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Forests of the Tertiary relict tree *Zelkova carpinifolia* in Colchis (South Caucasus) and their regional vegetation context

Wälder des tertiären Reliktbaums *Zelkova carpinifolia* in der Kolchis (Südkaukasus) und ihr regionaler Vegetationskontext

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Abstract

Zelkova (*Ulmaceae*) represents a relict woody genus comprising six extant species with a disjunctive distribution in eastern and southwestern Eurasia. *Zelkova carpinifolia* is a deciduous tree limited to the Caucasian Ecoregion and its surroundings. Most of its sites are located in the two essential Tertiary refugia of the Northern Hemisphere – Colchis (western Georgia, northeastern Turkey) and Hyrcania (northern Iran, southeastern Azerbaijan). In Georgia, *Z. carpinifolia* stands are recognized as a national priority habitat. However, data on their environmental conditions, structure and species composition were partial, sometimes contradicting and scattered in the literature. Our main goal was to describe Georgian Colchic *Z. carpinifolia* forests based a novel dataset of vegetation-plot records and to present them in the broader vegetation context using available phytosociological data. To address this issue we led a phytosociological survey of *Z. carpinifolia* forests in Georgian Colchis and obtained 35 vegetation-plot records supplemented by the original field data on slope inclination, aspect and soil pH. To explore *Z. carpinifolia* stands within the broader regional vegetation context, we combined our new dataset with relevés of similar vegetation types from northern Iran, northern Turkey and western Georgia extracted from databases and literature. We classified the vegetation datasets using classification algorithms (beta-flexible clustering and Modified TWINSPAN) and examined the resulting clusters with detrended correspondence analysis (DCA) in terms of diagnostic species and selected environmental variables. Colchic *Z. carpinifolia* forests exhibited a relatively uniform species composition and structure, with *Carpinus orientalis* and *Quercus robur* subsp. *imeretina* representing the most frequent canopy companions of *Z. carpinifolia*. The evergreen submediterranean species *Ruscus aculeatus* often dominated the understory, accompanied by forest generalists, while herbs of dry forests

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and evergreen species were also frequent. The average vascular plant richness was 24.7 species per 100 m^2. The investigated forests mainly inhabited soils of slightly acidic to subneutral reaction (average pH 6.2). A numerical comparison of Colchic and Hyrcanian *Z. carpinifolia* forests revealed significant differences: The Hyrcanian ones were much more mesophilous, with Hyrcanian endemics and forest mesophytes being diagnostic species. The underlying causes of this ecological discrepancy remain unclear. In the context of dry deciduous forests of the Euxinian Province, Colchic *Z. carpinifolia* forests were most similar to the Colchic-Caucasian association *Campanulo alliariifoliae-Carpinetum orientalis* described from western Georgia. However, *Z. carpinifolia* stands formed their own sharply delimited cluster, indicating deeper differences than just the canopy dominance. Based on the classification results, we described a new alliance *Smilaco excelsae-Carpinion orientalis* for the Colchic-Caucasian lowland and mid-mountain dry and xeromesophilous deciduous forests. A mixture of species characteristic of the Caucasus and Colchis is diagnostic for this alliance, including *Campanula alliariifolia*, *Klasea quinquefolia*, *Polygonatum glaberrimum*, *Quercus robur* subsp. *imeretina*, *Vinca major* subsp. *hirsuta*, *Z. carpinifolia*. Colchic *Z. carpinifolia* stands face numerous threats, especially overgrazing by cattle, invasions of alien species and infrastructure development.

Keywords: Caucasus, Colchic refugium, forest ecology, Georgia, habitat, phytosociology, *Ulmaceae*, vegetation classification

Erweitere deutsche Zusammenfassung am Ende des Artikels

1. Introduction

In Eurasia, Quaternary climatic oscillations with long periods of drought and cold brought dramatic waves of migrations and extinctions of numerous species of former Tertiary tropic and subtropic forests (Mai 1989, Magri et al. 2017). Nowadays, Tertiary relict floras are of great importance for nature conservation as they safeguard ancient biological heritage. Their global distribution is non-random, with concentration in several areas, including the Caucasus Ecoregion (Milne & Abbott 2002). This area is listed among the top 34 world biodiversity hotspots due to its extraordinarily rich biota (Mittermeier et al. 2004) and encompasses two Tertiary biota refugia of global significance – Colchis (W Georgia, NE Turkey) and Hyrcania (SE Azerbaijan, N Iran). They were sheltered from the Quaternary climatic oscillations by high mountain ranges and climatically mitigated by extensive water bodies of the Black and Caspian Seas, respectively (Denk et al. 2001, Kikvidze & Ohsawa 2001, Nakhutsrishvili et al. 2015, Gegechkori 2020). Deciduous forests represent their natural vegetation (Zohary 1973, Bohn et al. 2000–2003, Gholizadeh et al. 2020) and are considered their most important biome for biodiversity conservation (CEPF 2004). In Colchis, mesophilous deciduous forests are reconstructed as the prevailing biome during the Last Glacial Maximum based on paleoecological evidence (Tarasov et al. 2000). Both areas are very humid, with average annual precipitation exceeding 1300 mm, thus leading some authors to consider their forests as temperate rainforests (Nakhutsrishvili et al. 2011). While in the larger portion of Colchis, precipitation is mostly evenly distributed throughout the year, summers in Hyrcania can be relatively arid (Walter & Lieth 1967, Denk et al. 2001, Gegechkori 2020). The understory of the deciduous forests in this ecoregion often consists of relict evergreen broad-leaved shrubs and lianas, including genera such as *Danae*, *Hedera*, *Ilex*, *Osmanthus*, *Prunus* and *Rhododendron* (Gulisashvili et al. 1975, Browicz 1982, Denk et al. 2001, Dolukhanov 2010, Nakhutsrishvili 2013, Gholizadeh et al. 2020). In terms of global floristic regionalization, Colchis represents the eastern part of the Euxinian Province (Boreal Subkingdom of Holarctis) while Hyrcania constitutes its own Hyrcanian Province (Ancient Mediterranean Subkingdom of Holarctis; Takhtajan 1986).

