

# Calicolous rock-outcrop lime forests in the Cantabrian Mountains and the Western Pyrenees

## Kalkfels-Lindenwälder im Kantabrischen Gebirge und den westlichen Pyrenäen

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### Abstract

We present the first study of the forest vegetation dominated by *Tilia platyphyllos* growing on calcareous rock outcrops in the northern part of the Iberian Peninsula. This vegetation is confined to steep rocky slopes of mainly northern aspect in limestone areas. Based on a dataset of 53 relevés recorded during the summer of 2019 and compared with so far described associations of the order *Aceretalia pseudoplatani* (118 relevés), we describe the new association *Helictotricho cantabrici-Tilietum platyphylli*, distributed in the area stretching from the Picos de Europa in the west to the French Pyrenees in the east. Beside common species of mesophilous and thermophilous forests, numerous rock-outcrop specialists occur in this association. This vegetation is species-rich and of a high conservation value, as it also contains a high number of endemic species of the northern Iberian Peninsula, such as *Antirrhinum braun-blanquetii*, *Helictotrichon cantabricum*, *Oreochloa confusa*, *Petrocoptis pyrenaica*, *Saxifraga canaliculata* and *Seseli cantabricum*. Two subassociations of the *Helictotricho-Tilietum* are distinguished: *H. c.-T. p. typicum* represents more mesophytic stands occurring in the Basque-Cantabrian Mountains and the Pyrenees, while *H. c.-T. p. lauretosum nobilis*, with drought-tolerant submediterranean species, was recorded in the Cantabrian Range. We classify the *Helictotricho-Tilietum* in the *Melico-Tilion platyphylli* (order *Aceretalia pseudoplatani*, class *Carpino-Fagetea*), an alliance including xero-mesophilous scree and rock-outcrop forests of the European temperate zone.

**Keywords:** *Aceretalia pseudoplatani*, *Carpino-Fagetea*, classification, forest vegetation, Iberian Peninsula, *Melico-Tilion platyphylli*, phytosociology, syntaxonomy, *Tilia*

### Erweiterte deutsche Zusammenfassung am Ende des Artikels

## 1. Introduction

European scree and ravine forests dominated by the so-called noble-hardwood trees (i.e. *Acer platanoides*, *A. pseudoplatanus*, *Fraxinus excelsior*, *Tilia cordata*, *T. platyphyllos* and *Ulmus glabra*) are widely considered as an important refugium for numerous rare and relict vascular plant species (KOŠIR et al. 2008, PULLAIAH 2018, ZUKAL et al. 2020). Such forests represent azonal communities occurring in areas with rugged landscape on steep, often rocky

slopes in gullies and ravines, on cliffs and hillsides that are less favourable for the occurrence of the leading types of zonal vegetation, especially oak and oak-hornbeam forests in lower altitudes and beech forests in higher altitudes. *Tilio-Acerion* forests of slopes, screes and ravines are listed as a priority habitat within Annex I of the EU Habitats Directive (code 9180; EUROPEAN COMMISSION 2013), as they are of a high conservation value. Ravine woodland is also included in the European Red List of Habitats (code G1.Ab; JANSSEN et al. 2016) and evaluated as Near Threatened.

European scree and ravine forests have been traditionally classified within the broadly conceived alliance *Tilio-Acerion* Klika 1955. According to the EuroVegChecklist (MUCINA et al. 2016), they currently form the order *Aceretalia pseudoplatani* (within the class *Carpino-Fagetea*) with several alliances. In the Iberian Peninsula, forests belonging to *Aceretalia* are mainly confined to the northern and north-eastern part of Spain. They were studied by several authors, usually in smaller regions in the Pyrenees (VIGO et al. 1983, ROMO 1988, RIVAS-MARTÍNEZ & COSTA 1998), the Cantabrian Range (FERNÁNDEZ PRIETO & VÁZQUEZ 1987), the southern Iberian Range (CRESPO et al. 2008) and the Basque-Cantabrian Mountains (BIURRUN et al. 2011). CAMPOS et al. (2011) reviewed all the ravine forests belonging to *Aceretalia* in the Iberian Peninsula, resulting in six associations: *Viola mirabilis-Ulmetum glabrae* (ROMO 1988) and *Rosa pendulinae-Aceretum platanoidis* (CARRERAS et al. 1997) in the Pyrenees, *Hedero helioides-Tilietum platyphylli* in the Pyrenees (VIGO et al. 1983) and southern Basque-Cantabrian Mountains (BIURRUN et al. 2011), *Hyperico androsaemi-Ulmetum glabrae*, originally described from south-western France (VANDEN BERGHEN 1968), in the Basque Country (BIURRUN et al. 2011), *Helleboro occidentalis-Tilietum cordatae* in the Cantabrian Range (RIVAS-MARTÍNEZ 2011), and *Ononido aragonensis-Tilietum platyphylli* in the southern Iberian Range (CRESPO et al. 2008).

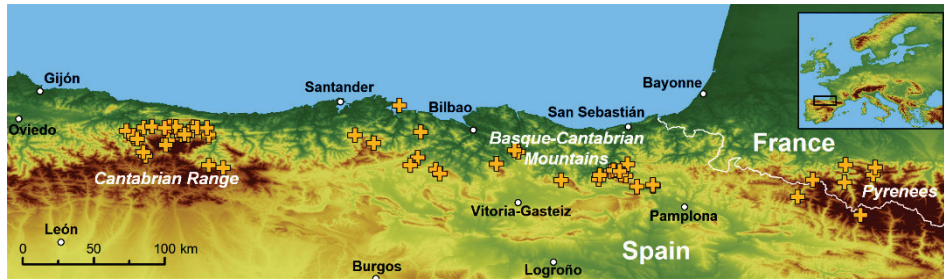
The above-mentioned associations include forests growing in ravines and on screes, but also among rock outcrops (CRESPO et al. 2008), although rock-outcrop forests were not distinguished as a distinct forest community. ZUKAL et al. (2020) reviewed calcicolous rock-outcrop lime forests (hereafter “CROLFs”) in central Europe and found their structure and floristic composition to differ from other forests of the *Aceretalia*. Tree canopy is rather open in CROLFs, and thus light-demanding species are frequent in the understorey, such as rock-outcrop and dry grassland species, some of them relict species of different periods (ZUKAL et al. 2020). During field research in the northern part of the Iberian Peninsula, we observed a similar forest type to occur there.

In this study, we focused our sampling on northern Iberian CROLFs. Our aims are to (1) describe the diversity, ecology and distribution of CROLFs in this area, and (2) compare them with the other communities of the *Aceretalia* in the Iberian Peninsula as well as with CROLFs occurring in central and western Europe.

## 2. Methods

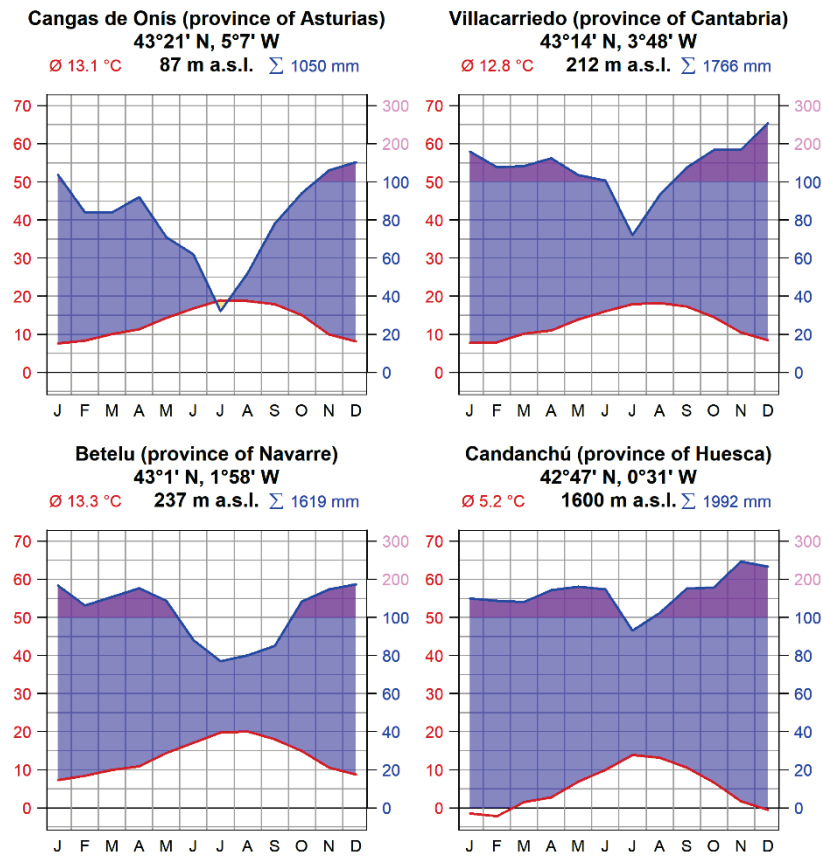
### 3.1 Study area

The study area comprises the northern part of the Iberian Peninsula in northern Spain and adjacent areas in south-western France, including the Cantabrian Mountains s.l. (Cantabrian Range on the west and Basque-Cantabrian Mountains on the east), and the Western Pyrenees (Fig. 1). It stretches from the Picos de Europa in the west (Cantabrian Range) to the French Western Pyrenees in the east (an area of nearly 400 km in length). The whole area belongs to the temperate macrobioclimatic zone (RIVAS-MARTÍNEZ et al. 2011) with a mild and humid climate. The studied localities occurred in both



**Fig. 1.** Study area showing the localities of sampled relevés (orange crosses).

**Abb. 1.** Verbreitungskarte der Vegetationsaufnahmen (orange Kreuze).



**Fig. 2.** Average Walter-type climate diagrams of the studied area based on data from Worldwide Bioclimatic Classification System (RIVAS-MARTÍNEZ & SÁENZ 2009) sorted from the west to the east. The blue curve represents precipitation and the red curve represents temperature. Note that precipitation amounts higher than 100 mm are shown on a different scale.

**Abb. 2.** Durchschnittliche Walter-Klimadiagramme aus dem Untersuchungsgebiet basierend auf Daten des Worldwide Bioclimatic Classification System (RIVAS-MARTÍNEZ & SÁENZ 2009), sortiert von West nach Ost. Die blaue Kurve repräsentiert den Niederschlag und die rote Kurve repräsentiert die Temperatur. Niederschlagsmengen über 100 mm werden in einem anderen Maßstab angezeigt.

mesotemperate and supratemperate thermotypes and both humid and hyperhumid ombrotypes (RIVAS-MARTÍNEZ et al. 2011). In general, continentality grows towards south-east in the study area. From the western part in the Cantabrian Range to the eastern part in the Western Pyrenees, there is a gradient of increasing temperature seasonality and decreasing precipitation seasonality, with a slight but noticeable summer drought in the Cantabrian Range (Fig. 2; RIVAS-MARTÍNEZ & SÁENZ 2009). Geology is very diverse along the study area, with Palaeozoic limestones as a dominant rock in the Picos de Europa, Mesozoic limestones and sandstones in the Basque-Cantabrian Mountains and Palaeozoic metamorphic and igneous rocks along with Mesozoic limestones in the Western Pyrenees. Due to ancient human settlement in the area, the landscape is quite transformed, but natural vegetation is still well preserved, especially in the mountains and in the steepest areas of lowlands. Zonal forests are mainly oak and beech forests in the mesotemperate humid and supratemperate hyperhumid belts, respectively (LOIDI et al. 2011). *Quercus robur* is the dominant oak in the Cantabrian Range and Basque-Cantabrian Mountains, while *Q. pubescens* forms the zonal forests on Pyrenean limestones below the beech belt. *Quercus petraea* is also common, but mostly on siliceous rocks. In the driest places of the Cantabrian Range and Basque-Cantabrian Mountains, *Q. faginea*, *Q. rotundifolia* and *Q. ilex* are also common, the former two especially in the southernmost mountains.

