietum platyphylli* und *Molinia caerulea-Oxalis acetosella*-Kiefernforst nachgewiesen werden. Das *Aceri-Tilietum* und auch das *Carici-Fagetum* stellen Gesellschaften mit vielen submediterranen Reliktarten dar. Insbesondere *Bupleurum longifolium* und *Arabis pauciflora* sind Elemente, die eine lückige Verbreitung entlang der Flusstäler von Donau, Altmühl, Main, Saale und Werra und angrenzender Wärmegebiete in Beckenlage wie dem Windsheimer Becken und dem Grabfeld zeigen (wie auch *Lithospermum purpurocaeruleum*). Die Anwesenheit dieser Arten könnte die Einwanderungsroute des Wildapfels nach der Eiszeit aus dem Submediterranraum bis nach Nordhessen nachzeichnen. Laut CORNILLE et al. (2013) gibt es drei genetische Subpopulationen des Wildapfels in Europa. Danach gehören sowohl die fränkischen als auch die nordhessischen zu einer westlichen Population. Nach HÖLTKEN et al. (2014) stehen die fränkischen und nordhessischen Vorkommen in enger genetischer Verwandtschaft zu den südwestdeutschen Vorkommen im Breisgau, was ebenfalls auf diese Einwanderungsroute hindeutet.

Der Wildapfel steht für eine vielfältige Landschaft mit starken ökologischen Gradienten auf kleinem Raum und ist darüber hinaus mit vielen seltenen oder gefährdeten Arten vergesellschaftet. Lichte Wälder, Waldränder und Sukzessionswaldgesellschaften sind wichtige Bestandteile einer zukunftsorientierten, multifunktionalen und risikoarmen Landnutzung, die wiederum konkurrenzschwachen, aber stresstoleranten Arten wie dem Wildapfel Nischenhabitate gewähren.

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## Supplements

**Supplement S1.** Forest communities from 13 vegetation plots of European crab apple (*Malus sylvestris*) in Northern Hesse.

**Beilage S1.** Waldgesellschaften aus 13 Aufnahmeflächen mit Wildapfel (*Malus sylvestris*) in Nordhessen.

**Supplement S2.** Plant communities from 18 vegetation plots of European crab apple (*Malus sylvestris*) in Upper Franconia.

**Beilage S2.** Pflanzengesellschaften aus 18 Aufnahmeflächen mit Wildapfel (*Malus sylvestris*) in Oberfranken.

**Additional supporting information may be found in the online version of this article.**

**Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.**

**Supplement E1.** Localities of the crabapple specimens and relevés in North Hesse and Upper Franconia.

**Anhang E1.** Fundorte der Wildapfel-Individuen der Vegetationsaufnahmeorte in Nordhessen und Oberfranken.

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**Supplement E1.** Localities of the crabapple individuals and relevés in I - North Hesse and II - Upper Franconia.

**Anhang E1.** Fundorte der Wildapfel-Individuen der Vegetationsaufnahmeorte in I - Nordhessen und II - Oberfranken.

| relevé no./Table | plot no. | height target *M. sylvestris* (m) | location | Gauss-Krueger coordinates | | altitude (m a.s.l.) |
|---|---|---|---|---|---|---|
| | | | | latitude | longitude | |
| | | | **North Hesse** | | | |
| 1/Supplement S1 | W22 | 10 | Hitzelrode | 51.230514 | 10.061489 | 440 |
| 2/Supplement S1 | W4 | 6 | Graburg | 51.115081 | 10.103799 | 504 |
| 3/Supplement S1 | W7/W10 | 6 | Graburg | 51.115473 | 10.098482 | 510 |
| 4/Supplement S1 | W1 | 7 | Graburg | 51.103315 | 10.103748 | 443 |
| 5/Supplement S1 | W11 | 6 | Graburg | 51.115428 | 10.098452 | 509 |
| 6/Supplement S1 | W5 | 7 | Graburg | 51.115999 | 10.098980 | 511 |
| 7/Supplement S1 | W18 | 6 | Hitzelrode | 51.244465 | 10.040485 | 510 |
| | W19 | 6 | Hitzelrode | 51.244286 | 10.041355 | 517 |
| | W20 | 6 | Hitzelrode | 51.260801 | 10.041725 | 518 |
| | W21 | 6 | Hitzelrode | 51.244302 | 10.041599 | 518 |
| 8/Supplement S1 | W2 | 7 | Graburg | 51.112848 | 10.118384 | 467 |
| 9/Supplement S1 | W6 | 8 | Graburg | 51.115571 | 10.098584 | 511 |
| 10/Supplement S1 | W3 | 2 | Graburg | 51.112754 | 10.119810 | 472 |
| 11/Supplement S1 | W12 | 5 | Hitzelrode | 51.243289 | 10.063315 | 449 |
| 12/Supplement S1 | W13 | 4 | Hitzelrode | 51.243503 | 10.039475 | 490 |
| 13/Supplement S1 | W14/W15 | 4 | Hitzelrode | 51.244714 | 10.039803 | 495 |
| | W16 | 4 | Wehretal | 51.244666 | 10.040146 | 504 |
| | W17 | 4 | Hitzelrode | 51.244603 | 10.040173 | 503 |
| | | | **Upper Franconia** | | | |
| 1/Supplement S2 | D5 | 6,5 | Destuben | 49.9064 | 11.56957 | 430 |
| 2/Supplement S2 | D4 | 12,5 | Destuben | 49.90584 | 11.56766 | 442 |
| 3/Supplement S2 | D101 | 6 | Destuben | 49.9048 | 11.56772 | 444 |
| 4/Supplement S2 | D8 | 5 | Destuben | 49.90501 | 11.56895 | 435 |
| 5/Supplement S2 | D6 | 10 | Destuben | 49.90549 | 11.5691 | 438 |
| 6/Supplement S2 | B2-b | 9 | Busbach | 49.95642 | 11.42183 | 555 |
| 7/Supplement S2 | B3ho | 9 | Busbach | 49.95643 | 11.42177 | 555 |
| 8/Supplement S2 | N103 | 13 | Busbach | 49.94957 | 11.41832 | 547 |
| 9/Supplement S2 | B8 | 12 | Busbach | 49.95128 | 11.41884 | 549 |
| 10/Supplement S2 | B9 | 15 | Busbach | 49.95087 | 11.41878 | 544 |
| 11/Supplement S2 | B1 | 5 | Busbach | 49.95734 | 11.42226 | 560 |
| 13/Supplement S2 | N101 | 6 | Busbach | 49.95725 | 11.45455 | 436 |
| 12/Supplement S2 | RM6 | 11 | Roter Main-Tal | 49.90642 | 11.61933 | 417 |
| 14/Supplement S2 | R4 | 10 | Roter Main-Tal | 49.9214 | 11.63415 | 361 |
| 15/Supplement S2 | WP38 | 8 | Roter Main-Tal | 49.90642 | 11.61933 | 382 |
| 16/Supplement S2 | R1 | 9,5 | Roter Main-Tal | 49.87881 | 11.61715 | 399 |
| 17/Supplement S2 | R3ho | 18 | Roter Main-Tal | 49.88388 | 11.6211 | 397 |
| 18/Supplement S2 | R2ho | 15 | Roter Main-Tal | 49.88386 | 11.62056 | 397 |