Another prominent tertiary relic of the Caucasian Ecoregion is *Zelkova carpinifolia*. In contrast to the aforementioned genera, it thrives in an ecologically different habitat, adapted to dry periods, avoiding those peculiar humid forests (Browicz 1982, Kozlowski et al. 2013, Nakhutsrishvili 2013, Dolukhanov 2010). *Zelkova* (*Ulmaceae*) is an ancient genus with the oldest known fossils from Northern America being ~55 million years old (Denk & Grimm 2005). It used to be a common component of Tertiary forests in the Northern Hemisphere (Mai 1989). The genus currently includes six species. Of these, three are limited to eastern Asia, while the other three occur in southwestern Eurasia. *Zelkova abelicea* is endemic to Crete and *Z. sicula* to Sicily. In contrast, *Z. carpinifolia* has a broader distribution (Kozlowski et al. 2013). It is almost exclusively limited to the Caucasus Ecoregion, known from Colchis and Eastern Greater Caucasus in Georgia, southern Armenia, western Azerbaijan and Hyrcania (Gulisashvili 1961, Browicz 1982, Kozlowski et al. 2013). Additionally, it persists at several isolated sites in eastern Turkey (Geven & Adigüzel 2016), western Iran (Akhani & Salimian 2003) and northeasternmost Iraq (Uzun & Galalaey 2022). The worldwide number of *Z. carpinifolia* sites is over one hundred, with an estimated area of occupancy exceeding 600 km^2 (Kozlowski et al. 2013, 2018).

Zelkova carpinifolia is a deciduous tree reaching an average height of 20–35 m (Kozlowski et al. 2013). However, it can form low shrubs in unsuitable conditions, including strong grazing pressure (Gulisashvili 1961). Details on its autecology are still somewhat blurred. Soil and light demands are often reported differently in various sources. Mostly, it is mentioned as a tree of deep and clay-loam humus-rich soils, but not waterlogged, swampy or salty. It is a relatively thermophilous species, preferring warm summers but with hardiness to -20 or -25 °C (Gulisashvili 1961, Sharashidze 1967, Gulisashvili et al. 1975). In the Georgian Holocene pollen spectra, *Z. carpinifolia* is reported as an indicator of climatic optima, i.e. periods of climatic amelioration and humidification associated with spreading of thermophilous woody taxa (Kvavadze & Connor 2005). Georgian populations occupy elevations between 100 and 600 m, whereas in Iran, Armenia or Azerbaijan, it reaches higher elevations, up to 1500 m (Kozlowski et al. 2013, Akhalkatsi 2019). Similar to its Asian relatives, *Z. carpinifolia* is frequently cultivated as an ornamental or even sacred tree, mainly in the vicinity of its native sites (Kozlowski et al. 2013, Mehdiyeva et al. 2017). In Colchis, it was planted in urban parks (e.g. Rokiti), cemeteries (e.g. Motsameta, Vartsikhe), monastery gardens (e.g. Martvili, Matkhoji) and alleys.

The dominant-based phytosociological approach formerly applied in Georgia recognized several community types of local *Z. carpinifolia* forests (Nakhutsrishvili 2013, Akhalkatsi 2019). There were six types named after accompanying taxa in Georgian Colchis: *Quercus robur* subsp. *imeretina*, *Ruscus colchicus*, *Brachypodium sylvaticum*, *Rhododendron luteum*, *Juncus effusus* and *Carpinus orientalis*. Kvachakidze (2009) presented a new classification of *Z. carpinifolia* forests, which only slightly modified the original division. These systems were generally derived from older classification schemes (e.g. Sharashidze 1967). *Zelkova carpinifolia* stands are assessed in the Georgian habitat typology as the priority habitat 92ZC-GE Zelkova forest (Akhalkatsi & Tarkhnishvili 2012). To date, only phytosociological plots of *Z. carpinifolia* forests have been available from Iran, but still they capture only a tiny fraction of its local sites (Gholizadeh et al. 2020). Additionally, several plots of mixed forests with a low proportion of *Z. carpinifolia* were published from eastern Georgia (Novák et al. 2020). The species is among the flagship species of Georgian nature protection (Akhalkatsi 2019). It is evaluated as a vulnerable species according to the criteria of IUCN (Kozlowski et al. 2018), and the same categorization was adopted for Georgia (Lachashvili et al. 2022). Moreover, it is listed in the national Red Book (Kacharava et al. 1982). *Zelkova carpinifolia* is subject to natural conservation in the reserves Ajameti and Sataplia in Georgian Colchis and Babaneuri in the eastern part of Georgia (Sokolova & Syroechkovskogo 1990, Akhalkatsi 2019).

Although *Z. carpinifolia* is considered an important species for nature protection, data on the species composition, structure, distribution and environmental conditions of its stands in Colchis have been lacking. In our study, we addressed the following questions: (1) What are the species composition and structure of the Colchic *Z. carpinifolia* forests? (2) What are their basic environmental conditions? (3) Are there differences in species composition between the Colchic and Hyrcanian *Z. carpinifolia* forests? If so, what are the possible determinants and which species are characteristic of each region? (4) Where do the Colchic *Z. carpinifolia* forests stand in the context of the dry deciduous forest vegetation of the Euxinian Province?

2. Methods

2.1 Study area

The study area (Fig. 1) included the main part of the *Zelkova carpinifolia* distribution in Colchis, western Georgia. It represents a slightly undulated landscape of old river terraces, plateaus and low hills. Mesozoic carbonate deposits, including Cretaceous limestones, along with younger volcanic rocks, constitute the prevailing pre-Quaternary geological bedrock in the area. Besides hillslopes, they