## 2.2 Data collection

We recorded phytosociological relevés of CROLFs in July and August 2019. Using aerial photographs and expert knowledge, we first selected localities with a presumable occurrence of CROLFs, especially in limestone areas with a noticeable presence of rock outcrops. As a rule, only the stands dominated by *Tilia* growing among rock outcrops were selected. Only one relevé per locality was recorded while keeping at least 1 km distance between the localities. Plot sizes of 100–225 m<sup>2</sup> (with a single exception of 50 m<sup>2</sup>) were used when recording relevés. The plot sizes were adjusted to individual stands, so their homogeneity was retained. In total, we recorded 53 relevés of CROLFs (see Fig. 1).

We estimated percentage cover of tree, shrub, herb and moss layers as well as the cover of each vascular plant species in each layer using the extended nine-degree Braun-Blanquet cover-abundance scale (WESTHOFF & VAN DER MAAREL 1978). For each plot, we recorded percentage cover of rocks, slope aspect and inclination, geographical coordinates and altitude. For the measurement of soil pH, soil samples were collected, each mixed from four subsamples taken in the same plot. Dried soil samples were sieved using 2 mm sieve and mixed in a laboratory with distilled water in a ratio of 2:5. pH was subsequently measured from the suspension using the GMH Greisinger pH meter.

Climatic data (Annual Mean Temperature, Temperature Seasonality, Annual Precipitation and Precipitation Seasonality) were obtained from the WorldClim model ver. 2 (FICK & HUIJMAN 2017).

## 2.3 Data analysis

We digitized the 53 relevés sampled by us in 2019 using the software TURBOVEG 2.1 (HENNEKENS & SCHAMINÉE 2001) and subsequently exported them to the JUICE software (ver. 7.1, TICHÝ 2002) forming the dataset (hereafter “CROLFs dataset”). To incorporate CROLFs into the general syntaxonomic framework of Iberian scree and ravine forests, we compared CROLF relevés with the relevés used by CAMPOS et al. (2011), who compiled the total amount of available data of *Aceretalia* in the Iberian Peninsula. We excluded two relevés of the association *Ononido-Tilietum platyphylli*, due to their small sampling area and low tree cover. The resulting dataset (hereafter “expanded dataset”) comprised 171 relevés. Vascular plant nomenclature was unified following EURO+MED (2020) with several species groups (see Supplement E1 and E2), higher syntaxa follow the EuroVegChecklist (MUCINA et al. 2016). Taxa recorded on the genus level were omitted. All records of a single species were merged into one layer according to the formula by FISCHER (2014) implemented in JUICE.

Similarly as CAMPOS et al. (2011), we used flexible-beta clustering ( $\beta = -0.25$ ) with Bray-Curtis distance measure and square-root transformation of mean percentage value of species covers for classification of relevés of the expanded dataset, using PC-ORD (MCCUNE & MEFFORD 1999) within the JUICE 7.1 environment (TICHÝ 2002). To identify diagnostic species, we calculated the *phi* coefficient

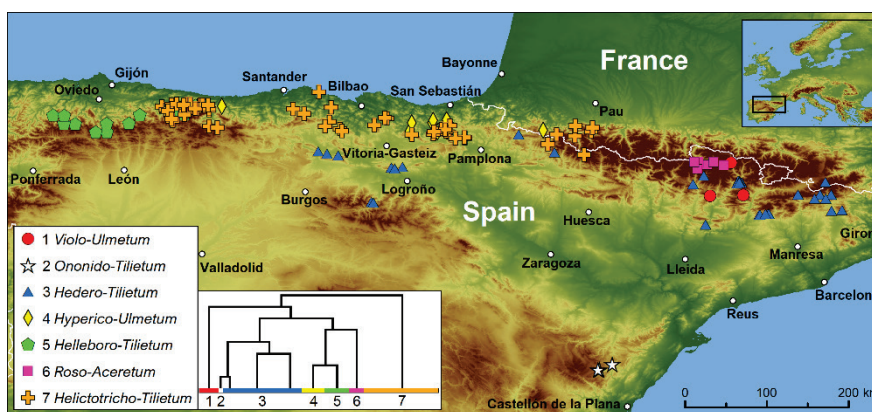
of association (CHYTRÝ et al. 2002) based on species presence-absence data. To omit rare species from the lists of diagnostic species, we performed Fisher's exact test ( $p \leq 0.001$ ). To avoid effects of different number of relevés per group on the calculation of the coefficient, all groups were virtually standardized to the same size (TICHÝ & CHYTRÝ 2006). Species with a *phi* value greater than 0.3 were considered as diagnostic and those with *phi* greater than 0.6 as highly diagnostic. However, only the species with a constancy ratio (DENGLER 2003) for a given group of at least 1.75 were selected as diagnostic species. The same settings were used when analyzing the inner variability of CROLFs, with the exception of using TWINSpan algorithm with three pseudospecies cut levels of 0, 5 and 25% (HILL 1979) for the identification of distinctive types of CROLFs. We preferred TWINSpan over flexible-beta clustering in this case because the latter is suitable to distinguish clusters along several major environmental variables as those behind the whole Iberian *Aceretalia*, but TWINSpan performs better highlighting of contrasting groups along a single dominant, conspicuous floristic gradient within a single association.

Species occurring in more than 50% of relevés of the group were considered as constant and those with a cover higher than 25% in at least 5% of relevés of the group were considered as dominant. The rules of the 4<sup>th</sup> edition of the International Code of Phytosociological Nomenclature (THEURILLAT et al. 2021) were followed for naming syntaxa.

To visualize the relationship between CROLFs and similar vegetation types forming the expanded dataset along environmental gradients, non-metric multidimensional scaling (NMDS) was computed using the package *vegan* (OKSANEN et al. 2019) in the R software (R CORE TEAM 2018). Altitude and climatic variables were passively projected to the ordination space. Differences among the forest types regarding these variables, as well as slope, were explored by means of boxplots.

### 3. Results and discussion

At the first hierarchical level, beta-flexible clustering separated a group formed by our original CROLF relevés plus a single relevé from the literature previously classified in the *Helleboro-Tilietum* (54 relevés in total; see map and dendrogram of the cluster analysis in Figure 3). This cluster is characterized by numerous diagnostic species of CROLFs, including rock-outcrop specialists that are generally absent in the other communities (see Table 1



**Fig. 3.** Distribution map of the associations of *Aceretalia* occurring in the Iberian Peninsula with embedded dendrogram of the cluster analysis. Numbers presented by the dendrogram denote the associations listed in the legend.

**Abb. 3.** Verbreitungskarte der auf der Iberischen Halbinsel vorkommenden *Aceretalia*-Assoziationen mit eingebettetem Dendrogramm der Clusteranalyse. Die vom Dendrogramm dargestellten Zahlen bezeichnen die in der Legende aufgeführten Assoziationen.

for the main differences in species composition between the distinguished vegetation types). We identify this cluster with a new association *Helictotricho cantabrici-Tilietum platyphylli*. The following text describes the new association and compares it with other related vegetation types.

**Table 1.** Shortened synoptic table showing the percentage frequencies (constancies) of diagnostic species (shaded) and other frequent species of the distinguished associations. Diagnostic species are sorted by decreasing *phi* value and non-diagnostic ones by decreasing frequency in the expanded dataset. Species with *phi* > 0.3 are considered as diagnostic and species with *phi* > 0.6 as highly diagnostic (in bold), but those with a constancy ratio lower than 1.75 or with non-significant Fisher's exact test ( $p > 0.001$ ) were excluded from the lists of diagnostic species. A maximum of 15 most diagnostic species of each cluster are shown for each association (see Supplement E3 for the full list). Abbreviations: VmU – *Viola mirabilis-Ulmetum*, OaT – *Ononido aragonensis-Tilietum*, HhT – *Hedero helioides-Tilietum*, HaU – *Hyperico androsaemi-Ulmetum*, HoT – *Helleboro occidentalis-Tilietum*, RpA – *Rosa pendulinae-Aceretum*, HcT – *Helictotricho cantabrici-Tilietum*.

**Tabelle 1.** Gekürzte synoptische Tabelle mit Stetigkeiten der diagnostischen Arten (schattiert) und der anderen häufigen Arten der verschiedenen Assoziationen. Diagnostische Arten werden nach sinkendem *phi*-Wert und andere Arten nach abnehmenden Stetigkeiten im erweiterten Datensatz sortiert. Arten mit *phi* > 0,3 gelten als diagnostisch und Arten mit *phi* > 0,6 sind hochdiagnostisch (fett), jedoch wurden Arten mit einem Konstanzverhältnis von weniger als 1,75 oder mit einem unbedeutenden Exakten Fisher-Test ( $p > 0,001$ ) als diagnostische Arten ausgeschlossen. Für jede Assoziation werden maximal 15 der am meisten diagnostischen Arten jedes Clusters angezeigt (eine vollständige Liste befindet sich im Anhang E3).

Association	VmU	OaT	HhT	HaU	HoT	RpA	HcT
Number of relevés	14	3	56	16	18	10	54
<b><i>Viola mirabilis-Ulmetum glabrae</i></b>							
<i>Viola mirabilis</i>	<b>64</b>	.	4	.	.	.	.
<i>Geranium pyrenaicum</i>	36	.	.	.	.	.	.
<i>Stellaria media</i>	29	.	.	.	.	.	.
<i>Anisantha sterilis</i>	29	.	.	.	.	.	.
<i>Galium aparine</i>	43	.	7	.	11	.	2
<i>Lapsana communis</i>	29	.	.	.	.	.	4
<i>Anthriscus sylvestris</i>	21	.	.	.	.	.	.
<i>Veronica triloba</i>	21	.	.	.	.	.	.
<i>Alliaria petiolata</i>	43	.	5	13	6	10	2
<b><i>Ononido aragonensis-Tilietum platyphylli</i></b>							
<i>Acer granatense</i>	.	<b>100</b>	.	.	.	.	.
<i>Cytisus heterochrous</i>	.	<b>100</b>	.	.	.	.	.
<i>Taxus baccata</i>	.	<b>100</b>	5	31	6	.	4
<i>Laserpitium gallicum</i>	.	<b>67</b>	.	.	.	.	.
<i>Viola willkommii</i>	.	<b>67</b>	.	.	.	.	.
<i>Ononis aragonensis</i>	.	<b>67</b>	.	.	.	.	.
<i>Satureja montana</i>	.	<b>67</b>	.	.	.	.	.
<b><i>Hedero helioides-Tilietum platyphylli</i></b>							
<i>Buxus sempervirens</i>	36	.	<b>63</b>	.	.	.	13
<i>Acer opalus</i>	.	.	30	.	.	.	7
<i>Luzula nivea</i>	.	.	20	.	.	.	.
<i>Malus sylvestris</i>	.	.	18	.	.	.	.
<i>Quercus pubescens</i>	14	.	34	19	.	.	2