**Supplement S1.** Forest communities from 13 vegetation plots of European crab apple (*Malus sylvestris* ) in North Hesse.

**Beilage S1.** Waldgesellschaften aus 13 Aufnahmeflächen mit Wildapfel (*Malus sylvestris* ) in Nordhessen.

Type 1 1a (1): fragment of *Aceri-Tilietum platyphylli* Faber 1936 without differential species
1b (2-5): *Aceri-Tilietum platyphylli* Faber 1936 typicum
1c (6-9): *Aceri-Tilietum platyphylli* Faber 1936 *vincetoxicetosum* (Winterhoff 1963) Hartmann et Jahn 1967 (Vincetoxico-Tilietum platyphylli Winterhoff 1963)
Type 2 (10-13): *Carici-Fagetum* Moor 1952

| S/N (serial number) | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Aufnahme-ID / plot ID | | W22 | W4 | W7 | W1 | W11 | W5 | W18 | W2 | W6 | W3 | W12 | W13 | W14 |
| Aufnahmefläche / Relevé area ($m^2$) | | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 |
| Aufnahmedatum / date of investigation | | 20170905 | 20170706 | 20170706 | 20170706 | 20170706 | 20170706 | 20170905 | 20170706 | 20170706 | 20170706 | 20170905 | 20170905 | 20170905 |
| Altitude [m] | | 440 | 504 | 510 | 443 | 510 | 511 | 510 | 467 | 511 | 472 | 450 | 490 | 495 |
| Aspect [degrees] | | 270 | 0 | 180 | 180 | 315 | 315 | 0 | 180 | 315 | 180 | 270 | 0 | 0 |
| Slope [degrees] | | 40 | 0 | 2 | 20 | 2 | 2 | 0 | 15 | 2 | 50 | 40 | 1 | 0 |
| Cover tree layer [%] | | 80 | 30 | 55 | 50 | 50 | 90 | 60 | 50 | 50 | 60 | 60 | 90 | 90 |
| Cover shrub layer [%] | | 0 | 0 | 35 | 30 | 30 | 5 | 30 | 50 | 0 | 10 | 8 | 10 | 30 |
| Cover herb layer [%] | | 0 | 80 | 75 | 55 | 90 | 50 | 40 | 65 | 85 | 50 | 40 | 35 | 70 |
| Cover moss layer [%] | | 10 | 0 | 0 | 1 | 4 | 0 | 10 | 0 | 5 | 7 | 4 | 0 | 10 |
| Height [highest] trees [m] | | 20 | 6 | 10 | 20 | 30 | 18 | 20 | 20 | 10 | 10 | 20 | 15 | 15 |
| Height lowest trees [m] | | 10 | 6 | 6 | 7 | 10 | 7 | 10 | 7 | 8 | 7 | 5 | 8 | 15 |
| Height [highest] shrubs [m] | | 0.0 | 6.0 | 3.0 | 3.0 | 3.0 | 3.0 | 6.0 | 3.0 | 0.0 | 2.0 | 3.0 | 4.0 | 4.0 |
| Height lowest shrubs [m] | | 0.0 | 6.0 | 3.0 | 1.0 | 3.0 | 3.0 | 2.0 | 3.0 | 0.0 | 2.0 | 3.0 | 4.0 | 1.0 |
| Number of species | | 6 | 33 | 22 | 22 | 24 | 29 | 18 | 29 | 22 | 19 | 27 | 21 | 20 |
| **Trees** | | | | | | | | | | | | | | |
| Malus sylvestris | t1, t2 | . | 30 | 7 | 30 | 10 | 2 | 20 | 20 | 5 | . | 20 | . | . |
| Malus sylvestris | s1 | 40 | . | 2 | . | . | . | . | . | . | 2 | . | 3 | 10 |
| Fraxinus excelsior | t1, t2 | . | . | 25 | . | 20 | 5 | . | 10,5 | 50,10 | . | . | 5 | . |
| Fraxinus excelsior | jl | . | 1 | 2 | 1 | 2 | 0.5 | 5,1 | 5 | 20 | . | 2 | 2 | 5 |
| Fagus sylvatica (***predominating*** ) | t1, t2 | . | . | . | 20 | . | 30 | 30 | 10 | . | 10,20 | ***60*** | ***75*** | ***50*** |
| Fagus sylvatica | s1,s2 | . | . | . | 20,4 | . | 2 | . | 5 | . | . | . | . | 2 |
| Fagus sylvatica | jl | . | . | 1 | . | 5 | 0.5 | . | . | . | . | 1 | . | . |
| Acer pseudoplatanus | t1 | 10 | . | 25 | . | . | . | . | . | . | . | . | . | . |
| Acer pseudoplatanus | jl, s1 | . | . | . | . | . | . | 1 | 1 | 1 | 2 | 0.5 | . | . |
| Acer platanoides | t1, jl | . | 1 | 2 | . | 30 | 0.5 | . | 10 | . | 0.5 | . | . | . |
| Taxus baccata | t2 | 10 | . | . | . | . | . | . | . | . | . | . | . | . |
| Taxus baccata | jl, s2 | . | . | 0.5 | 1 | . | 1 | . | . | . | 0.5 | 1 | 0.5 | . |
| Carpinus betulus | t2 | . | . | 40 | . | 20 | 2 | . | . | 10 | . | . | . | . |
| Carpinus betulus | jl, s1 | . | 10 | . | . | 5,10 | 1 | . | . | 1 | . | . | . | . |
| Sorbus torminalis | jl, s1 | . | 1 | . | . | . | . | 1,2 | 0.5 | . | 1 | . | . | . |
| Sorbus aria | t2 | . | . | . | . | . | 3 | . | . | . | 40 | . | . | . |
| Sorbus aria | jl, s1 | . | 1 | . | . | . | . | . | . | . | 3,4 | . | . | . |
| Ulmus glabra | t2 | . | . | . | 2 | . | . | . | . | . | . | . | . | . |
| Ulmus glabra | jl, s1 | . | . | . | 2,10 | . | . | . | . | . | . | . | . | 1 |
| Picea abies | t1 | . | . | . | 10 | . | . | . | . | . | . | . | . | . |
| Acer campestre | jl | . | 2 | . | . | . | . | . | . | . | . | . | . | . |
| Quercus robur | t2 | . | . | 10 | . | . | . | . | . | . | . | . | . | . |
| **Shrubs** | | | | | | | | | | | | | | |
| Corylus avellana | t2, s1 | 30 | . | . | 15 | . | . | . | 25 | . | . | . | 5 | . |
| Corylus avellana | jl, s2 | . | 1 | . | 5 | . | . | . | 10 | 1 | . | . | . | . |
| Lonicera xylosteum | s1,s2 | . | . | 2 | 1 | . | . | . | . | . | . | . | . | . |
| Lonicera xylosteum | jl | . | . | . | . | . | . | . | . | . | . | 0.5 | . | . |
| Cornus sanguinea | jl, s1 | . | . | . | . | . | . | . | 1 | . | 2 | 0.5 | . | . |
| Rhamnus cathartica | jl,s2 | . | . | . | 0.5 | . | . | . | . | . | . | . | . | 0.5 |
| Sorbus aucuparia | jl, s1 | . | . | . | . | . | . | . | 1 | . | . | . | 1 | . |
| Rosa species | s2 | . | . | . | 1 | . | . | . | . | . | . | . | . | . |