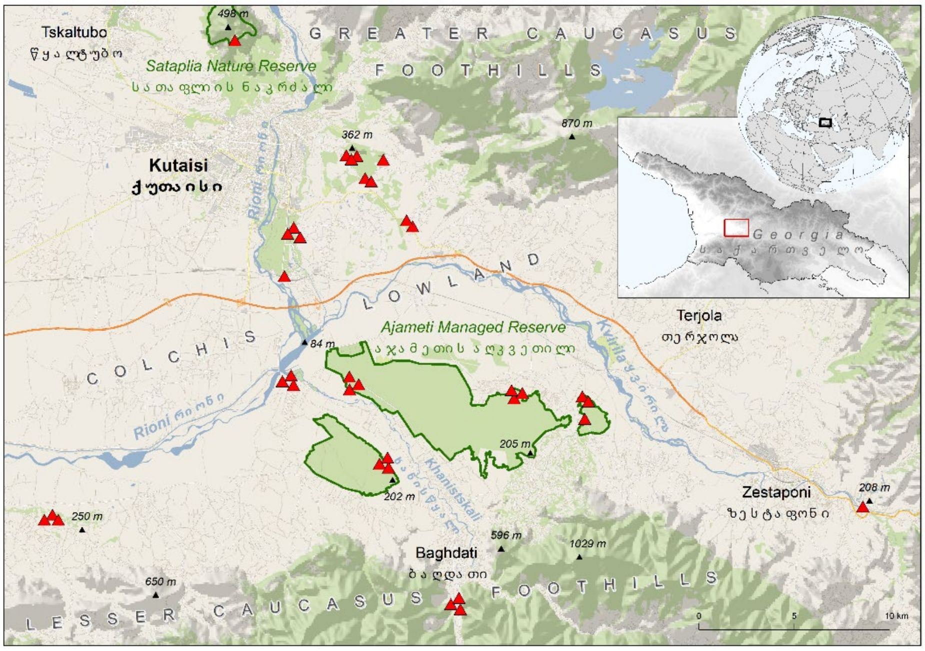

Fig. 1. Map of the study area with sampling sites of *Zelkova carpinifolia* forests (red triangles).

Abb. 1. Karte des Untersuchungsgebiet mit Aufnahmeflächen von *Zelkova carpinifolia*-Wäldern (rote Dreiecke).

are often overlaid by various Quaternary sediments, such as alluvial and fluvioglacial deposits (Connor et al. 2007, Adamia 2010). The climatic conditions of the studied region, derived from data measured at the Ajameti Managed Reserve in the central part of the Colchic *Z. carpinifolia* range (Sokolova & Syroechkovskogo 1990), indicate an annual mean temperature of 14 °C (4.4 °C in January and 23.5 °C in August) with temperatures ranging between -20 and 42 °C. Annual precipitation is ~1500 mm, of this ~550 mm during the vegetation season. Arid episodes might appear, especially in July and August.

Colchic deciduous mixed oak forests are considered the natural vegetation of the region (Bohn et al. 2000–2003). Due to millennia of human impact (Connor et al. 2007, Nikolaishvili et al. 2015), the landscape is nowadays largely deforested. Moreover, the Colchis Lowland has undergone a dramatic transformation to make way for the cultivation of subtropical crops over the last century (Ponnert 1977, Bondyrev et al. 2015). A significant portion of *Z. carpinifolia* stands was damaged to obtain valuable timber (Kozlowski et al. 2013, 2018). Within the Georgian floristic division, the sampled sites are located in the Imereti Region, which has relatively fewer species of vascular plants compared to other regions in the country, with around 900 species recorded (Gagnidze 2005).

2.2 Datasets

Our field sampling took place during the vegetation seasons of 2019 and 2022, with the majority of fieldwork done in August 2022. We extracted data on distribution of *Z. carpinifolia* in Colchis, Georgia, from the literature (e.g. Gulisashvili 1961, Ketskhoveli 1975, Kacharava et al. 1982, Maharramova et al. 2015) and investigated the reported sites to inspect the current occurrence of *Z. carpinifolia*. Moreover, we searched for new occurrences in the vicinity of known localities. We aimed to record vegetation where our target species was dominant, defined as having *Z. carpinifolia* cover in the tree layer exceeding 25%, with no other species exhibiting higher cover. We applied the Braun-Blanquet approach (Dengler et al. 2008) and sampled phytosociological relevés (100 m^2), usually of square shape. We acquired their geographic position (WGS84) and elevation by a portable receiver and determined slope aspect and inclination. The heat load index (McCune & Keon 2002, Equation 1) was calculated from these variables. Total percentage covers of the vegetation layers (moss, herb, shrub, tree) and their average heights were estimated. Covers of vascular plants in the vegetation layers were assessed using the nine-degree Braun-Blanquet scale (Dengler et al. 2008). In each plot, we collected a sample of the uppermost 15 cm of soil layer, dried it, and measured its pH in a suspension with deionized water (2:5) using a portable Greisinger instrument. From the BIOCLIM+ dataset included in the Chelsa database (Brun et al. 2022), we acquired plot annual mean temperature (BIO1), temperature seasonality (BIO4), annual precipitation (BIO12), precipitation seasonality (BIO15), growing season length (gsl) and climate moisture index (the difference between precipitation amount and potential evapotranspiration; cmi). We used QGIS 3.8 (QGIS Development Team 2021) to manage spatial data. As Colchis is a hotspot of alien plant diversity within Georgia (Ponert 1977), we also counted the number of aliens (sensu Kikodze et al. 2010) for each relevé. The relevés from Colchis were compiled into a dataset hereafter referred to as the "Colchic Dataset".

To compare species composition of the *Z. carpinifolia* stands in Colchis with those in Hyrcania, we extracted relevés dominated by this species (cover ≥25%) from the Hyrcanian Forest Vegetation Database (Gholizadeh et al. 2019). These relevés were then analysed together with the Colchic Dataset, creating a merged dataset hereafter referred to as the "Zelkova Dataset". To provide a broader context of the Euxinian Province for the Georgian *Z. carpinifolia* forests, we compiled a dataset called the "Euxinian Dataset", consisting of relevés from dry deciduous forests covering nearly the entire Euxinian Province. It included the Colchic Dataset and relevés of associations dominated or co-dominated by *Carpinus orientalis*, the most abundant canopy companion of *Z. carpinifolia* in the Colchic stands, extracted from the following sources: Quézel et al. 1980 (association *Carpinetum betulo-orientalis*, *n* = 11 relevés; *Crataego curvisepalae-Quercetum cerridis*, *n* = 7; *Erico arboreae-Carpinetum orientalis*, *n* = 16; *Rusco aculeatae-Carpinetum orientalis*, *n* = 7; missing association assignment of the community, *n* = 3), Kutbay & Kilinç 1995 (*Carpino orientalis-Quercetum cerridis*, *n* = 15; *Carpino orientalis-Phillyrietum latifoliae*, *n* = 6), Yarcı 2002 (*Querco cerridis-Carpinetum orientalis*, *n* = 10) and Korkmaz et al. 2011 (*Corno mari-Quercetum cerridis*, *n* = 10). Moreover, we included relevés of the association *Campanulo alliariifoliae-Carpinetum orientalis* (n = 20; Novák et al. 2021) representing xeromesophilous *Carpinus orientalis* forests with sparse occurrence of *Z. carpinifolia*, described from limestone areas bordering the Colchis Lowland in the north.