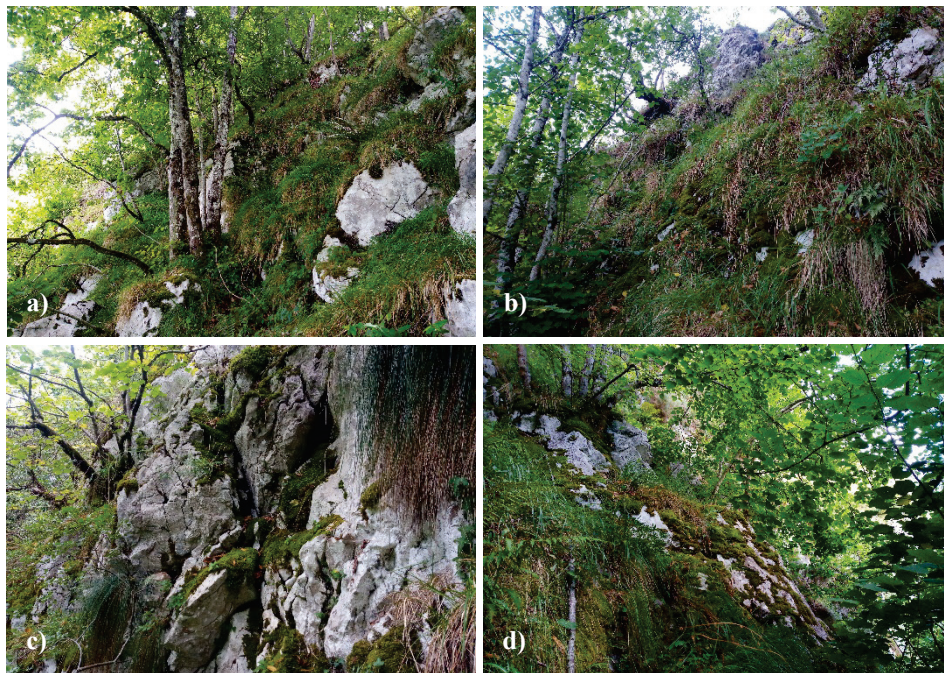
Association	VmU	OaT	HhT	HaU	HoT	RpA	HcT
Number of relevés	14	3	56	16	18	10	54
<b><i>Hyperico androsaemi-Ulmetum glabrae</i></b>							
<i>Hypericum androsaemum</i>	.	.	.	<b>81</b>	6	.	19
<i>Arum italicum</i>	.	.	.	<b>63</b>	6	.	.
<i>Quercus robur</i>	.	.	5	<b>56</b>	6	.	.
<i>Cardamine pratensis</i>	.	.	.	<b>50</b>	6	.	2
<i>Dryopteris affinis</i> agg.	.	.	.	63	33	.	.
<i>Asplenium scolopendrium</i>	.	.	4	69	39	.	17
<i>Ajuga reptans</i>	.	.	7	44	6	.	2
<i>Alnus glutinosa</i>	.	.	2	31	.	.	.
<i>Glechoma hederacea</i>	.	.	.	25	.	.	.
<i>Veronica montana</i>	.	.	.	25	.	.	.
<i>Potentilla sterilis</i>	.	.	9	38	11	.	.
<i>Circaea lutetiana</i>	.	.	2	31	.	10	.
<i>Euphorbia amygdaloides</i>	.	.	25	63	33	.	24
<i>Blechnum spicant</i>	.	.	.	19	.	.	.
<i>Lysimachia nemorum</i>	.	.	.	19	.	.	.
<b><i>Helleboro occidentalis-Tilietum cordatae</i></b>							
<i>Primula acaulis</i>	.	.	2	.	<b>72</b>	.	6
<i>Quercus petraea</i>	.	.	34	.	<b>94</b>	.	6
<i>Astrantia major</i>	.	.	4	.	<b>56</b>	.	4
<i>Acer pseudoplatanus</i>	.	.	.	19	56	.	4
<i>Lonicera periclymenum</i>	.	.	5	19	50	.	6
<i>Crepis lamsanoides</i>	.	.	4	19	56	20	.
<i>Pimpinella siifolia</i>	.	.	.	.	22	.	.
<i>Agrostis capillaris</i>	.	.	.	.	22	.	2
<i>Quercus pyrenaica</i>	.	.	.	.	22	.	2
<i>Bromopsis ramosa</i>	.	.	4	25	44	10	2
<i>Hyacinthoides non-scripta</i>	.	.	.	.	17	.	.
<b><i>Roso pendulinae-Aceretum platanoidis</i></b>							
<i>Acer platanoides</i>	.	.	2	.	.	<b>90</b>	.
<i>Rosa pendulina</i>	.	.	2	.	.	<b>90</b>	.
<i>Abies alba</i>	.	.	7	.	.	<b>90</b>	2
<i>Calamagrostis arundinacea</i>	.	.	.	.	.	<b>80</b>	.
<i>Geranium sylvaticum</i>	.	.	4	.	.	<b>80</b>	.
<i>Sorbus aucuparia</i>	.	.	2	.	.	<b>80</b>	2
<i>Rubus saxatilis</i>	.	.	.	.	.	<b>70</b>	.
<i>Melica nutans</i>	.	.	.	.	.	<b>70</b>	.
<i>Pulmonaria affinis</i>	.	.	11	13	.	<b>90</b>	2
<i>Rubus idaeus</i>	.	.	2	.	.	<b>70</b>	.
<i>Lathyrus laevigatus</i> subsp. <i>occidentalis</i>	.	.	2	6	17	<b>90</b>	2
<i>Salix caprea</i>	7	.	7	.	.	<b>80</b>	.
<i>Prunus padus</i>	.	.	.	.	.	<b>60</b>	.
<i>Lonicera nigra</i>	.	.	.	.	.	<b>60</b>	.
<i>Ribes petraeum</i>	.	.	.	.	.	<b>60</b>	.
<b><i>Helictotricho cantabrigi-Tilietum platyphylli</i></b>							
<i>Asplenium ruta-muraria</i>	.	.	.	.	.	.	<b>67</b>
<i>Helictotrichon cantabrigicum</i>	.	.	.	6	.	.	<b>69</b>

Association	VmU	OaT	HhT	HaU	HoT	RpA	HcT
Number of relevés	14	3	56	16	18	10	54
<i>Galium mollugo</i> agg.	.	.	.	.	.	.	<b>61</b>
<i>Globularia nudicaulis</i>	.	.	4	.	.	.	<b>63</b>
<i>Genista hispanica</i> subsp. <i>occidentalis</i>	.	.	.	.	.	.	<b>48</b>
<i>Asplenium trichomanes</i> s.l.	.	33	16	25	22	10	<b>100</b>
<i>Erucastrum nasturtiifolium</i> subsp. <i>sudrei</i>	.	.	2	.	.	.	<b>43</b>
<i>Silene italica</i>	.	.	.	.	.	.	39
<i>Campanula rotundifolia</i>	.	33	.	.	11	.	67
<i>Vincetoxicum hirundinaria</i>	.	.	2	.	33	10	67
<i>Dianthus hyssopifolius</i>	.	.	7	.	.	.	43
<i>Picris hieracioides</i>	.	.	.	6	.	.	39
<i>Polypodium vulgare</i> agg.	.	.	25	13	28	10	70
<i>Sedum sediforme</i>	.	.	.	.	.	.	28
<i>Sesleria caerulea</i>	.	.	5	.	.	.	33
<b>Species diagnostic for two associations</b>							
<i>Lamium galeobdolon</i>	.	.	7	88	6	90	26
<i>Ruscus aculeatus</i>	.	.	7	69	17	.	56
<i>Athyrium filix-femina</i>	.	.	5	56	.	50	.
<i>Helleborus viridis</i> subsp. <i>occidentalis</i>	.	.	23	75	89	.	20
<i>Polystichum setiferum</i>	.	.	14	88	94	10	74
<i>Mercurialis perennis</i>	.	.	27	63	89	.	81
<b>Other frequent species (f &gt; 33% of the expanded dataset)</b>							
<b>Trees and shrubs</b>							
<i>Corylus avellana</i>	21	100	86	100	94	80	74
<i>Tilia platyphyllos</i>	.	100	93	44	78	.	100
<i>Fraxinus excelsior</i>	50	.	70	81	100	90	72
<i>Crataegus monogyna</i>	14	.	59	63	100	.	41
<i>Sorbus aria</i>	.	100	32	13	50	40	48
<i>Ulmus glabra</i>	100	67	18	88	33	70	17
<i>Acer campestre</i>	29	.	61	63	6	.	17
<b>Other species</b>							
<i>Hedera helix</i> agg.	50	100	63	100	89	.	80
<i>Hepatica nobilis</i>	.	67	70	31	50	80	74
<i>Geranium robertianum</i> agg.	14	33	55	94	50	30	63
<i>Viola riviniana</i> agg.	.	.	73	81	67	80	31
<i>Brachypodium sylvaticum</i>	57	33	59	81	67	.	19
<i>Vicia sepium</i>	29	.	66	56	39	.	31
<i>Poa nemoralis</i>	64	.	77	.	17	80	17
<i>Stellaria holostea</i>	21	.	48	19	78	80	28
<i>Dioscorea communis</i>	29	.	23	69	67	.	52
<i>Saxifraga hirsuta</i>	.	.	11	56	39	.	72
<i>Fragaria vesca</i>	.	.	70	.	44	80	7
<i>Rubus</i> sect. <i>Rubus</i>	.	.	13	63	50	.	61
<i>Primula veris</i>	.	.	55	.	39	10	37
<i>Brachypodium rupestre</i>	.	.	2	31	56	.	78



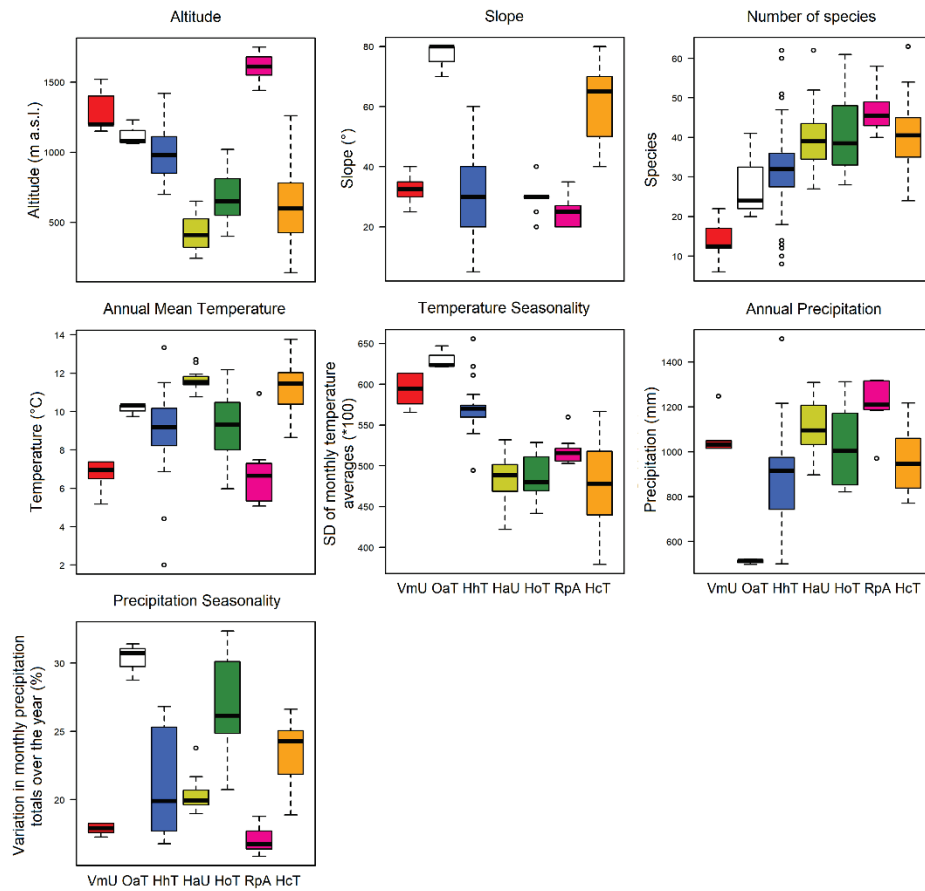
***Helictotricho cantabrics-Tilietum platyphylli* ass. nova (nomenclatural type: this paper, Appendix 1, relevé TR1, holotypus)**