| Juniperus communis | s1 | . | . | . | . | . | . | . | . | . | . | 1 | . | . |
| Frangula alnus | s1 | . | . | . | . | . | . | . | . | . | . | 5 | . | . |
| Viburnum opulus | jl, s1 | . | . | . | . | . | . | . | 1,2 | . | . | . | . | . |
| Prunus spinosa | s2 | . | . | . | . | . | . | . | . | . | . | . | . | 5 |
| **Differential species (type 1b, 1c, 2)** | | | | | | | | | | | | | | |
| Mercurialis perennis | hl | . | 1 | 20 | 3 | 20 | 10 | 2 | . | 1 | . | 1 | . | 5 |
| Laserpitium latifolium | hl | . | 1 | 10 | . | 25 | . | 1 | 0.5 | 5 | . | 1 | 0.5 | . |
| Convallaria majalis | hl | . | . | . | . | 5 | 10 | 1 | 2 | 4 | 5 | 3 | 2 | . |
| Lathyrus vernus | hl | . | . | 1 | . | 2 | 4 | . | 0.5 | 2 | . | . | . | 0.5 |
| Crataegus laevigata | s1,s2 | . | . | . | . | 20 | 2 | 10,4 | 40 | . | . | . | 2 | 20,5 |
| Crataegus laevigata | jl | . | . | . | . | . | 4 | . | . | . | . | . | 1 | . |
| Crataegus monogyna (inkl. C. x media) | t2,s1 | . | . | 30 | . | . | . | . | . | 15 | . | . | . | . |
| Crataegus monogyna (inkl. C. x media) | jl | . | . | . | 1 | . | . | . | . | 5 | . | 1 | . | . |
| Primula veris | | . | 1 | 5 | . | 2 | . | . | . | . | . | . | . | 3 |
| **Differential species (type 1b, 1c)** | | | | | | | | | | | | | | |
| Tilia platyphyllos | t1,t2 | | . | . | . | . | 25 | 10 | . | . | . | . | . | . |
| Tilia platyphyllos | jl | | 1 | 1 | . | . | . | . | . | 5 | . | . | . | . |
| Phyteuma spicatum | hl | . | 1 | 5 | 0.5 | 1 | . | . | 0.5 | 2 | . | . | . | . |
| Galium sylvaticum | hl | . | . | 20 | . | 5 | 1 | . | 0.5 | 1 | . | . | . | . |
| Lilium martagon | hl | . | . | 2 | . | 1 | 2 | . | 2 | 3 | . | . | . | . |
| Bupleurum longifolium | hl | . | 0.5 | 5 | . | 5 | 5 | . | . | 10 | . | . | . | . |
| **Differential species (type 1c, 2)** | | | | | | | | | | | | | | |
| Quercus petraea | t1,jl | . | . | . | . | . | 30 | 30 | . | 1 | . | . | . | 20 |
| Hedera helix | hl | . | . | . | . | . | 10 | 1 | 5 | 10 | . | . | 1 | 1 |
| Sesleria albicans | hl | . | . | . | . | . | 0.5 | . | 0.5 | . | 20 | 3 | 25 | 30 |
| Vincetoxicum hirundinaria | hl | . | . | . | . | . | . | . | 5 | 10 | 1 | 10 | 1 | 1 |
| Carex montana | hl | . | . | . | . | . | . | 1 | 20 | . | 10 | . | . | 20 |
| **Differential species (type 2)** | | | | | | | | | | | | | | |
| Pinus sylvestris | t1,t2 | . | . | . | 3 | . | . | . | . | . | 5 | . | 10,2 | 10 |
| Pyrus pyraster | t1,t2 | . | . | . | . | . | . | . | . | . | . | . | 8 | 10 |
| Pyrus pyraster | s1 | . | . | . | . | . | . | . | . | . | . | 2 | . | . |
| Hieracium bifidum | | . | . | . | . | . | . | . | . | . | 0.5 | 1 | 0.5 | . |
| Campanula persicifolia | | . | . | . | . | . | . | . | . | . | . | 0.5 | 0.5 | . |
| **Companion species** | | | | | | | | | | | | | | |
| Brachypodium pinnatum | hl | . | 30 | . | 40 | 5 | . | 20 | 5 | . | 10 | . | 2 | 5 |
| Dactylis polygama | hl | . | . | 1 | . | . | . | . | 0.5 | 1 | . | . | . | . |
| Clematis vitalba | hl | . | 5 | . | 0.5 | . | . | . | 1 | . | . | . | . | . |
| Melica uniflora | hl | . | 1 | . | . | . | 0.5 | . | . | . | . | . | . | . |
| Fragaria vesca | hl | . | 0.5 | . | . | . | . | . | 1 | . | . | . | . | . |
| Polygonatum multiflorum | hl | . | 0.5 | . | . | . | 2 | . | . | 2 | . | . | . | . |
| Hieracium murorum | hl | . | . | . | . | . | 0.5 | . | . | . | . | 1 | 0.5 | . |
| Hieracium glaucinum | hl | . | . | . | . | 2 | 0.5 | 3 | . | . | . | . | . | . |
| Origanum vulgare | hl | . | 1 | . | . | . | . | . | . | . | . | 3 | 1 | . |
| Hordelymus europaeus | hl | . | . | . | 1 | 0.5 | . | . | . | . | . | . | . | . |
| Euphorbia cyparissias | hl | . | 2 | . | 1 | . | . | . | . | . | . | . | . | . |
| Anemone nemorosa | hl | . | . | . | 1 | . | . | . | 2 | . | . | . | . | . |
| Campanula trachelium | hl | . | . | . | . | 1 | 1 | . | . | . | . | . | . | . |
| Bromus benekenii | hl | . | 1 | . | . | . | . | . | . | . | . | . | . | . |
| Solidago virgaurea | hl | . | 0.5 | . | . | . | . | . | 0.5 | . | . | . | . | . |
| Sanicula europaea | hl | . | 0.5 | . | . | . | 0.5 | . | . | . | . | . | . | . |
| Arabis pauciflora | hl | . | . | . | . | 1 | 0.5 | . | . | . | . | . | . | . |
| Hypericum hirsutum | hl | . | 1 | 2 | . | . | . | . | . | . | . | . | . | . |
| Epipactis atrorubens | hl | . | . | . | . | . | . | . | 0.5 | . | 0.5 | . | . | . |
| **Bryophytes** | | | | | | | | | | | | | | |
| Ctenidium molluscum | ml | 8 | . | . | . | . | . | . | . | . | 5 | 2 | . | . |
| Polytrichum formosum | ml | . | . | . | . | 2 | . | 10 | . | . | . | . | . | 10 |
| Brachythecium rutabulum | ml | . | . | . | 1 | . | . | . | . | . | . | . | . | . |
| Tortella tortuosa | ml | . | . | . | . | . | . | . | . | . | 1 | 2 | . | . |
| Hypnum cupressiforme | ml | . | . | . | . | 2 | . | . | . | 2 | . | . | . | . |