2.3 Data processing and analyses

Field data were stored in the Turboveg 2.1 database (Hennekens & Schaminée 2001) and are available in the Transcaucasian Vegetation Database (Novák et al. 2023a). Afterwards, they were exported to Juice 7.1 (Tichý 2002) where they were mostly processed. Taxonomic concepts and nomenclature were unified according to the Euro+Med (2006–) supplemented by information from the WFO (2023) for species exclusive to the Hyrcanian subset from Iran. Additionally, we merged *Carex divulsa*, *C. muricata* and *C. spicata* into *Carex muricata* aggr. and adopted the *Rubus* taxonomic concept from Sochor & Trávníček (2016). The Zelkova and Euxinian datasets were subjected to further classification analyses. Same-name species records were merged across the vegetation layers (Fischer 2015) and taxa determined only at the genus level were deleted prior to the analyses. The optimal clustering algorithm and the number of final clusters for interpretations were determined by the OptimClass1 method (Tichý et al. 2010). The Zelkova Dataset was classified using beta-flexible clustering (*beta* = -0.2) and Bray-Curtis metric as a measure of similarity between plots. Species covers were square-root transformed prior to the analyses (Tichý et al. 2020). The classification of the Euxinian Dataset was conducted using Modified TWINSPAN (Roleček et al. 2009) with *Whittaker's beta* as a measure of heterogeneity of the clusters and three pseudospecies cover cut levels (0, 5, 25%). To select diagnostic species, species-to-cluster fidelity was expressed by a *phi* coefficient (Sokal & Rohlf 1995) based on virtually equalized clusters (Tichý & Chytrý 2006). Moreover, we calculated Fisher Exact Test, and species with statistically insignificant concentration ($p > 0.05$) in a cluster were excluded from the diagnostic species lists. Highly diagnostic species ($phi \geq 0.5$) and diagnostic species ($phi \geq 0.25$) were calculated for each cluster. We applied detrended correspondence analysis (hereafter DCA) to visualize differences in species composition among clusters within the Zelkova Dataset and their relationships with the analysed environmental variables, whose vectors were passively projected onto the ordination space. Percentage species covers were square-root transformed prior to the analysis. It was performed in R 4.2.2 (R Core Team 2022) using the package *vegan* (Oksanen et al. 2020). Data on species distribution were extracted from relevant sources (the compendium Flora of Georgia vol. 1-16 – e.g. Ketskhoveli 1975, Donner 1990, EURO+MED 2006–, Gholizadeh et al. 2019, Novák et al. 2023b). In the syntaxonomic outline, we followed the rules of the International Code of Phytosociological Nomenclature (Theurillat et al. 2021).

3. Results and discussion

3.1 Colchic *Zelkova carpinifolia* forests – distribution, ecology, species composition

During the fieldwork, we recorded 35 relevés of forest vegetation dominated by *Zelkova carpinifolia* (Fig. 1 and 2) in Colchis. They were recorded mainly in the area between Kutaisi and the Lesser Caucasus foothills (~600 km^2). Besides *Z. carpinifolia*, the tree layer (average cover 78%, average height 19 m) often contained two deciduous trees: *Carpinus orientalis* and *Quercus robur* subsp. *imeretina*, a Colchic endemic taxon. The shrub layer was developed in 86% of the relevés (having average cover 15% and average height 1.8 m in them) with *Z. carpinifolia* being its most frequent component. This suggests the fundamental capability of *Z. carpinifolia* to grow successfully under a relatively closed canopy. *Crataegus monogyna* and *Carpinus orientalis* were often admixed. The herb layer (29%, 0.36 m) was regularly dominated by low thick stands of the evergreen submediterranean element *Ruscus aculeatus*, which spreads by creeping rhizomes and features spiny phylloclades that protect its stems from grazing. Forest xeromesophytes and mesophytes were common, including *Carex muricata* aggr., *Hedera helix*, *Primula acaulis* subsp. *rubra*, *Viola alba* and *V. reichenbachiana*. The Colchic-Caucasian and Euxino-Caucasian-Hyrcanian floral elements were represented by herbs (e.g. *Klasea quinquefolia*, *Sedum stoloniferum*, *Veronica peduncularis*) and evergreen species (*Hypericum xylosteifolium*, *Smilax excelsa* and *Vinca major* subsp. *hirsuta*). Common pasture weeds (e.g. unpalatable or toxic species) included *Helleborus orientalis*, *Hypericum perforatum* and *Prunella vulgaris*. Abundant occurrence of seedlings and young individuals of *Z. carpinifolia* indicated its ongoing generative reproduction. However, generative regeneration of the stands is often hindered by the heavy browsing pressure from cattle. Moreover, a portion of the young specimens were sucker shoots originating from horizontal roots. Other abundant juveniles included *Fraxinus excelsior* and *Quercus robur* subsp. *imeretina*. The moss layer reached only low covers (4% on average). Average species richness per plot reached 25 vascular plant species. Aliens were recorded in 54% of relevés, with average frequency one species per plot. The most commonly observed were seedlings of *Gleditsia triacanthos*, a North American tree ordinarily cultivated in windbreaks and alleys near the sampled sites. However, their successful establishment in forests remains questionable, as older individuals were not detected. Trees of *Robinia pseudoacacia* occurred in several plots as well as its rejuvenation. Of other cultivated alien plants, we discovered escaping individuals of hedgerow ornamental shrubs *Citrus trifoliata* and *Ligustrum japonicum*, both evergreen zoochoric species.