The association includes CROLFs occurring in the northern Iberian Peninsula: Picos de Europa in the Cantabrian Range, the Basque-Cantabrian Mountains and the Western Pyrenees. Stands of this association (Fig. 4) inhabit xero-mesophilous limestone rocky slopes of mainly northern aspect. As their occurrence is confined to special environmental conditions, they can either be of very limited extent or cover larger areas in rocky regions. They have been recorded across a broad altitudinal range, occurring from 140 m at the northern foothills of the Picos de Europa to 1260 m in the Pyrenees (mean altitude 609 m; for boxplots of selected variables see Fig. 5). Annual mean temperature of the recorded relevés mostly



**Fig. 4.** Photos of the studied sites of the *Helictotricho cantabrics-Tilietum platyphylli*: **a)** Amezketa (province of Gipuzkoa), Sierra de Aralar, northern slopes of the peak Azpiko gaina (1129 m a.s.l.); **b)** Villasana de Mena (province of Burgos), Montes la Peña, north-western slopes of the peak Portillejos (1066 m a.s.l.); **c)** Trucios-Turtzioz (province of Bizkaia), rocky northern slopes to the north-east of the peak Armañón (856 m a.s.l.); **d)** Oseja de Sajambre (province of León), Picos de Europa, western slopes of the peak Pica Arancón (988 m a.s.l.). Photos a + b show the subassociation *H. c.-T. p. typicum*, while c + d represent *H. c.-T. p. lauretosum nobilis* (see further text) (Photos: D. Zukal, July and August 2019).

**Abb. 4.** Photographien der untersuchten Wuchsorte des *Helictotricho cantabrics-Tilietum platyphylli*: **a)** Amezketa (Provinz Gipuzkoa), Sierra de Aralar, Nordhänge des Gipfels Azpiko Gaina (1129 m ü. N.N.); **b)** Villasana de Mena (Provinz Burgos), Montes la Peña, nordwestliche Hänge des Gipfels Portillejos (1066 m ü. N.N.); **c)** Trucios-Turtzioz (Provinz Bizkaia), felsige Nordhänge nordöstlich vom Gipfel Armañón (856 m ü. N.N.); **d)** Oseja de Sajambre (Provinz León), Picos de Europa, Westhänge des Gipfels Pica Arancón (988 m ü. N.N.). Photographien a + b zeigen die Subassoziation *H. c.-T. p. typicum*, c + d die Subassoziation *H. c.-T. p. lauretosum nobilis* (Fotos: D. Zukal, Juli und August 2019).



**Fig. 5.** Boxplots showing differences in selected measures between the associations. Abbreviations: VmU – *Viola mirabilis*-*Ulm*etum, OaT – *Ononido aragonensis*-*Tilietum*, HhT – *Hedero heli*cis-*Tilietum*, HaU – *Hyperico androsaemi*-*Ulm*etum, HoT – *Helleboro occidentalis*-*Tilietum*, RpA – *Roso pendulinae*-*Aceretum*, HcT – *Helictotricho cantabrigi*-*Tilietum*. Note that we excluded *Hyperico-Ulm*etum in the slope diagram, as the slope information is missing for most of its relevés.

**Abb. 5.** Box-plots mit Unterschieden in den ausgewählten Variablen zwischen den Assoziationen. Wir haben das *Hyperico-Ulm*etum im Hangneigungdiagramm ausgeschlossen, da Informationen zur Hangneigung für die meisten ihrer Vegetationsaufnahmen fehlen.

ranges between 10–12 °C and annual precipitation between 800–1100 mm. The inclination of slopes is rather steep, ranging between 40–80° (mean value 62°). Substrate varies between solid rock with patches of fine soil, and steep loamy or scree slopes with numerous rock outcrops. Based on the occurrence of species with different nutrient-requirements within a single plot, it may be inferred that the soil nutrient content varies in a fine grain; the shallow layer of soil filling small hollows is nutrient-poor, while patches of soil accumulations under rocks are richer in nutrients. The soil is base-rich (mean pH 7.4).

The tree canopy of the *Helictotricho-Tilietum* usually reaches 70–85% in its cover and is dominated exclusively by *Tilia platyphyllos*. Unlike in central Europe, *T. cordata* occurs rarely in habitats typical of CROLFs in the northern Iberian Peninsula. Less frequently and

with lower cover, several other trees co-occur with lime, especially *Fagus sylvatica*, *Fraxinus excelsior*, *Quercus ilex* and *Sorbus aria*. The shrub layer varies in its cover (typically between 5–15%) and its main constituent is *Corylus avellana*, present at most of the sites. Besides younger individuals of tree species, *Crataegus monogyna*, *Rhamnus alaternus*, *R. alpina* and *Rosa* sp. often form the shrub layer. *Laurus nobilis* is often occurring in the western part of the study area, while *Buxus sempervirens* is abundant in the Pyrenees. The herb layer varies in its cover (mostly 35–65%) and is species-rich (usually 30–50 species per relevé). *Brachypodium rupestre*, *Sesleria autumnalis* and *S. caerulea* are typical dominants of the herb layer, although *Hedera hibernica* and *Mercurialis perennis* can also reach relatively high cover. Its species composition is rather diverse, although the species of the main ecological groups are constant, especially regarding mesophilous forest species (e.g. *Euphorbia amygdaloides*, *Geranium robertianum* agg., *Hepatica nobilis*, *Lactuca muralis*, *Saxifraga hirsuta*) and numerous species of rock-outcrops (e.g. *Asplenium ceterach*, *A. ruta-muraria*, *A. trichomanes* s.l., *Erinus alpinus*, *Globularia nudicaulis*, *Hypericum nummularium*, *Saxifraga paniculata*, *S. trifurcata*, *Sedum dasyphyllum*, *S. sediforme*). Drought-tolerant forest species (e.g. *Aegonychon purpureocaeruleum*, *Melittis melissophyllum*, *Primula veris*, *Rubia peregrina*, *Vincetoxicum hirundinaria*) were present at the driest sites. An open canopy of trees growing among rock outcrops on steep slopes leads to a lot of light in the understorey, thus species of open habitats (e.g. *Dianthus hyssopifolius*, *Erica vagans*, *Genista hispanica* subsp. *occidentalis*, *Scabiosa columbaria*, *Teucrium pyrenaicum*) also occur frequently. Endemic species of the Cantabrian Mountains and the Western Pyrenees (e.g. *Antirrhinum braun-blanquetii*, *Digitalis parviflora*, *Erysimum duriaei*, *Helictotrichon cantabricum*, *Seseli cantabricum*) including also some rare species (e.g. *Oreochloa confusa*, *Petrocoptis pyrenaica* s.l., *Saxifraga canaliculata*) were recorded as well.

**Diagnostic species in the context of Iberian *Aceretalia*** (highly diagnostic species in bold): *Allium ericetorum*, *Antirrhinum braun-blanquetii*, *Asplenium ceterach*, ***A. ruta-muraria***, ***A. trichomanes* s.l.**, *Campanula rotundifolia*, *Carex sempervirens*, *Dactylis glomerata*, *Dianthus hyssopifolius*, *Erinus alpinus*, ***Erucastrum nasturtiifolium* subsp. *sudrei***, *Erysimum duriaei*, *Festuca piceo-europeana*, ***Galium mollugo* agg.**, ***Genista hispanica* subsp. *occidentalis***, ***Globularia nudicaulis***, ***Helictotrichon cantabricum***, *Hypericum nummularium*, *Laurus nobilis*, *Leucanthemum vulgare* agg., *Melica ciliata*, *Picris hieracioides*, *Pimpinella tragiium* subsp. *lithophila*, *Polypodium vulgare* agg., *Quercus ilex* agg., *Rhamnus alaternus*, *Saxifraga paniculata*, *S. trifurcata*, *Scabiosa columbaria*, *Sedum dasyphyllum*, *S. sediforme*, *Seseli libanotis*, *Sesleria autumnalis*, *S. caerulea*, *Silene italica*, *Smilax aspera*, *Teucrium pyrenaicum*, *T. scorodonia*, *Valeriana montana*, *Vincetoxicum hirundinaria*, *Viscum album*.

**Constant species:** *Asplenium ruta-muraria*, *A. trichomanes* s.l., *Brachypodium rupestre*, *Campanula rotundifolia*, *Corylus avellana*, *Dioscorea communis*, *Fraxinus excelsior*, *Galium mollugo* agg., *Geranium robertianum* agg., *Globularia nudicaulis*, *Hedera helix* agg., *Helictotrichon cantabricum*, *Hepatica nobilis*, *Mercurialis perennis*, *Polypodium vulgare* agg., *Polystichum setiferum*, *Rubus* sect. *Rubus*, *Ruscus aculeatus*, *Saxifraga hirsuta*, *Tilia platyphyllos*, *Vincetoxicum hirundinaria*.

**Dominant species:** *Brachypodium rupestre*, *Sesleria autumnalis*, *S. caerulea*, *Tilia platyphyllos*.

### 3.1 Variability of the *Helictotricho cantabrigi-Tilietum platyphylli*

Two distinct geographically vicariant types can be distinguished as subassociations (Table 2). The *H. c.-T. p. typicum* represents the eastern type of the study area occurring especially in the Basque-Cantabrian Mountains and Pyrenees, while its western counterpart *H. c.-T. p. lauretosum nobilis* occurs mostly at lower altitudes of the Cantabrian Range.

**Table 2.** Synoptic tables showing the percentage frequencies (constancies) of diagnostic species (shaded) of the distinguished subassociations of *Helictotricho-Tilietum* based on CROLFs dataset. The table on the left shows the diagnostic species of *H. c.-T. p. typicum*, while the one on the right of *H. c.-T. p. lauretosum nobilis*. The species are sorted by decreasing phi value. Species with  $\phi > 0.3$  are considered as diagnostic and species with  $\phi > 0.6$  as highly diagnostic (in bold), but those with a constancy ratio lower than 1.75 or with non-significant Fisher's exact test ( $p > 0.001$ ) were excluded from the lists of diagnostic species. Abbreviations: typ – *H. c.-T. p. typicum*, lau – *H. c.-T. p. lauretosum nobilis*.

**Tabelle 2.** Synoptische Tabellen der *Helictotricho-Tilietum*-Subassoziation mit Stetigkeiten diagnostischer Arten (schattiert), basierend auf dem CROLF-Datensatz. Die Tabelle links zeigt die diagnostischen Arten des *H. c.-T. p. typicum*, die rechte Tabelle die des *H. c.-T. p. lauretosum nobilis*. Die Arten werden nach abnehmendem  $\phi$ -Wert sortiert. Arten mit  $\phi > 0,3$  gelten als diagnostisch und Arten mit  $\phi > 0,6$  sind hochdiagnostisch (fett), jedoch wurden Arten mit einem Konstanzverhältnis von weniger als 1,75 oder mit einem unbedeutenden Exakten Fisher-Test ( $p > 0,001$ ) als diagnostische Arten ausgeschlossen.