**Species noted in one reléve only:**
**Herb layer:** Allium ursinum 2: 0.5; Dactylis glomerata 2: 10; Aethusa cynapium 2: 0.5; Aegopodium podagraria 2: 5; Anthemis tinctoria 2: 0.5; Picris hieracioides 2: 0.5; Senecio sylvaticus 2: 0.5; Coronilla varia 2: 1; Mycelis muralis 3: 0.5; Viola riviniana 4: 0.5; Cephalanthera damasonium 4: 0.5; Aquilegia vulgaris 5: 3; Polygonatum verticillatum 5: 1; Carlina vulgaris 6: 0.5; Melampyrum nemorosum 6: 0.5; Carex digitata 6: 0.5; Brachypodium sylvaticum 6: 0.5; Epipactis helleborine 7: 1; Hieracium lachenalii 7: 1; Carex sylvatica 8: 0.5; Gymnocarpium robertianum 11: 5; Galium odoratum: 11: 1; Daphne mezereum 11: 2; Epipactis muelleri 11: 1: Gentianella ciliata 11: 1; Viola hirta 12: 0.5; Calamagrostis varia 12: 0.5; Viola reichenbachiana 13: 4.
**Bryophytes:** Homalothecium lutescens 1: 2; Isothecium myosuroides 9: 3; Anomodon attenuatus 10: 1.