Based on our observations, the Colchic *Z. carpinifolia* forests were usually associated with specific sites in the landscape in terms of geomorphology and land use. We recorded them along the edges of large forested areas, especially in the Ajameti Managed Reserve. Other habitats included the upper edges of plateaus and old river terraces, river valley slopes, as well as bottoms of shallow valleys with summer-dry streams. Generally, it appeared that *Z. carpinifolia* forests preferentially inhabit sites with soil water shortage, presumably limiting other potential canopy competitors. However, to confirm this hypothesis, a comprehensive environmental study would be necessary. The soils in the stands were mostly slightly acidic to subneutral (mean pH 6.2), often loamy or containing gravel and silt admixture. Stands on carbonate hills around Kutaisi were found to occupy skeletal rendzina soils. These observations suggest a broad tolerance of *Z. carpinifolia* to various soil pH levels, as also reported from Iran (Dorostkar & Noirfalise 1976). Most of the recorded stands were developed on mild slopes (up to 15°) or planes, except for those on steeper slopes of river valleys (Khanitskali, Kvirila, Rioni). The stands are situated in a warm-temperate climate, with mean annual temperature 14.0 °C and abundant precipitation averaging 1431 mm per year. Climate moisture index ranges in positive values (mean value 4.04 kg m^{-2} $month^{-1}$), indicating a predominance of precipitation over evapotranspiration as the sites probably experience only occasional summer drought events. Selected variables characterizing environmental conditions of the Colchic *Z. carpinifolia* stands are shown in boxplots (Fig. 3).

Many of the observed *Z. carpinfolia* individuals exhibited signs of former coppicing management, suggesting that these stands presumably served as coppice-with-standards in the past. Forest cow grazing remains broadly practised in the sampled stands.

Our research has revealed a broad niche of *Z. carpinifolia* Colchic stands regarding soil pH. However, its suggested avoidance of swampy or waterlogged sites, as reported in some sources (e.g. Gulisashvili 1961, Bétrisey et al. 2018), remains blurred. During our fieldwork, we did not encounter a specific habitat subtype "*Zelkoveto-Querceta juncosa* (*Juncus effusus*)" (Sharashidze 1967, Nakhutsrishvili 2013) inhabiting heavy clay soils prone to periodical waterlogging. Moreover, *Z. carpinifolia* is mentioned as a species of riparian forests in some sources (e.g. Kozlowski et al. 2018), noting its affinity for alluvial soils (Sharashidze 1967). To inspect this interesting ecological topic, comprehensive year-round measurements of soil moisture content in the *Z. carpinifolia* stands would be helpful.

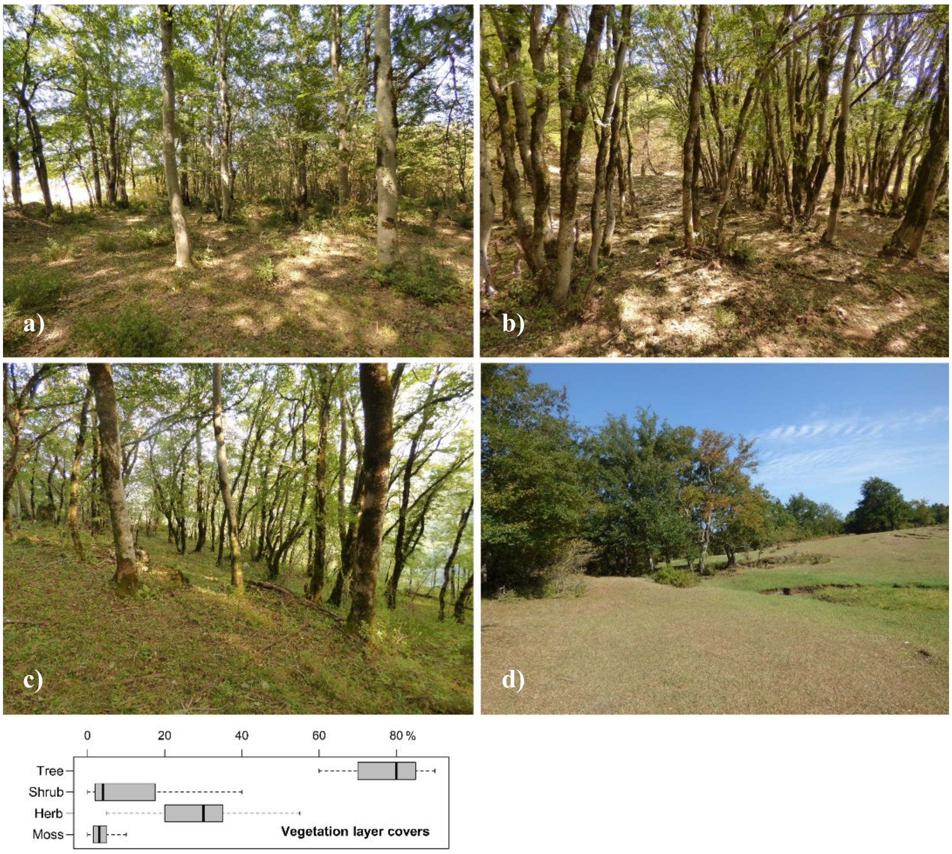

Fig. 2. Colchic *Zelkova carpinifolia* forests. **a)** Stand on an old river terrace near Akhali Tsviri (distr. Zestaphoni), 28. August 2022. **b)** Stand with multi-trunk trees at the bottom of a dry valley near Godogani (distr. Terjola), 30. August 2022. **c)** Stand on the upper edge of a limestone plateau near Banoja (distr. Tskaltubo), 29. August 2022. **d)** Edge of a stand in a heavily grazed landscape near Broliskedi (distr. Terjola), 29. August 2022 (all photos by P. Novák). **e)** Boxplots of vegetation layer covers in the Colchic *Zelkova carpinifolia* plots. Medians, interquartile ranges and whiskers are provided.