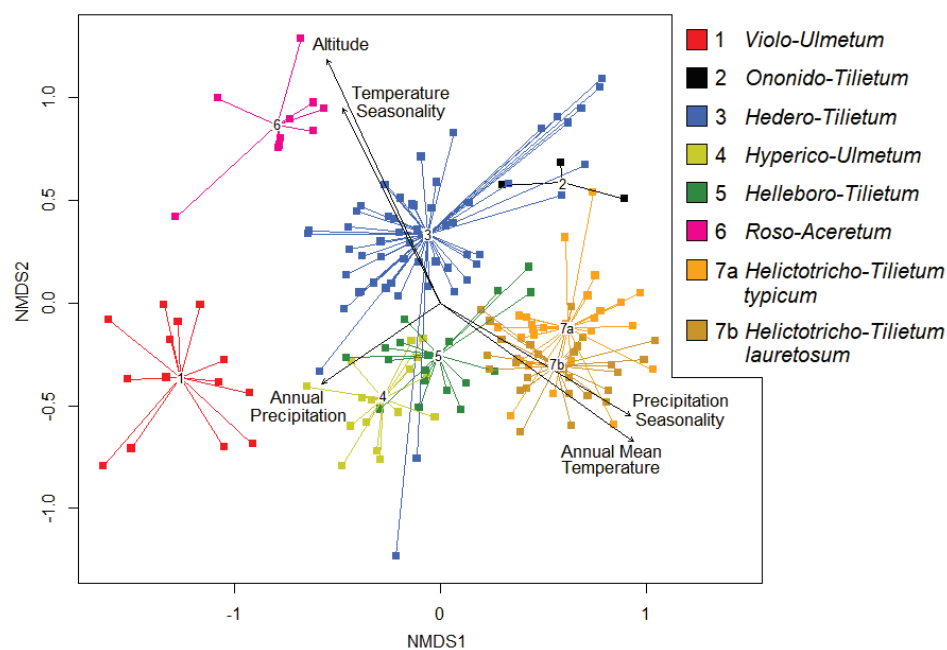
Subassociation	typ	lau	Subassociation	typ	lau
Number of relevés	26	28	Number of relevés	26	28
<b><i>H. c.-T. p. typicum</i></b>			<b><i>H. c.-T. p. lauretosum nobilis</i></b>		
<i>Fagus sylvatica</i>	54	4	<i>Aegonychon purpureocaeruleum</i>	.	<b>61</b>
<i>Sorbus aria</i>	77	21	<i>Dioscorea communis</i>	23	79
<i>Sesleria autumnalis</i>	58	11	<i>Laurus nobilis</i>	4	54
<i>Lonicera xylosteum</i>	35	.	<i>Helleborus foetidus</i>	4	50
<i>Seseli libanotis</i>	31	.	<i>Viola alba</i>	4	50
<i>Buxus sempervirens</i>	27	.	<i>Antirrhinum braun-blanquetii</i>	.	39
<i>Rhamnus cathartica</i>	23	.	<i>Carex caudata</i>	.	32
<i>Campanula trachelium</i>	23	.	<i>Dactylis glomerata</i>	15	57
<i>Acer campestre</i>	31	4	<i>Smilax aspera</i>	4	36
<i>Lamium galeobdolon</i>	42	11	<i>Festuca picoeuropeana</i>	.	25
			<i>Asplenium ceterach</i>	4	32

#### ***Helictotricho cantabrigi-Tilietum platyphylli typicum***

The typical variant was recorded to occur from the westernmost border of the Basque Country to the French Pyrenees, at middle and higher altitudes (mean 724 m). It is characterized by a higher proportion of mesophilous forest species (e.g. *Campanula trachelium*, *Hepatica nobilis*, *Lamium galeobdolon*, *Lonicera xylosteum*, *Rhamnus cathartica*) which are distributed throughout the temperate zone of the European continent. *Fagus sylvatica* and *Sorbus aria* are common in the tree and shrub layers. *Buxus sempervirens* is abundant in the south-eastern part of the study area including both the Pyrenees and the transitional area to the Mediterranean bioclimatic zone, while it is absent in the northern part of the Basque-Cantabrian Mountains.

***Helictotricho cantabrici-Tilietum platyphylli lauretosum nobilis* subass. nova (nomenclatural type: this paper, Appendix 1, relevé TR2, holotypus)**

The *H. c.-T. p. lauretosum nobilis* represents the submediterranean counterpart to the typical subassociation, occurring in the Cantabrian Range (Picos de Europa), in the western part of the study area, where summer drought is more conspicuous than in the eastern part (Fig. 2). It is differentiated by drought-tolerant species (e.g. *Aegonychon purpureocaeruleum*, *Asplenium ceterach*, *Viola alba*), submediterranean species (e.g. *Dioscorea communis*, *Laurus nobilis*, *Smilax aspera*) and some typical species of the Cantabrian Mountains (e.g. *Antirrhinum braun-blanquetii*, *Carex caudata*, *Festuca picoeuropeana*). It was usually recorded at slightly lower altitudes (mean 498 m) than the previous subassociation, mainly due to the fact that forests at higher altitudes are very difficult to reach in this part of the study area, especially the Picos de Europa, where it can be found also at relatively low altitudes. However, we assume it also occurs at higher altitudes of the Cantabrian Mountains, as it is a common vegetation type in the Picos de Europa, where it inhabits large areas on steep, often almost vertical rocky places.



**Fig. 6.** NMDS diagram of the forests of *Aceretalia* distinguished in the Iberian Peninsula. Selected environmental variables were superimposed on the ordination plot. The stress of the analysis is 0.21.

**Abb. 6.** NMDS-Diagramm der Wälder von *Aceretalia* auf der Iberischen Halbinsel. Ausgewählte Variable wurden nachträglich im Diagramm aufgetragen.

### 3.3 Comparison with other Iberian forests of *Aceretalia*

NMDS ordination separates relevés of the *Helictotricho cantabrici-Tilietum platyphylli* on the right periphery of the diagram, forming a rather distinct cluster (Fig. 6). *Ononido aragonensis-Tilietum platyphylli* is an association from the precipitation-poor southern Iberian Range (CRESPO et al. 2008), represented by only three relevés. Besides shady ravines and canyons, it also occurs on cliffs and steep rocky slopes. It is however well distinguished from the other associations by the occurrence of species absent in the northern part of the Iberian Peninsula (e.g. *Acer granatense*, *Cytisus heterochrous*, *Ononis aragonensis*). The stands of the *Helleboro-Tilietum* are also often developed on rocky slopes, sometimes even with rock outcrops (CRESPO et al. 2008). Several drought-tolerant species (e.g. *Aegonychon purpureocaeruleum*, *Brachypodium rupestre*, *Melittis melissophyllum*, *Scabiosa columbaria*, *Vincetoxicum hirsutinaria*) are common in stands of both associations, *Helleboro-Tilietum* and *Helictotricho-Tilietum*, while they are usually absent in the other forests of the *Aceretalia*. However, the *Helictotricho-Tilietum* differs from the former by the prominent occurrence of rock-outcrop specialists. The *Hedero helici-Tilietum platyphylli* was described to occur on deep soils of mainly siliceous bedrocks on cold, shady, north-facing slopes at relatively high altitudes in the Catalan Pyrenees (775–1160 m a.s.l.; VIGO et al. 1983). Common species of mesophilous forests are prevailing in its species composition, most of them shared with the other associations. Several relevés of the *Hedero-Tilietum* including drought-tolerant woody species (e.g. *Acer opalus*, *Buxus sempervirens*, *Quercus pubescens*) are situated to the upper right corner of the NMDS diagram, close to *Ononido-Tilietum*. They represent the thermophilous subassociation *H.-T. festucetosum gautieri* (syn. *Poo nemoralis-Tilietum platyphylli* Romo 1989; see CRESPO et al. 2008) inhabiting stony ravines and limestone cliffs in the Pre-Pyrenees. As the cluster analysis also classified these relevés together with the *Ononido-Tilietum* until the last division of the dataset (see the dendrogram in Fig. 3), it can be inferred that the vegetation of this subassociation is transitional to the *Ononido-Tilietum*. The *Hyperico androsaemi-Ulmetum glabrae* is characterized mainly by mesophilous and hygrophilous forest species (e.g. *Alnus glutinosa*, *Carex sylvatica*, *Circaea lutetiana*, *Hypericum androsaemum*, *Lysimachia nemorum*). The remaining two associations, *Violo mirabilis-Ulmetum glabrae* and *Roso pendulinae-Aceretum platanoidis*, form separate clusters in the left part of the diagram, linked to the highest elevations, especially the *Roso-Aceretum* (occurring in 1500–1750 m a.s.l.), which is very well distinguished by numerous montane and subalpine species absent in the other associations (e.g. *Geranium sylvaticum*, *Lonicera alpigena*, *L. nigra*, *Ribes petraeum*, *Rosa pendulina*; CARRERAS et al. 1997). Finally, the *Violo-Ulmetum* is a peculiar association characterized by nutrient-demanding species (e.g. *Alliaria petiolata*, *Galium aparine*, *Stellaria media*, *Urtica dioica*), which represents anthropized species-poor forest patches near human settlements (ROMO 1988).

Regarding the species richness of the association, the *Helictotricho-Tilietum* belongs among the species-richest communities among Iberian *Aceretalia*, with only *Roso-Aceretum* being slightly richer (Fig. 5). Based on the obtained climatic variables, the *Helictotricho-Tilietum* has one of the highest Annual Mean Temperature. Conversely, the Temperature Seasonality is rather low, especially compared to the associations in the Pyrenees.

### 3.3 Comparison with CROLFs in other parts of Europe

During the last decades, calcicolous lime forests have been studied in various parts of Europe. In his comprehensive study dealing primarily with maple forests, CLOT (1990) addressed also lime forests reported from western and central Europe. Although there is no evidence on similar forest vegetation occurring in the adjacent area in western France, several vegetation types resembling CROLFs were described from eastern France and Switzerland. The *Asperulo taurinae-Tilietum* Trepp 1947 includes species-rich lime forests occurring on slopes of warm and precipitation-rich föhn valleys in the Swiss Prealps (e.g. TREPP 1947, KELLER 1974). Comparing this association with Iberian CROLFs, it shares some subatlantic-submediterranean species (*Daphne laureola*, *Dioscorea communis*), but it differs in occurrence of species missing in Atlantic Europe (*Asperula taurina*, *Coronilla coronata*, *Cyclamen purpurascens*). RAMEAU (1974) reported the association *Seslerio caeruleae-Tilietum platyphylli* from limestone areas in Côte-d'Or department in Eastern France. This association represents more thermophilous communities, sharing species of thermophilous forests (*Melittis melissophyllum*, *Vincetoxicum hirundinaria*) with the *Helictotricho-Tilietum*, though it clearly differs from the latter by the general absence of rock-outcrop species. KISSLING (1985) distinguished the *Aceri-Tilietum polypodietosum* to include CROLFs occurring on southeast-facing limestone pavements in the Swiss Jura Mountains, containing numerous rock-outcrop specialists. However, as this synatxon does not include species with south-western European distribution, stands of the *Aceri-Tilietum polypodietosum* might represent the eastern vicariant community to the Iberian *Helictotricho-Tilietum*.