**Supplement S2.** Plant communities from 18 vegetation plots of European crabapple (*Malus sylvestris*) in Upper Franconia

**Beilage S2.** Pflanzengesellschaften aus 18 Aufnahmeflächen mit Wildapfel (*Malus sylvestris*) in Oberfranken

Type 1 (1-5): *Molinia caerulea-Oxalis acetosella-* Scots pine forest ex *Calamagrostio arundinaceae-Quercetum petraeae* (Hartmann 1934) Scamoni et Passarge 1959
Type 2 (6-7): residuals of secondary (semi-natural) mesoxerophytic grasslands of *Bromion erecti Koch 1926* overgrown with encroaching bushes and trees (replacement vegetation of Carici-Fagetum Moor 1952)
Type 3 (8-10): *mixed pine-hardwood stands* ex *Hordelymo-Fagetum Kuhn* 1937
Type 4 (11-13): *Stellario-Carpinetum* Oberd. 1957 (11-12: early successional stages with *Pinus sylvestris, Betula pendula, Populus tremula*)
Type 5 (14-18): *Stellario nemorum-Alnetum glutinosae* Lohmeyer 1957

| S/N (serial number) | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Aufnahme-ID / plot ID | | D5 | D4 | D101 | D8 | D6 | B2-b | B3 ho | N103 | B8 | B9 | B1 | RM6 | N101 | R4 ho | WP38 | R1 | R3ho | R2ho |
| Aufnahmefläche / Relevé area ($m^2$) | | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 |
| Aufnahmedatum / date of investigation | | 20170703 | 20170703 | 20170824 | 20170824 | 20170824 | 20170620 | 20170620 | 20170529 | 20170529 | 20170529 | 20170620 | 20170908 | 20170529 | 20170620 | 20170612 | 20170612 | 20170711 | 20170711 |
| Altitude (m) | | 430 | 442 | 444 | 435 | 438 | 555 | 555 | 547 | 549 | 544 | 560 | 417 | 436 | 361 | 382 | 399 | 397 | 397 |
| Aspect (degrees) | | 45 | - | 160 | 200 | 225 | 200 | 200 | 200 | 200 | 200 | 290 | 67 | 90 | 200 | 225 | 337 | 270 | 337 |
| Slope (degrees) | | 8 | 0 | 10 | 7 | 6 | 1 | 1 | 25 | 25 | 15 | 5 | 10 | 3 | 57 | 25 | 10 | 2 | 10 |
| Cover tree layer (%) | | 75 | 60 | 50 | 50 | 40 | 50 | 50 | 50 | 80 | 50 | 80 | 60 | 50 | 50 | 30 | 20 | 50 | 100 |
| Cover shrub layer (%) | | 10 | 4 | 30 | 50 | 70 | 40 | 40 | 50 | 15 | 5 | 80 | 50 | 70 | 15 | 5 | 30 | 30 | 30 |
| Cover herb layer (%) | | 65 | 100 | 90 | 30 | 40 | 80 | 100 | 80 | 90 | 90 | 95 | 60 | 40 | 70 | 80 | 80 | 100 | 90 |
| Cover moss layer (%) | | 70 | 0 | 90 | 70 | 50 | 0 | 0 | 0 | 0 | 0 | 0 | 10 | 0 | 0 | 0 | 0 | 0 | 0 |
| Height (highest) trees (m) | | 30 | 30 | 30 | 30 | 30 | 25 | 9 | 25 | 25 | 25 | 12 | 25 | 20 | 18 | 15 | 15 | 20 | 20 |
| Height lowest trees (m) | | 7 | 20 | 8 | 6 | 10 | 6 | 6 | 15 | 15 | 15 | 10 | 11 | 15 | 10 | 8 | 10 | 15 | 15 |
| Height (highest) shrubs (m) | | 3.0 | 3.0 | 6.0 | 4.0 | 6.0 | 5.0 | 5.0 | 8.0 | 5.0 | 1.5 | 5.0 | 6.0 | 8.0 | 5.0 | 5.0 | 2.0 | 4.0 | 5.0 |
| Height lowest shrubs (m) | | 2.0 | 1.0 | 3.0 | 1.5 | 2.0 | 0.5 | 4.0 | 1.0 | 5.0 | 1.5 | 1.5 | 1.5 | 3.0 | 1.0 | 1.0 | 1.5 | 2.5 | 1.5 |
| Number of species | | 28 | 18 | 19 | 26 | 20 | 22 | 15 | 16 | 28 | 30 | 15 | 20 | 14 | 14 | 32 | 21 | 22 | 29 |
| **Trees** | | | | | | | | | | | | | | | | | | | |
| Malus sylvestris | t1, t2 | 15 | 15 | . | 30 | 30 | 10, 15 | 30 | 30 | 1 | 20 | 15 | 15 | 50 | 20 | 30 | 20 | 10 | 20 |
| Malus sylvestris | s1, s2 | . | . | 10, 5 | . | . | 15 | 10 | . | . | . | . | . | . | . | . | . | . | . |
| Malus sylvestris | jl | 1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Pinus sylvestris | t1, t2 | 40 | 60 | 50 | 45 | 40 | . | . | 30 | 2 | . | 40 | 20 | . | . | . | . | . | . |
| Quercus robur | t1, t2 | . | 10 | 10 | 5 | . | 15 | 40 | . | 40 | . | . | . | 50 | . | . | . | . | 20 |
| Quercus robur | s1, s2 | . | . | 20 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Quercus robur | jl | 1 | . | 3 | 0.1 | . | . | . | . | . | . | . | 0.1 | . | . | . | . | . | . |
| Sorbus aucuparia | s1, s2 | 1 | 2 | 1 | . | 1 | 5 | 15 | . | . | . | . | 1 | . | . | . | . | . | . |
| Sorbus aucuparia | jl | 1 | 5 | 1 | 1 | 1 | 5 | 1 | . | . | . | . | . | . | . | . | . | . | . |
| Betula pendula | t1, t2 | 25 | . | . | . | . | 0.1 | . | . | . | . | . | 20 | . | . | . | . | . | . |
| Betula pendula | s1, s2 | . | . | 2 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Acer pseudoplatanus | t1, t2 | . | . | . | . | . | . | . | . | 40 | 20 | . | . | . | . | . | . | . | 20 |
| Acer pseudoplatanus | s1 | . | . | . | . | . | . | . | . | . | 0.5 | . | . | . | . | . | . | 2 | . |
| Acer pseudoplatanus | jl | . | . | . | . | . | . | . | 2 | . | . | . | . | . | . | . | . | . | . |
| Acer campestre | t2 | . | . | . | . | . | . | . | . | 1 | . | . | . | . | . | . | . | . | . |
| Acer campestre | s | . | . | . | . | . | . | . | . | | 1 | . | . | . | . | . | . | . | . |
| Acer campestre | jl | . | . | . | . | . | . | 1 | . | 1 | 1 | . | . | . | . | . | . | . | . |
| Fraxinus excelsior | t1 | . | . | . | . | . | . | . | . | . | . | . | . | . | 20 | . | . | . | . |
| Fraxinus excelsior | t2 | . | . | . | . | . | . | . | 3 | . | . | . | . | . | . | . | . | 5 | . |
| Fraxinus excelsior | s1, s2 | . | . | . | 0.1 | . | . | . | 5 | 0.1 | 2 | . | . | . | . | . | . | . | . |
| Fraxinus excelsior | jl | . | . | . | . | . | . | . | 1 | . | . | . | . | . | . | . | . | . | . |
| Prunus avium | t1, t2 | . | . | . | . | . | 15 | 15 | . | . | . | . | . | . | . | . | . | . | . |
| Prunus avium | s1, s2 | . | . | . | . | . | . | 2 | . | . | . | . | . | 10 | . | . | . | . | . |
| Prunus avium | jl | . | . | . | . | . | . | . | . | . | . | 1 | . | . | . | . | . | . | . |
| Picea abies | t1, t2 | . | 15 | . | . | . | . | . | . | . | 5 | . | . | . | . | . | . | . | . |