Abb. 2. Kolchische *Zelkova carpinifolia*-Wälder. **a)** Bestand auf einer alten Flussterrasse in der Nähe von Akhali Tsviri (Bezirk Zestaphoni), 28. August 2022. **b)** Bestand mit mehrstämmigen Bäumen am Boden eines trockenen Tals in der Nähe von Godogani (Bezirk Terjola), 30. August 2022. **c)** Bestand am oberen Rand eines Kalksteinplateaus in der Nähe von Banoja (Bezirk Tskaltubo), 29. August 2022. **d)** Rand eines Bestandes in einer stark beweideten Landschaft in der Nähe von Broliskedi (Bezirk Terjola), 29. August 2022 (alle Fotos von P. Novák). **e)** Boxplots der Vegetationsschichtbedeckungen in den kolchischen *Zelkova carpinifolia*-Plots. Mediane, Interquartilbereiche und Whiskers sind dargestellt.

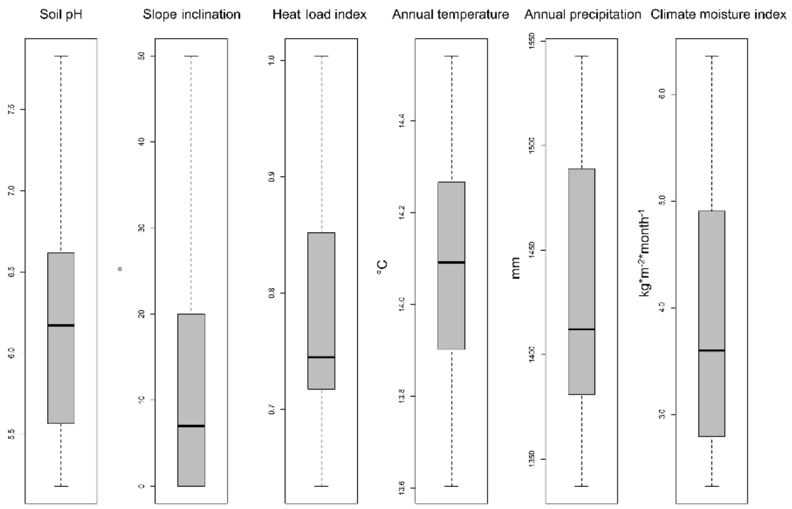

Fig. 3. Boxplots of selected variables characterizing environmental conditions of the Colchic *Zelkova carpinifolia* stands. Medians, interquartile ranges and whiskers are provided.

Abb. 3. Boxplots ausgewählter Variablen, die die Umweltbedingungen der kolchischen *Zelkova carpinifolia*-Bestände charakterisieren. Mediane, Interquartilsbereiche und Whiskers sind dargestellt.

3.2 Colchic and Hyrcanian *Zelkova carpinifolia* forests – a comparison

The Zelkova Dataset was classified using the beta-flexible algorithm. Colchic communities formed one cluster in this partitioning, while Hyrcanian communities formed two clusters. Furthermore, the Colchic stands were significantly more homogeneous, as they remained a solid cluster even in the seven-cluster dataset partitioning. The comparison of the communities is provided in Table 1 and the DCA diagram (Fig. 4).

The Hyrcanian clusters (2 and 3) often exhibited the canopy co-dominated by local endemics (*Parrotia persica* and *Quercus castaneifolia*), along with more widely distributed trees *Carpinus betulus* and *Diospyros lotus*. While their understory varies slightly in species composition, diagnostic species of both clusters include numerous forest mesophytes, suggesting their ecology is probably very similar in terms of soil moisture availability. These clusters shared some forest species with the Colchic cluster (1) (e.g. *Lamium album*, *Sanicula europaea*). However, numerous species differed, including geographically-restricted species specific for these refugia (e.g. *Hypericum xylosteifolium*, *Veronica peduncularis*, *Vinca major* subsp. *hirsuta* for Colchis vs. *Primula heterochroma*, *Quercus castaneifolia*, *Ruscus hyrcanus* for Hyrcania). A similar biogeographically determined pattern was detected in some other forest types like oak-hornbeam (Novák et al. 2023b) or oriental beech forests (Gholizadeh et al. 2020). The Hyrcanian and Colchic clusters of *Z. carpinifolia* forests also differed in the presence of broadly distributed mesophytes and xerophytes. Xerophilous woody species, such as *Carpinus orientalis* and *Crataegus monogyna*, were scarce within the Hyrcanian clusters, whereas mesophilous trees were more prevalent. Similarly, some understory mesophytes (e.g. *Euphorbia amygdaloides*, *Hypericum androsaemum*, *Viola odorata*) were exclusive to the Hyrcanian types, despite being common in Colchis but largely absent from the *Z. carpinifolia* stands. Conversely, xerophilous and drought-tolerant herbs limited to the Colchic type encompassed e.g. *Carex flacca* subsp. *serrulata*, *Hypericum perforatum* and *Ruscus aculeatus*.

Table 1. Shortened frequency table of the Colchic and Hyrcanian *Zelkova carpinifolia* forests. Top ten diagnostic species and all woody diagnostic species (*phi* ≥ 0.25; grey shaded) and highly diagnostic species (*phi* ≥ 0.5; grey shaded, in bold) for each cluster are shown, sorted according to decreasing *phi* values. At the bottom, the ten most frequent other species, sorted by decreasing frequency, are given. Species occurring as native in the Colchic Region (Col) and missing in the Hyrcanian Region (Hyr) and vice versa are marked by asterisk (*). See Supplement E3 for the full version of this table.

Tabelle 1. Gekürzte Häufigkeitstabelle der kolchischen und hyrkanischen *Zelkova carpinifolia*-Wälder. Die zehn am häufigsten vorkommenden Arten und alle holzigen Arten (*phi* ≥ 0,25; grau schattiert) sowie die am häufigsten vorkommenden Arten (*phi* ≥ 0,5; grau schattiert, fett) für jeden Cluster werden angezeigt, sortiert nach abnehmenden *phi*-Werten. Unten werden die zehn häufigsten anderen Arten angegeben, sortiert nach abnehmender Häufigkeit. Arten, die in der kolchischen Region (Col) heimisch sind und in der hyrkanischen Region (Hyr) fehlen und umgekehrt, sind mit einem Sternchen (*) gekennzeichnet. Die vollständige Version dieser Tabelle findet sich in Anhang E3.