CROLFs have been also studied in central Europe (e.g. ŠOMŠÁK & HÁBEROVÁ 1979, CHYTRÝ & SÁDLO 1998, KLIMENT et al. 2010). Recently, ZUKAL et al. (2020) reviewed all the studies dealing with central European CROLFs together with supplementary original relevés. They found that three associations occur in east-central Europe, following the biogeographical gradient: *Seslerio caeruleae-Tilietum cordatae* Chytrý et Sádlo 1998 nom. corr. (Czech Republic, northern Austria, northern Hungary, western Slovakia and southern Poland), *Tilio platyphylli-Fraxinetum excelsioris* Zólyomi 1936 (central Slovakia and northern Hungary), and *Spiraeo chamaedryfoliae-Tilietum cordatae* Zukal et al. 2020 (northern and western Romania). Comparing these associations with the *Helictotricho-Tilietum*, they are similar in their physiognomy and ecology, generally occurring on steep rocky slopes of predominantly northern exposition in limestone areas. They share the main ecological species groups, including mesophilous forest species (e.g. *Euphorbia amygdaloides*, *Geranium robertianum* agg., *Hepatica nobilis*, *Mercurialis perennis*) and rock-outcrop specialists (e.g. *Asplenium ruta-muraria*, *Polypodium vulgare* agg., *Saxifraga paniculata*, *Sesleria caerulea*). Drought-tolerant forest species (e.g. *Aegonychon purpurocaeruleum*, *Melittis melissophyllum*, *Primula veris*, *Vincetoxicum hirundinaria*) confined to thermophilous forests in central Europe are also shared with the *Helictotricho-Tilietum*. However, they differ in species with specific biogeography: continental species with central and eastern European distribution (e.g. *Euonymus verrucosus*, *Galium intermedium*, *Melica picta*, *Spiraea chamaedryfolia*) and submediterranean species with central and south-eastern European distribution (e.g. *Euphorbia epithymoides*, *Quercus cerris*, *Seseli osseum*, *Tilia tomentosa*) are absent in CROLFs in the Iberian Peninsula.

Regarding the uniqueness of Iberian CROLFs among all above-mentioned calcicolous lime forests in Europe, they are clearly distinguished by the occurrence of species with south-western European distribution (e.g. *Erica vagans*, *Genista hispanica* subsp. *occiden-*

*talis*, *Hypericum nummularium*, *Saxifraga hirsuta*), including endemic species of the Iberian Peninsula (e.g. *Antirrhinum braun-blanquetii*, *Helictotrichon cantabricum*, *Petrocoptis pyrenaica* s.l., *Saxifraga canaliculata*).

### 3.4 Syntaxonomy

Classification of the northern Iberian CROLFs in higher-level syntaxa is a matter for discussion and further analyses. Scree and ravine forests of the Iberian Peninsula have been traditionally classified within the broadly understood alliance *Tilio-Acerion* (e.g. CRESPO et al. 2008, BIURRUN et al. 2011, CAMPOS et al. 2011), also used in the other parts of Europe. The EuroVegChecklist classifies the European scree and ravine forests in the order *Aceretalia*, with six alliances reflecting mainly biogeography and moisture gradients (MUCINA et al. 2016). Following the scheme proposed by KOŠIR et al. (2008) and refined by ČARNI in WILLNER et al. (2016), the *Tilio-Acerion* is currently conceived much narrower in the EuroVegChecklist, including only cool temperate maple forests of central Europe, while the thermophilous ones form a separate alliance *Melico-Tilion platyphylli* in central Europe. The Atlantic ash-maple scree forests of Western Europe are classified in the alliance *Dryopterido affinis-Fraxinion excelsioris*, to include forests where typical Atlantic mesophilous forest species are prevailing (e.g. *Hypericum androsaemum*, *Polystichum setiferum*, *Saxifraga hirsuta*, *Scilla lilio-hyacinthus*). Drought- and light-demanding species are mostly absent in the original description, as well as rock-outcrop specialists. Moreover, stands of the *Dryopterido-Fraxinion* are dominated by *Acer campestre*, *Fagus sylvatica*, *Fraxinus excelsior* and *Ulmus glabra*, not by *Tilia* spp.

While the EuroVegChecklist considers *Dryopterido-Fraxinion* a mesophytic counterpart in the Atlantic part of Europe to the central European *Tilio-Acerion*, it is unclear whether xero-mesophilous scree and rock-outcrop forests in Atlantic Europe should be classified to *Melico-Tilion* based on similar ecology or to *Dryopterido-Fraxinion* based on shared biogeography. The absence of a syntaxon comprising xerophilous scree forests in Atlantic Europe is likely caused either by (a) a long tradition of classifying all scree forests of that area to *Tilio-Acerion*, or (b) non-existence of any characteristic species of xerophilous scree forests in Atlantic Europe. It can be assumed that most of the typical Atlantic species (e.g. *Hyacinthoides non-scripta*, *Hypericum androsaemum*, *Polystichum setiferum*, *Saxifraga hirsuta*, *Scilla lilio-hyacinthus*) prefer rather humid oceanic climate, having their optimum in the *Dryopterido-Fraxinion*.

As there is no comparative study dealing with the inner variability of *Aceretalia* within Europe, we decided to prefer the ecological criterion rather than the biogeographic one, and thus we suggest to provisionally classify the *Helictotricho-Tilietum* in the *Melico-Tilion*. Such classification is supported by the clear differences between *Helictotricho-Tilietum* and *Dryopterido-Fraxinion*, and by the numerous shared similarities with the analogous vegetation in central Europe also classified to the *Melico-Tilion*. Consequently, we propose the following syntaxonomical scheme, currently compatible with the EuroVegChecklist (MUCINA et al. 2016):

Class.: *Carpino-Fagetea sylvaticae* Jakucs ex Passarge 1968

Order: *Aceretalia pseudoplatani* Moor 1976

Alliance: *Melico-Tilion platyphylli* Passarge et G. Hofmann 1968

Association: *Helictotricho cantabrici-Tilietum platyphylli* Zukal et Biurrun 2022

Subassociation: *H. c.-T. p. typicum*

Subassociation: *H. c.-T. p. lauretosum nobilis* Zukal et Biurrun 2022



As there are some clear uncertainties at the alliance level of the order *Aceretalia* in the EuroVegChecklist, a comprehensive study based on numerical analysis of this vegetation at the European level is required. How many alliances should be recognized among European *Aceretalia*, and whether biogeography or ecology is the main criterion for their division are among the main questions to be answered. It is also a question for further research to explore if CROLFs may also be separated at the level of association in other mountain systems of the Iberian Peninsula where ravine forests have already been described, such as the Central and Eastern Pyrenees and Iberian Ranges.

#### 4. Conclusions

We provide the first description of the forest vegetation dominated by *Tilia platyphyllos* growing on rock outcrops in limestone areas of the Cantabrian Mountains and the Western Pyrenees. It is ecologically and floristically different from other *Aceretalia* forests occurring there, forming a new association *Helictotricho cantabrici-Tilietum platyphylli*. Due to the presence of relict and endemic species, the studied forests are of a high conservation value. However, they do not currently seem to require any special protection, as they are not directly endangered by human activities thanks to their linkage to steep rocky habitats. In any case, further studies addressing their bryophyte and lichen diversity would be required for a comprehensive overview of their plant diversity and conservation value, as it is expected that these forests host a diverse epilithic and epiphytic cryptogam flora (MEŽAKA et al. 2012, VICOL 2016, JÜRIADO & PAAL 2018).

#### Erweiterte deutsche Zusammenfassung

**Einleitung** – Europäische Gesteinsschutt- und Schluchtwälder sind wertvolle Habitate von hohem Naturschutzwert, da sie zahlreiche seltene und reliktsche Gefäßpflanzenarten beherbergen. Nach aktueller Syntaxonomie (MUCINA et al. 2016) bilden sie die Ordnung *Aceretalia pseudoplatani*. Gesteinsschutt- und Schluchtwälder der Iberischen Halbinsel sind mehrfach studiert worden, zuletzt in einer Übersicht von CAMPOS et al. (2011), in der sechs Assoziationen unterschieden werden: *Viola mirabilis-Ulmetum glabrae*, *Rosa pendulinae-Aceretum platanoidis*, *Hedero helcis-Tilietum platyphylli*, *Hyperico androsaemi-Ulmetum glabrae*, *Helleboro occidentalis-Tilietum cordatae* and *Ononido aragonensis-Tilietum platyphylli*. Bei Feldstudien im nördlichen Teil der Iberischen Halbinsel beobachteten wir auf Kalkfelsvorsprüngen einen anderen von *Tilia platyphyllos* dominierten Waldvegetationstyp, hier als Kalkfels-Lindenwälder bezeichnet (CROLFs).

**Methoden** – Das Untersuchungsgebiet schließt den nördlichen Teil der Iberischen Halbinsel in Nordspanien und angrenzende Gebiete in Südwestfrankreich ein (Abb. 1). Das Gebiet gehört zur temperaten Zone mit mildem und feuchtem Klima. Die Geologie ist vielfältig. Für die Datenerhebung fertigten wir im Juli und August 2019 53 Vegetationsaufnahmen in Kalkfels-Lindenwäldern auf Probenflächen von 100–225 m<sup>2</sup> an. Zusammen mit der Erfassung der Arten und ihrer Abundanz nach der erweiterten neun-teiligen Braun-Blanquet-Skala erfassten wir die Gesamtdeckung der einzelnen Vegetationsschichten sowie des zutage tretenden Gesteins, Hangneigung und -exposition, geografische Koordinaten, Höhe und Boden-pH. Klimadaten wurden mittels WorldClim vs. 2 ermittelt. Die Datenanalyse der Vegetationsaufnahmen erfolgte mit der Software JUICE (TICHÝ 2002). Um unsere Aufnahmen mit anderen *Aceretalia*-Aufnahmen der Iberischen Halbinsel zu vergleichen, haben wir sie mit den Aufnahmen bei CAMPOS et al. (2011) in einer Datenbank vereinigt. Wie CAMPOS et al. (2011) haben wir die Clusteranalyse Flexible-Beta verwendet. Wir bestimmten die diagnostischen Arten mithilfe des *phi*-Koeffizienten (CHYTRÝ et al. 2002). Zur Veranschaulichung der standörtlichen Beziehung der untersuchten Kalkfels-Lindenwälder mit anderen iberischen *Aceretalia*-Einheiten errechneten wir

eine Ordination mit nicht-metrischer multidimensionaler Skalierung (NMDS) und projizierten nachträglich ausgewählte Umweltvariablen in den Ordinationsraum. Um verschiedene Typen von Kalkfels-Lindenwäldern herauszuarbeiten, klassifizierten wir den Datensatz mit TWINSPAN.

**Ergebnisse und Diskussion** – Flexible-Beta trennte eine Gruppe von Kalkfels-Lindenwald-Aufnahmen auf der ersten Hierarchiestufe (Abb. 3). Die Gruppe ist charakterisiert durch zahlreiche diagnostische Arten. Wir erkannten sie als neue Assoziation *Helictotricho cantabricsi-Tilietum platyphylli*, deren xero-mesophile Bestände Kalkfelshänge meist in Nordexposition einnehmen. Die Nachweise stammen von Steilhängen (40–80°) mit basenreichen Böden (mittlerer pH 7,4) entlang einer breiten Höhenspanne (140–1260 m). Die Baumschicht erreicht gewöhnlich 70–85% Deckung und ist dominiert von *Tilia platyphyllos*, begleitet von *Fagus sylvatica*, *Fraxinus excelsior*, *Quercus ilex* und *Sorbus aria*. Die Strauchschicht ist variabel mit Deckungswerten von 5–15% und wird hauptsächlich durch *Corylus avellana*, *Crataegus monogyna*, *Rhamnus alaternus*, *R. alpina* und Jungbäume gebildet. Die Krautschicht ist artenreich (30–50 Arten pro Aufnahme) und erreicht typischerweise 35–65% Deckung. Typisch sind *Brachypodium rupestre*, *Sesleria autumnalis* und *S. caerulea* als dominante Gräser. Die Artenzusammensetzung stellt eine Mischung dar aus mesophilen Waldarten (z. B. *Euphorbia amygdaloides*, *Hepatica nobilis*, *Saxifraga hirsuta*), trockenheitsverträglichen Waldarten wie *Melittis melissophyllum*, *Rubia peregrina* und *Vincetoxicum hirundinaria*, Arten von Felsvorsprüngen (z. B. *Asplenium trichomanes*, *Globularia nudicaulis*, *Saxifraga paniculata*) und von Offenhabitaten (z. B. *Dianthus hyssopifolius*, *Genista hispanica* subsp. *occidentalis*, *Teucrium pyrenaicum*). Auch endemische Arten des Kantabrischen Gebirges und der West-Pyrenäen konnten wir nachweisen wie z. B. *Antirrhinum braun-blanquetii*, *Digitalis parviflora* und *Seseli cantabricum*, einschließlich einiger Seltenheiten wie *Oreochloa confusa*, *Petrocoptis pyrenaica* s.l. und *Saxifraga canaliculata*.