| Pyrus pyraster | t2 | . | . | . | 0.1 | 10 | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Populus tremula | t1, t2 | . | . | . | . | . | . | . | . | . | 30 | . | 10 | . | . | . | . | . | . |
| Populus tremula | s1, s2 | . | . | . | . | . | . | . | . | 10 | . | . | 10 | . | . | . | . | . | . |
| Carpinus betulus | t1, t2 | . | . | . | . | . | . | . | . | . | 30 | . | . | . | . | . | . | . | . |
| Carpinus betulus | s1, s2 | . | . | . | . | . | . | . | . | . | . | . | 5 | . | . | . | . | . | . |
| Populus alba | s1 | 1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Juglans regia | s2 | . | . | . | . | 1 | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Juglans regia | jl | . | . | . | . | 1 | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Fagus sylvatica | t1, t2 | . | . | . | . | . | 10 | . | . | . | . | . | . | . | . | . | . | . | . |
| Fagus sylvatica | s1, jl | . | . | . | . | . | . | . | . | 1 | . | . | . | . | . | . | . | . | . |
| Acer platanoides | s1 | . | . | . | . | . | . | . | . | . | . | . | . | . | 0.1 | . | . | . | . |
| Prunus padus | s1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 10 | . |
| Salix alba | t1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 5 |
| **Shrubs** | | | | | | | | | | | | | | | | | | | |
| Prunus spinosa | s1, s2 | 2 | 3 | 10 | 15 | 20 | 15 | . | . | . | . | . | 5 | 5 | . | . | . | . | 5 |
| Prunus spinosa | jl | 1 | . | . | . | . | . | . | . | . | . | 2 | . | . | . | . | . | . | . |
| Crataegus x macrocarpa | s1 | . | . | . | 5 | 10 | 5 | . | 1 | . | . | . | . | 5 | . | . | . | . | . |
| Crataegus x macrocarpa | s2 | . | . | . | 10 | . | . | . | . | . | . | . | . | 50 | . | . | . | . | . |
| Crataegus laevigata | s1, s2 | 2 | . | . | 20 | 10 | 5 | 5 | . | . | . | 3 | . | 3 | . | . | . | . | . |
| Crataegus laevigata | jl | . | . | . | 0.1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Crataegus monogyna | s1, s2 | . | . | . | 2 | . | . | . | . | . | . | . | 20 | . | . | . | . | . | . |
| Crataegus monogyna | jl | . | . | . | . | . | . | . | . | . | . | . | 15 | . | . | . | . | . | . |
| Crataegus x media | s1, s2 | 5 | 2 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Crataegus x media | jl | . | 0.1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Crataegus rhipidophylla | s2 | . | . | . | . | . | . | . | . | . | . | . | . | 2 | . | . | . | . | . |
| Rosa canina | s1, s2 | . | . | . | . | . | . | . | . | . | . | . | . | 1 | . | 1 | . | . | 1 |
| Rosa canina | jl | 0.1 | . | . | . | . | . | . | . | . | 0.1 | . | . | . | . | . | . | . | . |
| Rosa tomentosa | s2 | . | . | 2 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Rosa sp. | jl | . | . | . | . | 1 | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Lonicera xylosteum | s1, s2 | . | . | . | . | . | . | . | 9 | 1 | 1 | 3 | . | . | . | . | . | . | . |
| Corylus avellana | t2 | . | . | . | . | . | . | . | 30 | . | . | . | . | . | . | . | . | . | . |
| Corylus avellana | s1, jl | . | . | . | . | . | . | . | 35 | . | 0.5 | . | . | . | . | . | . | 2 | . |
| Ribes uva-crispa | hl | . | . | . | . | . | . | . | . | . | . | 1 | . | . | . | . | . | . | . |
| Cornus mas | s1 | . | . | . | . | . | . | . | . | . | 0.1 | . | . | . | . | . | . | . | . |
| Juniperus communis | s2 | . | . | 3 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Sorbus pannonica | s1 | . | . | . | . | . | 5 | . | . | . | . | . | . | . | . | . | . | . | . |
| Salix triandra | s1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 5 | . |
| **Differential species (type 1)** | | | | | | | | | | | | | | | | | | | |
| Vaccinium myrtillus | hl | 25 | 5 | 80 | 5 | 10 | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Carex flacca | hl | 5 | 2 | . | 20 | 20 | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Thuidium tamariscinum | ml | 5 | . | 5 | 10 | 25 | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Frangula alnus | s, jl | 5 | . | 5 | . | 1 | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Scleropodium purum | ml | 50 | . | . | . | 25 | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Deschampsia flexuosa | hl | 5 | . | 2 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Molinia caerulea | hl | 20 | 1 | 10 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Oxalis acetosella | hl | 0.1 | 10 | . | 0.1 | . | . | . | . | . | . | . | 1 | . | . | . | . | . | . |
| Vaccinium vitis-idaea | hl | 1 | . | 5 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Viola riviniana | hl | 0.1 | . | . | 0.1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Rubus fruticosus ag. L. | s2, hl | . | . | . | 0.1 | 1 | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Dicranum scoparium | ml | 2 | . | . | 1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Pleurozium schreberi | ml | . | . | 80 | 60 | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Polytrichum formosum | ml | . | . | 1 | 2 | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| **Differential species (type 2)** | | | | | | | | | | | | | | | | | | | |
| Vicia cracca | hl | . | . | . | . | . | 10 | 30 | . | . | . | 1 | . | . | . | . | . | . | . |
| Euphorbia cyparissias | hl | . | . | . | . | . | 1 | 1 | . | . | . | . | . | . | . | . | . | . | . |
| Viola hirta | hl | . | . | . | . | . | 10 | 10 | . | . | . | . | . | . | . | . | . | . | . |