Cluster number	1	2	3
Number of plots	35	18	7
Region	Col	Hyr	Hyr
Diagnostic species			
*Ruscus aculeatus**	**97**	.	.
*Hedera helix**	**94**	.	.
*Viola reichenbachiana**	**69**	.	.
Vinca major subsp. *hirsuta**	**66**	.	.
*Veronica peduncularis**	**66**	.	.
Viola alba	**86**	22	.
Smilax excelsa	**60**	11	.
Poa trivialis	**46**	.	.
Primula acaulis subsp. *rubra**	**40**	.	.
Quercus robur subsp. *imeretina**	**40**	.	.
Prunella vulgaris	**40**	.	.
*Hypericum xylosteifolium**	**37**	.	.
Ligustrum vulgare	**34**	.	.
Carpinus orientalis	57	11	14
Crataegus monogyna	43	.	14
Crataegus microphylla	.	**61**	.
*Viola caspia**	.	50	14
Acer cappadocicum	.	50	14
*Viola sintenisii**	.	28	.
Alliaria petiolata	.	22	.
Viscum album	.	22	.
Vincetoxicum scandens	.	17	.
Buxus sempervirens subsp. *hyrcana**	.	17	.
Carpesium cernuum	.	17	.
Prunus cerasifera	3	33	14
*Ruscus hyrcanus**	.	28	14
Viola odorata	.	.	**86**
Euphorbia amygdaloides	.	17	**86**
*Danae racemosa**	.	.	**57**
*Poa masenderana**	.	.	**57**
Oplismenus hirtellus subsp. *undulatifolius*	9	17	**71**
Hypericum androsaemum	.	11	**57**
Galium odoratum	.	.	**43**
Vicia crocea	.	6	**43**

Cluster number	1	2	3
Circaea lutetiana	.	6	**43**
*Crataegus ambigua**	.	.	29
*Hedera pastuchovii**	.	11	43
Carpinus betulus	6	50	71
Ulmus glabra	.	6	29
Diospyros lotus	.	22	43
Species diagnostic for two clusters			
*Quercus castaneifolia**	.	83	86
*Parrotia persica**	.	61	71
*Acer velutinum**	.	50	57
Other frequent species			
Zelkova carpinifolia	100	100	100
Brachypodium sylvaticum	69	39	57
Carex sylvatica	43	39	71
Geum urbanum	37	11	43
Asplenium adiantum-nigrum	34	28	.
Lamium album	17	33	.
Sanicula europaea	17	17	43
Fraxinus excelsior	26	11	14
Poa nemoralis	9	28	43
Crataegus germanica	11	22	14

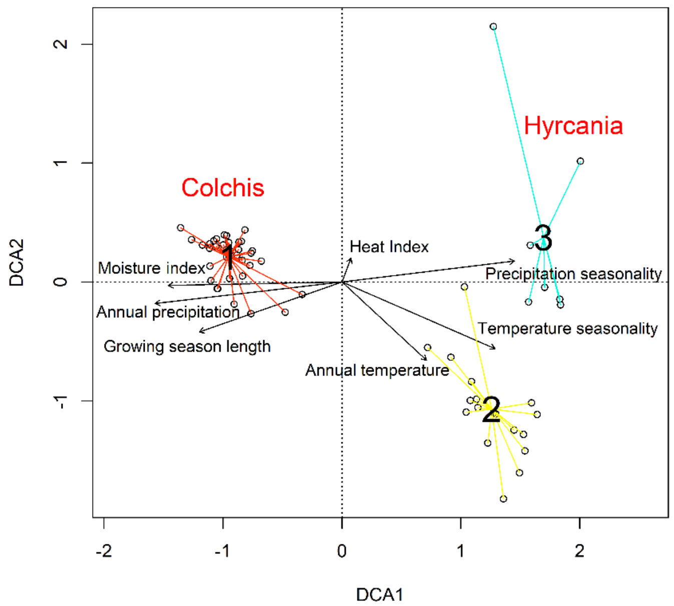

Fig. 4. DCA diagram with the three clusters defined within the Zelkova Dataset and vectors of environmental variables passively projected onto the ordination space. The first two ordination axes are shown: the first explained 8.45% of the dataset variability while the second 5.08%.

Abb. 4. DCA-Diagramm mit den drei im Zelkova-Datensatz definierten Clustern und Vektoren von Umweltvariablen, die passiv auf den Ordinationsbereich projiziert werden. Die ersten beiden Ordinationachsen werden angezeigt: Die erste erklärte 8,45 % der Variabilität des Datensatzes, die zweite 5,08 %.

From the syntaxonomic viewpoint, Hyrcanian *Z. carpinifolia* stands are assigned to the association *Zelkovo carpinifoliae-Quercetum castaneifoliae* Dorostkar et Noirfalise 1976. This association is included within the alliance of the Hyrcanian oak-hornbeam forests *Parrotio persicae-Carpinion betuli* Djazirei ex Gholizadeh, Naqinezhad et Chytrý 2020, reflecting its mesophilous character. The association is characteristic of flat areas of the Caspian Lowland (Gholizadeh et al. 2020).

We found significant differences between the Colchic and Hyrcanian *Z. carpinifolia* stands. While some differential species can be attributed to biogeographical patterns, such as endemics and subendemics, others highlight differences in their ecology. Specifically, the Hyrcanian stands appeared to be more mesophilous compared to their Colchic counterparts as reported also by some earlier studies (e.g. Gulisashvili et al. 1975). Previous researchers partly ascribed this difference to the putative taxonomic affiliation of Hyrcanian *Zelkova* as a distinct species, *Z. hyrcania*, while *Z. carpinifolia* was believed to be absent in that region. However, the validity of this taxonomic concept remains unconfirmed, as molecular studies on *Z. carpinifolia* yielded ambiguous findings (e.g. Christe et al. 2014 vs. Maharramova et al. 2015). Hyrcanian stands occur in warmer but more seasonal climates, with regular hot and dry periods in the summer (Fig. 4). However, data on their pedological conditions are missing. Consequently, the underlying causes of this ecological discrepancy remain unknown and require further investigation, encompassing both environmental and genetic aspects.