Wir unterscheiden zwei vikariierende Subassoziationen des *Helictotricho cantabricsi-Tilietum platyphylli*. Das *H. c.-T. p. typicum* ist charakteristisch für den östlichen Teil des Untersuchungsgebietes und zeichnet sich durch einen höheren Anteil an mesophilen Waldarten wie *Campanula trachelium*, *Lamium galeobdolon* und *Lonicera xylosteum* aus. Ihr westliches Gegenstück, die Subassoziation *H. c.-T. p. lauretosum nobilis*, enthält trockenheitsverträgliche Arten wie *Aegonychon purpureocaeruleum* und *Asplenium ceterach*, submediterrane Arten (z. B. *Dioscorea communis* und *Smilax aspera*) und typische Arten des Kantabrischen Gebirges wie *Antirrhinum braun-blanquetii* und *Carex caudata*.

Beim Vergleich mit anderen iberischen *Aceretalia*-Wäldern bilden die Aufnahmen des *Helictotricho-Tilietum* eine recht eigenständige Gruppe rechts außen im NMDS-Ordinationsdiagramm (Fig. 6). Diese Gruppe der Kalkfels-Lindenwälder unterscheidet sich durch zahlreiche diagnostische Arten, insbesondere Spezialisten der Felsvorsprünge, die in anderen iberischen *Aceretalia*-Wäldern im Allgemeinen fehlen.

Das *Helictotricho cantabricsi-Tilietum platyphylli* ähnelt in seinem Aussehen und seiner Ökologie mehreren anderen Lindenwald-Syntaxa in verschiedenen Regionen des gemäßigten Europas. Die iberischen Kalkfels-Lindenwälder unterscheiden sich jedoch deutlich durch das Vorkommen von Arten mit südwesteuropäischer Verbreitung und durch das Fehlen von zentral- und osteuropäisch sowie von ost-submediterran verbreiteten Arten.

**Syntaxonomie:** Iberische Gesteinsschutt- und Schluchtwälder sind traditionell in einem breit angelegten Verband *Tilio-Acerion* klassifiziert worden. In der EuroVegChecklist wird dieser Verband jedoch viel enger gefasst und umfasst vor allem kühl-temperate zentraleuropäische Ahornwälder, während die thermophilen Wälder einen eigenen zentraleuropäischen Verband *Melico-Tilion platyphylli* bilden (MUCINA et al. 2016). Die atlantisch geprägten Eschen-Ahorn-Wälder auf Gesteinsschutt in Westeuropa werden in der EuroVegChecklist im Verband *Dryopterido affinis-Fraxinion* klassifiziert; sie enthalten typische atlantische mesophile Waldarten wie *Hypericum androsaemum*, *Saxifraga hirsuta* und *Scilla lilio-hyacinthus*. Es bleibt zu klären, ob xero-mesophile Gesteinsschutt- und Felswälder im atlantischen Südwesteuropa aufgrund ihrer Ökologie im *Melico-Tilion* zu klassifizieren sind oder im Hinblick auf biogeografische Gemeinsamkeiten im *Dryopterido-Fraxinion*. Wir ziehen das ökologische Kriterium vor und klassifizieren das *Helictotricho-Tilietum* vorläufig im *Melico-Tilion*. Daraus folgt das folgende syntaxonomische Schema, das kompatibel ist mit der aktuellen EuroVegChecklist (MUCINA et al. 2016):

Klasse: *Carpino-Fagetea sylvaticae* Jakucs ex Passarge 1968  
Ordnung: *Aceretalia pseudoplatani* Moor 1976  
Verband: *Melico-Tilion platyphylli* Passarge et G. Hofmann 1968  
Assoziation: *Helictotricho cantabrics-Tilietum platyphylli* Zukal et Biurrun 2022  
Subassoziation: *H. c.-T. p. typicum*  
Subassoziation: *H. c.-T. p. lauretosum nobilis* Zukal et Biurrun 2022


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## Author contributions

DZ designed the study, organized and conducted the field sampling, led the writing, performed the statistical analyses and prepared tables and figures. IB participated in the field sampling and critically revised the manuscript.

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## Appendices and Supplements

**Appendix 1.** Nomenclature types of the new syntaxa.

**Anhang 1.** Nomenklatorische Typen der neuen Syntaxa.

### TR1. *Helictotricho cantabrics-Tilietum platyphylli* Zukal et Biurrun 2022

**Holotypus:** Spain, province of Navarre, Arribe: forest on a steep rocky slope, 4.4 km SW from the church in the village; 745 m a.s.l.; coordinates: 43.01314 N, 2.02672 W; relevé area: 120 m<sup>2</sup> (15 m × 8 m); aspect: 50°; slope: 65°; covers: tree layer 85%, shrub layer 5%, herb layer 60%, moss layer 35%; cover of rocks: 65%; soil pH: 7.6. Recorded by D. Zukal on July 22, 2019.

**Tree layer:** *Tilia platyphyllos* 4, *Fagus sylvatica* 2b, *Fraxinus excelsior* 1, *Sorbus aria* 1.

**Shrub layer:** *Corylus avellana* 1, *Hedera hibernica* 1, *Fraxinus excelsior* +, *Lonicera xylosteum* +, *Sorbus aria* +, *Tilia platyphyllos* +, *Acer campestre* r, *Rhamnus alpina* r.

**Herb layer:** *Brachypodium rupestre* 3, *Hedera hibernica* 2b, *Sesleria autumnalis* 2a, *Helictotrichon cantabricum* 1, *Asplenium adiantum-nigrum* +, *A. trichomanes* s.l. +, *Bromopsis erecta* +, *Campanula rotundifolia* +, *Dactylis glomerata* +, *Dianthus hyssopifolius* +, *Erica vagans* +, *Erucastrum nasturtiifolium* subsp. *sudrei* +, *Galium mollugo* agg. +, *Globularia nudicaulis* +, *Hepatica nobilis* +, *Laserpitium nestleri* +, *Lathyrus linifolius* +, *Mercurialis perennis* +, *Picris hieracioides* +, *Rubus* sect. *Rubus* +, *Saxifraga hirsuta* +, *S. paniculata* +, *Silene italica* +, *Stachys officinalis* +, *Vicia sepium* +, *Asplenium ruta-muraria* r, *A. scolopendrium* r, *Campanula trachelium* r, *Dioscorea communis* r, *Genista hispanica* subsp. *occidentalis* r, *Helleborus viridis* subsp. *occidentalis* r, *Polystichum setiferum* r, *Primula veris* r, *Ruscus aculeatus* r, *Sedum dasyphyllum* r, *Solidago virgaurea* r, *Teucrium pyrenaicum* r, *Vincetoxicum hirundinaria* r, *Viola riviniana* agg. r, *Corylus avellana* +, *Crataegus monogyna* +, *Fraxinus excelsior* +, *Fagus sylvatica* r, *Rosa* sp. r.

## TR2. *Helictotricho cantabrici-Tilietum platyphylli lauretosum nobilis* Zukal et Biurrun 2022

**Holotypus:** Spain, province of Asturias, Alles: forest on a steep rocky slope, 0.7 km NE from the peak Pica la Jaya (874 m); 590 m a.s.l.; coordinates: 43.30786 N, 4.70956 W; relevé area: 100 m<sup>2</sup> (12.5 m × 8 m); aspect: 90°; slope: 75°; covers: tree layer 70%, shrub layer 4%, herb layer 65%, moss layer 25%; cover of rocks: 50%; soil pH: 7.2. Recorded by D. Zukal on July 9, 2019.

**Tree layer:** *Tilia platyphyllos* 4, *Quercus ilex* 2a.

**Shrub layer:** *Laurus nobilis* 1, *Quercus ilex* +, *Sorbus aria* +.

**Herb layer:** *Brachypodium rupestre* 3, *Mercurialis perennis* 2a, *Vincetoxicum hirundinaria* 2a, *Bromopsis erecta* 1, *Dactylis glomerata* 1, *Hedera hibernica* 1, *Helictotrichon cantabricum* 1, *Hepatica nobilis* 1, *Laserpitium nestleri* 1, *Primula veris* 1, *Stachys officinalis* 1, *Aegonychon purpureocaeruleum* +, *Allium ericetorum* +, *Asplenium adiantum-nigrum* +, *A. ruta-muraria* +, *A. trichomanes* s.l. +, *Campanula rotundifolia* +, *Carduus defloratus* subsp. *argemone* +, *Dianthus hyssopifolius* +, *Dioscorea communis* +, *Erucastrum nasturtiifolium* subsp. *sudrei* +, *Euphorbia characias* +, *Festuca piceo-europeana* +, *Galium mollugo* agg. +, *Leucanthemum vulgare* agg. +, *Picris hieracioides* +, *Polypodium cambricum* +, *Pseudoturritis turrata* +, *Ruscus aculeatus* +, *Saxifraga hirsuta* +, *S. trifurcata* +, *Silene italica* +, *S. vulgaris* +, *Scabiosa columbaria* +, *Teucrium scorodonia* +, *Viola alba* +, *Antirrhinum braun-blanchetii* r, *Aquilegia vulgaris* r, *Genista hispanica* subsp. *occidentalis* r, *Helleborus foetidus* r, *Hypericum montanum* r, *Polystichum setiferum* r, *Ranunculus polyanthemus* r, *Valeriana montana* r, *Vicia sepium* r, *Quercus ilex* +.

**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.** Primary data of the association *Helictotricho cantabrici-Tilietum platyphylli*.

**Anhang E1.** Primärdaten des *Helictotricho cantabrici-Tilietum platyphylli*.

**Supplement E2.** A list of species groups used in this study.

**Anhang E2.** Eine Liste von Artengruppen, die in dieser Studie verwendet wurden.

**Supplement E3.** Complete synoptic table showing the percentage frequencies (constancies) of diagnostic species (shaded), sorted by decreasing phi value.

**Anhang E3.** Vollständige Übersichtstabelle mit den prozentualen Häufigkeiten (Stetigkeiten) diagnostischer Arten (schattiert), sortiert nach abnehmendem phi-Wert.