| Rosa rubiginosa | s1 | . | . | . | . | . | 5 | 5 | . | . | . | . | . | . | . | . | . | . | . |
| Cornus sanguinea | s, jl | . | . | . | . | . | 5 | 5 | . | . | . | . | . | . | . | . | . | . | . |
| Festuca rubra | hl | . | . | . | . | . | 5 | 5 | . | . | . | . | . | . | . | . | . | . | . |
| Rhamnus cathartica | s1, jl | . | . | . | . | . | 1 | 1 | . | . | . | . | . | . | . | . | . | . | . |
| Heracleum sphondylium | hl | . | . | . | . | . | 1 | 1 | . | . | . | . | . | . | . | . | . | . | . |
| Veronica teucrium | hl | . | . | . | . | . | 0.1 | . | . | . | . | . | . | . | . | . | . | . | . |
| **Differential species (type 3-5)** | | | | | | | | | | | | | | | | | | | |
| Aegopodium podagraria | hl | . | . | . | . | . | . | . | 2 | . | 80 | . | . | . | 3 | 10 | 2 | 50 | 40 |
| Galium aparine | hl | . | . | . | . | . | . | . | . | . | . | 0.1 | 0.1 | 15 | . | 20 | 15 | 50 | . |
| Lamiastrum galeobdolon | hl | . | . | . | . | . | . | . | . | 4 | 0.1 | . | . | . | . | . | 2 | 2 | 5 |
| **Differential species (type 3)** | | | | | | | | | | | | | | | | | | | |
| Ulmus glabra | s, jl | . | . | . | . | . | . | . | 1 | 0.1 | 1 | . | . | . | . | . | . | . | . |
| Sanicula europaea | hl | . | . | . | . | . | . | . | 2 | 2 | 15 | . | . | . | . | . | . | . | . |
| Galium odoratum | hl | . | . | . | . | . | . | . | 15 | 5 | 10 | . | . | . | . | . | . | . | . |
| Polygonatum multiflorum | hl | . | . | . | . | . | . | . | 1 | 1 | 40 | . | . | . | . | . | . | . | . |
| Melica uniflora | hl | . | . | . | . | . | . | . | 1 | 25 | 2 | . | . | . | . | . | . | . | . |
| Actaea spicata | hl | . | . | . | . | . | . | . | 2 | 0.5 | . | . | . | . | . | . | . | . | . |
| Asarum europaeum | hl | . | . | . | . | . | . | . | . | 5 | 1 | . | . | . | . | . | . | . | . |
| Pulmonaria obscura | hl | . | . | . | . | . | . | . | . | 0.1 | 0.1 | . | . | . | . | . | . | . | . |
| Lathyrus vernus | hl | . | . | . | . | . | . | . | . | 1 | 2 | . | . | . | . | . | . | . | . |
| **Differential species (type 4-5)** | | | | | | | | | | | | | | | | | | | |
| Geum urbanum | hl | . | . | . | . | . | . | . | . | . | 0.1 | . | 1 | . | 30 | 1 | . | . | 2 |
| Alliaria petiolata | hl | . | . | . | . | . | . | . | . | . | . | . | . | 5 | . | 1 | 2 | 2 | 2 |
| Sambucus nigra | s, jl | . | . | . | . | . | . | . | . | . | . | 3 | 10 | 2 | . | 5 | . | . | . |
| Festuca gigantea | hl | . | . | . | . | . | . | . | . | . | 0.1 | . | . | . | 2 | . | . | 5 | 10 |
| Carex brizoides | hl | . | . | . | . | . | . | . | . | . | . | . | 50 | . | . | . | 20 | 15 | 20 |
| Euonymus europaeus | s, jl | . | . | . | . | . | . | . | . | . | . | . | 0.1 | 0.1 | . | . | 1 | 2 | 20 |
| Stellaria holostea | hl | . | . | . | . | . | . | . | . | . | . | . | 1 | . | . | 2 | 2 | . | 10 |
| Rubus caesius | hl | . | . | . | . | . | . | . | . | . | . | 1 | . | . | . | 1 | 5 | . | 5 |
| **Differential species (type 6)** | | | | | | | | | | | | | | | | | | | |
| Alnus glutinosa | t1, t2 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 20 | 10 | . | 5 |
| Alnus incana | t1, t2 | . | . | . | . | . | . | . | . | . | . | . | . | . | 20 | . | . | 30 | 40 |
| Alnus incana | s1, jl | . | . | . | . | . | . | . | . | . | . | . | . | . | 7 | . | . | . | 10 |
| Salix fragilis | t1, t2 | . | . | . | . | . | . | . | . | . | . | . | . | . | 10 | 20 | . | 10 | . |
| Humulus lupulus | s1 | . | . | . | . | . | . | . | . | . | . | . | . | . | 7 | 0.1 | . | 15 | 5 |
| Urtica dioica | hl | . | . | . | . | . | . | . | . | . | . | . | . | . | 30 | 50 | 10 | 70 | . |
| Stachys sylvatica | hl | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 5 | . | 4 | 5 |
| Impatiens glandulifera | hl | . | . | . | . | . | . | . | . | . | . | . | . | . | 30 | 10 | 5 | . | 5 |
| Stellaria nemorum | hl | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 40 | 30 | 10 | . |
| Circaea x intermedia | hl | . | . | . | . | . | . | . | . | . | . | . | . | . | 1 | . | . | 2 | 5 |
| Phalaris arundinacea | hl | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 2 | 30 | . | 5 |
| **Companion species** | | | | | | | | | | | | | | | | | | | |
| Anemone nemorosa | hl | 1 | 0.1 | . | 1 | . | . | . | . | 10 | 2 | . | . | . | . | 20 | . | . | . |
| Ajuga reptans | hl | 0.1 | . | . | 0.1 | 0.1 | . | . | . | 0.1 | 1 | . | . | . | . | . | . | . | . |
| Brachypodium pinnatum (***facies-forming***) | hl | . | . | . | 2 | 2 | ***70*** | ***70*** | . | . | . | 40 | . | . | . | . | . | . | . |
| Rubus idaeus | hl, s | . | 1 | . | . | . | . | . | . | . | . | 1 | 15 | . | . | . | 30 | . | 5 |
| Brachypodium sylvaticum | hl | . | 0.1 | . | . | . | . | . | . | 1 | 1 | . | . | . | . | . | . | . | 5 |
| Convallaria majalis | hl | . | 2 | . | . | . | . | . | . | 25 | . | . | . | . | . | . | . | . | . |
| Fragaria moschata | hl | . | . | . | . | 1 | . | . | . | . | 1 | . | . | . | . | . | . | . | . |
| Carex montana | hl | . | . | . | . | 20 | . | . | . | 1 | . | . | . | . | . | . | . | . | . |
| Arrhenatherum elatius | hl | . | . | . | . | . | . | . | . | . | . | 60 | 10 | . | . | . | . | . | . |
| Dactylis glomerata | hl | . | . | . | . | . | . | . | . | . | . | . | . | . | 5 | 5 | . | . | . |
| Elymus caninus | hl | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 8 | . | . | 2 |
| Myosoton aquaticum | hl | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 20 | 0.1 | . | . |
| Athyrium filix-femina | hl | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 1 | 2 | . |