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## Header data / Kopfdaten:

#	Country	Locality	Altitude (m a.s.l.)	Latitude	Longitude	Area (m <sup>2</sup> )	Aspect (°)	Slope (°)	Covers (%)					Soil pH	Date	Authors	Syntaxon
									Tree layer	Shrub layer	Herb layer	Moss layer	Rocks				
1	Spain	Camporrioni	240	43.25389 N	5.11175 W	150	340	75	70	6	45	40	65	7.5	03.07.2019	D. Zukal	<i>H. c.-T. p. lauretosum nobilis</i>
2	Spain	Vega de Cien	370	43.24197 N	5.10669 W	100	30	45	75	5	15	15	40	7.7	03.07.2019	D. Zukal	<i>H. c.-T. p. lauretosum nobilis</i>
3	Spain	Cuadonga	315	43.30803 N	5.04858 W	100	330	45	85	8	55	30	40	7.1	06.07.2019	D. Zukal	<i>H. c.-T. p. lauretosum nobilis</i>
4	Spain	Argada	430	43.31453 N	4.99422 W	50	60	80	50	40	60	25	85	7.9	06.07.2019	D. Zukal	<i>H. c.-T. p. lauretosum nobilis</i>
5	Spain	La Molina	420	43.30406 N	4.91458 W	100	280	60	70	25	45	40	70	7.4	07.07.2019	D. Zukal	<i>H. c.-T. p. lauretosum nobilis</i>
6	Spain	Berodía	420	43.31314 N	4.88536 W	100	340	40	60	40	40	25	65	6.9	07.07.2019	D. Zukal	<i>H. c.-T. p. lauretosum nobilis</i>
7	Spain	Carreña	345	43.31225 N	4.84489 W	100	350	55	85	3	85	35	30	6.8	07.07.2019	D. Zukal	<i>H. c.-T. p. lauretosum nobilis</i>
8	Spain	Oceño	425	43.29544 N	4.74425 W	100	210	45	75	30	35	30	80	7.1	08.07.2019	D. Zukal	<i>H. c.-T. p. lauretosum nobilis</i>
9	Spain	Tielve	780	43.25842 N	4.77022 W	100	40	70	70	3	65	30	40	7.2	08.07.2019	D. Zukal	<i>H. c.-T. p. lauretosum nobilis</i>
10	Spain	Poncebos	460	43.25853 N	4.80867 W	100	350	80	90	4	35	25	60	7.6	08.07.2019	D. Zukal	<i>H. c.-T. p. lauretosum nobilis</i>
11	Spain	Trescares	590	43.30786 N	4.70956 W	100	90	75	70	4	65	25	50	7.2	09.07.2019	D. Zukal	<i>H. c.-T. p. lauretosum nobilis</i>
12	Spain	Cáraves	140	43.30981 N	4.73197 W	100	340	70	85	2	70	40	45	7.4	10.07.2019	D. Zukal	<i>H. c.-T. p. lauretosum nobilis</i>
13	Spain	Bores	550	43.30433 N	4.64783 W	100	30	75	60	15	80	70	50	7.7	10.07.2019	D. Zukal	<i>H. c.-T. p. lauretosum nobilis</i>
14	Spain	Urgoiti	1020	43.07953 N	2.81564 W	100	360	50	85	2	75	30	45	7.2	16.07.2019	D. Zukal	<i>H. c.-T. p. typicum</i>
15	Spain	Intza	600	43.00247 N	1.99681 W	100	360	65	80	25	55	40	65	7.8	22.07.2019	D. Zukal	<i>H. c.-T. p. typicum</i>
16	Spain	Gaintza	745	43.01314 N	2.02672 W	120	50	65	85	5	60	35	65	7.6	22.07.2019	D. Zukal	<i>H. c.-T. p. typicum</i>
17	Spain	Azkarate	1095	43.03261 N	2.03631 W	100	340	60	80	3	65	40	70	7.3	22.07.2019	D. Zukal	<i>H. c.-T. p. typicum</i>
18	Spain	Latasa	615	42.9385 N	1.82333 W	100	30	55	80	5	50	40	80	7.3	22.07.2019	D. Zukal	<i>H. c.-T. p. typicum</i>
19	Spain	Latasa	670	42.94681 N	1.82411 W	100	310	60	70	1	45	25	75	7.3	22.07.2019	D. Zukal	<i>H. c.-T. p. typicum</i>
20	Spain	Amezketeta	560	43.03828 N	2.07525 W	225	30	60	85	15	60	40	50	7.3	23.07.2019	D. Zukal	<i>H. c.-T. p. typicum</i>
21	Spain	Larraitz	725	43.02975 N	2.09008 W	160	290	50	75	25	65	35	45	7.3	23.07.2019	D. Zukal	<i>H. c.-T. p. typicum</i>
22	Spain	Ataun	555	42.98219 N	2.16869 W	150	10	65	85	6	60	35	25	7.3	26.07.2019	D. Zukal	<i>H. c.-T. p. typicum</i>
23	Spain	San Martin	680	43.0085 N	2.16094 W	100	320	80	80	3	55	15	75	7.1	26.07.2019	D. Zukal	<i>H. c.-T. p. typicum</i>
24	Spain	Encima Angulo	985	43.04156 N	3.19825 W	100	40	75	75	2	45	25	40	7.7	28.07.2019	D. Zukal	<i>H. c.-T. p. typicum</i>
25	Spain	Encima Angulo	885	43.01781 N	3.17428 W	100	50	70	70	10	65	40	40	7.5	28.07.2019	D. Zukal	<i>H. c.-T. p. typicum</i>
26	Spain	Cadagua	755	43.06861 N	3.36003 W	150	360	50	75	15	70	25	30	7.4	29.07.2019	D. Zukal	<i>H. c.-T. p. typicum</i>
27	Spain	Ordejon	560	43.11744 N	3.31375 W	100	350	65	80	1	55	40	70	7.6	29.07.2019	D. Zukal	<i>H. c.-T. p. typicum</i>
28	Spain	Turtzioz	460	43.27939 N	3.29364 W	150	350	75	60	15	35	55	80	6.4	29.07.2019	D. Zukal	<i>H. c.-T. p. lauretosum nobilis</i>
29	Spain	Orozketeta	620	43.15444 N	2.67753 W	100	350	75	55	35	50	35	75	7.4	01.08.2019	D. Zukal	<i>H. c.-T. p. typicum</i>
30	Spain	Bernagoitia	580	43.16228 N	2.70067 W	100	40	70	85	2	60	35	60	7.2	01.08.2019	D. Zukal	<i>H. c.-T. p. typicum</i>
31	Spain	Santoña	225	43.44647 N	3.42844 W	150	340	60	80	8	10	30	35	7.4	06.08.2019	D. Zukal	<i>H. c.-T. p. lauretosum nobilis</i>
32	Spain	Urdón	200	43.26106 N	4.63711 W	100	320	70	80	5	70	25	25	7.7	10.08.2019	D. Zukal	<i>H. c.-T. p. lauretosum nobilis</i>
33	Spain	La Quintana	360	43.24969 N	4.63644 W	120	10	50	70	12	55	45	50	7.3	11.08.2019	D. Zukal	<i>H. c.-T. p. lauretosum nobilis</i>
34	Spain	Tielve	695	43.26303 N	4.78881 W	150	20	45	70	0	35	40	75	7.2	11.08.2019	D. Zukal	<i>H. c.-T. p. lauretosum nobilis</i>
35	Spain	Ceneya	350	43.23686 N	5.08861 W	100	30	65	85	5	45	50	40	7.7	11.08.2019	D. Zukal	<i>H. c.-T. p. lauretosum nobilis</i>
36	Spain	Ribota de Sajambre	850	43.15086 N	5.05031 W	100	50	50	70	2	60	50	40	7.3	12.08.2019	D. Zukal	<i>H. c.-T. p. lauretosum nobilis</i>
37	Spain	Oseha de Sajambre	685	43.12836 N	5.03628 W	125	10	70	90	4	45	60	65	7.8	12.08.2019	D. Zukal	<i>H. c.-T. p. lauretosum nobilis</i>
38	Spain	Cáin	585	43.22625 N	4.89386 W	160	40	60	85	3	70	25	40	8.3	12.08.2019	D. Zukal	<i>H. c.-T. p. lauretosum nobilis</i>
39	Spain	Cáin	595	43.19681 N	4.90769 W	100	50	60	90	2	65	15	15	7.8	12.08.2019	D. Zukal	<i>H. c.-T. p. lauretosum nobilis</i>
40	Spain	Dobres	1025	43.06972 N	4.63717 W	100	320	45	60	35	65	15	25	7.4	13.08.2019	D. Zukal	<i>H. c.-T. p. lauretosum nobilis</i>
41	Spain	Vandejo	785	43.05367 N	4.54569 W	100	350	70	70	5	45	50	70	7.7	13.08.2019	D. Zukal	<i>H. c.-T. p. lauretosum nobilis</i>
42	Spain	Ajanedo	520	43.25889 N	3.711 W	160	310	55	55	65	30	25	60	7.6	17.08.2019	D. Zukal	<i>H. c.-T. p. lauretosum nobilis</i>
43	Spain	Ason	635	43.20858 N	3.59269 W	120	50	70	85	2	70	10	45	7.6	17.08.2019	D. Zukal	<i>H. c.-T. p. lauretosum nobilis</i>
44	Spain	Oñati	645	42.97508 N	2.40606 W	180	100	65	90	5	35	25	70	7.6	21.08.2019	D. Zukal & I. Biurrun	<i>H. c.-T. p. typicum</i>
45	Spain	Orexa	355	43.07656 N	1.98597 W	120	20	65	90	2	30	45	80	7.4	21.08.2019	D. Zukal & I. Biurrun	<i>H. c.-T. p. typicum</i>
46	Spain	Isaba	830	42.87042 N	0.90917 W	105	70	45	65	60	5	15	45	7.3	22.08.2019	D. Zukal	<i>H. c.-T. p. typicum</i>
47	France	Sainte-Engrâce	940	42.97858 N	0.81328 W	100	330	70	70	3	75	30	50	7.3	22.08.2019	D. Zukal	<i>H. c.-T. p. typicum</i>
48	France	Bielle	655	43.056 N	0.41722 W	100	250	60	75	3	15	50	90	7.6	23.08.2019	D. Zukal	<i>H. c.-T. p. typicum</i>
49	France	Laruns	815	43.01044 N	0.43003 W	100	340	40	85	10	25	25	15	6.1	23.08.2019	D. Zukal	<i>H. c.-T. p. typicum</i>
50	France	Escot	365	43.07208 N	0.60542 W	100	340	70	80	15	12	75	90	7.5	24.08.2019	D. Zukal	<i>H. c.-T. p. typicum</i>
51	France	Lees	535	42.96283 N	0.61136 W	100	30	60	85	15	40	25	35	7.4	24.08.2019	D. Zukal	<i>H. c.-T. p. typicum</i>
52	Spain	Canfranc	1260	42.75683 N	0.51067 W	120	290	75	70	70	3	25	30	7.4	24.08.2019	D. Zukal	<i>H. c.-T. p. typicum</i>
53	Spain	Irañeta	785	42.93572 N	1.92561 W	100	360	65	90	20	15	55	95	7.4	25.08.2019	D. Zukal	<i>H. c.-T. p. typicum</i>



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**Supplement E2.** A list of species groups used in this study.

**Anhang E2.** Eine Liste von Artengruppen, die in dieser Studie verwendet wurden.

*Aquilegia vulgaris* agg.: *Aquilegia pyrenaica*, *A. vulgaris*.

*Dryopteris affinis* agg.: *Dryopteris affinis*, *D. borrieri*.

*Galium mollugo* agg.: *Galium album*, *G. mollugo*.

*Geranium robertianum* agg.: *Geranium purpureum*, *G. robertianum*.

*Hedera helix* agg.: *Hedera helix*, *H. hibernica*.

*Leucanthemum vulgare* agg.: *Leucanthemum ircutianum*, *L. vulgare*.

*Polypodium vulgare* agg.: *Polypodium cambricum*, *P. interjectum*, *P. vulgare*.

*Quercus ilex* agg.: *Quercus ilex*, *Q. rotundifolia*.

*Viola riviniana* agg.: *Viola reichenbachiana*, *V. riviniana*.



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