**Species noted in one reléve only:**
**Herb layer:** Dryopteris carthusiana 1: 0.1; Inula salicina 1: 0.1; Carex flava ag. 1: 0.1; Lathyrus montanus 1: 0.1; Rubus schleicheri 2: 80; Impatiens parviflora 2: 2; Dryopteris dilatata 2: 2; Calluna vulgaris 3: 1; Fragaria vesca 4: 0.1; Stachys officinalis 4: 0.1; Frangula alnus 4: 0.1; Veronica officinalis 4: 1; Galeopsis speciosa 6: 1; Epipactis helleborine 6: 0.1; Mercurialis perennis 8: 70; Hieracium murorum 8: 1; Galium sylvaticum 9: 0.5; Daphne mezereum 9: 0.1; Carex digitata 9: 0.1; Paris quadrifolia 9: 1; Maianthemum bifolium 10: 1; Senecio ovatus 10: 0.1; Aquilegia vulgaris 10: 0.1; Convolvulus arvensis 11: 1; Dactylis polygama 12: 5; Ranculus ficaria 13: 30; Galeopsis tetrahit 13: 1; Elymus repens 14: 1; Lamium maculatum 15: 2; Myosotis scorpioides 15: 1; Callitriche palustris 15: 5; Scutellaria galericulata 15: 1; Rumex obtusifolius 15: 0.1; Lysimachia nummularia 15: 2; Veronica beccabunga 15: 1; Solanum dulcamara 15: 1; Carex remota 15: 1; Holcus lanatus 15: 1; Poa trivialis 15: 0.1; Petasites hybridus 16: 20; Juncus effusus 16: 5; Filipendula ulmaria 16: 0.1; Potentilla erecta 16: 0.1; Aconitum lycoctonum 17: 2; Poa nemoralis 18: 5.
**Bryophytes:** Dicranum polysetum 1: 2; Sphagnum sp. 3: 3; Lophocolea bidentata 3: 1; Hypnum cupressiforme 5: 10; Eurhynchium striatum 12: 5; Plagiomnium affine 12: 5; Plagiomnium undulatum 18: 4; Eurhynchium praelongum 18: 1; Mnium spinosum 18: 1.

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