3.3 Colchic *Zelkova carpinifolia* forests in the context of Euxinian forests

Euxinian dry forests with *Carpinus orientalis*, the most common companion of *Z. carpinifolia* in Colchis, occur across the entire province. We analysed the composition of the Euxinian Dataset by Modified TWINSPAN. We provide a frequency table of diagnostic species for the six distinguished clusters (Table 2), along with an interpreted classification dendrogram (Fig. 5) and their distribution (Fig. 6).

Here, we give a syntaxonomic interpretation of two levels of the classification hierarchy resulting from the unsupervised classification. We specifically focus on the position of the Colchic-Caucasian clusters (1 and 2), which are in the main scope of this study. At the first level, three clusters delineate three coherent biogeographical groups that could be identified as alliances. The first, Colchic-Caucasian group (clusters 1 and 2), involves dry forests of the Western Caucasus, including the Colchis Lowland. Its diagnostic species are regionally characteristic taxa, including *Campanula alliariifolia*, *Clinopodium umbrosum*, *Hypericum xylosteifolium*, *Klasea quinquefolia*, *Oplismenus hirtellus* subsp. *undulatifolius*, *Sedum stoloniferum*, *Symphytum grandiflorum*, *Veronica peduncularis*, *Vinca major* subsp. *Hirsute* and *Z. carpinifolia*. Its negative delimitation is determined by species which are missing or rare in Colchis (see below). The second group (cluster 3), Eastern Euxinian, included stands recorded in the eastern section of the Euxinian Province, but far away from the Caucasus. Its diagnostic species combination reflects well this biogeographic position; they often include species limited to central Euxinia (e.g. *Asperula cimulosa*, *Salvia forsskaolei*) and species with Mediterranean affinities, including evergreen small trees and shrubs (e.g. *Arbutus andrachne*, *Cistus creticus*, *Erica arborea*) that reach their eastern distribution limits in central Euxinia (Donner 1990) and are almost absent in Georgian Colchis (Nakhutsrishvili 2013). The third group (clusters 4, 5 and 6) encompasses dry forests of western Euxinia. They are positively delimited by a group of species shared by western Euxinia and

Table 2. Shortened frequency table of the Euxinian Dataset. Top five diagnostic species (*phi* ≥ 0.25; grey shaded) and highly diagnostic species (*phi* ≥ 0.5; grey shaded, in bold) for each cluster are shown, sorted according to decreasing *phi* values. At the bottom, the ten most frequent other species, sorted by decreasing frequency, are given. Alliance acronyms: *Smilaco excelsae-Carpinion orientalis* (Sm-Car), *Castaneo sativae-Carpinion orientalis* (Ca-Car), *Quercion confertae* (Que co). See Supplement E4 for the full version of the table.

Tabelle 2. Gekürzte Stetigkeitstabelle des Euxinischen Datensatzes. Die fünf häufigsten diagnostischen Arten (*phi* ≥ 0,25; grau schattiert) und die hoch diagnostischen Arten (*phi* ≥ 0,5; grau schattiert, fett) für jeden Cluster werden angezeigt, sortiert nach abnehmenden *phi*-Werten. Unten werden die zehn häufigsten anderen Arten, sortiert nach abnehmender Häufigkeit, angegeben. Allianz-Akronyme: *Smilaco excelsae-Carpinion orientalis* (Sm-Car), *Castaneo sativae-Carpinion orientalis* (Ca-Car), *Quercion confertae* (Que co). Die vollständige Version der Tabelle findet sich in Anhang E4.

Cluster number	1	2	3	4	5	6
Number of relevés	21	34	38	17	20	10
Alliance	Sm-Car	Sm-Car	Ca-Car	Que con	Que con	Que con
Diagnostic species						
Klasea quinquefolia	**76**	15	.	.	.	.
Carex digitata	**57**	.	.	.	.	.
Campanula alliariifolia	**81**	9	21	.	.	.
Clinopodium umbrosum	**57**	12	.	.	.	.
Oplismenus hirtellus subsp. *undulatifolius*	**57**	9	5	.	.	.
Zelkova carpinifolia	19	**100**	.	.	.	.
Carex muricata aggr.	43	**97**	.	12	.	.
Poa trivialis	.	**47**	.	.	.	.
Quercus robur subsp. *imeretina*	.	**41**	.	.	.	.
Viola reichenbachiana	38	**68**	.	.	.	.
Epimedium pubigerum	.	.	**55**	.	5	.
Salvia forsskaolei	.	.	**55**	.	10	.
Erica arborea	.	.	**42**	.	.	.
Lathyrus aureus	.	.	**37**	.	.	.
Genista tinctoria	.	.	**32**	.	.	.
Tanacetum parthenium	.	.	11	**65**	.	.
Vicia cracca	.	.	8	**59**	.	.
Cephalanthera rubra	.	.	5	**53**	.	.
Asperula involucrata	.	.	.	**47**	.	.
Viola odorata	.	.	.	**41**	.	.
Phillyrea latifolia	.	.	3	.	**35**	.
Rubus ulmifolius	.	.	.	.	**30**	.
Styrax officinalis	.	.	.	.	25	.
Teucrium polium	.	.	.	.	20	.
Festuca heterophylla	.	.	21	.	35	.
Potentilla reptans	.	.	.	.	.	**80**
Festuca jeanpertii	.	.	.	.	.	**60**
Agrimonia eupatoria	.	3	.	.	.	**60**
Quercus hartwissiana	5	.	11	.	.	**60**
Euphorbia amygdaloides	5	.	5	.	40	**80**
Species diagnostic for more clusters						
Vinca major subsp. *hirsuta*	**90**	65	.	.	.	.
Viola alba	**86**	**85**	.	.	.	.
Carex sylvatica	48	41	5	.	.	.
Veronica peduncularis	52	**65**	.	.	.	.

Cluster number	1	2	3	4	5	6
Hedera helix	90	94	61	35	65	.
Prunella vulgaris	33	38	.	.	10	.
Quercus petraea	62	21	55	.	5	.
Drymochloa drymeja	48	18	50	.	.	.
Brachypodium pinnatum	5	.	47	47	.	.
Asyneuma rigidum	.	.	37	47	.	.
Daphne pontica	.	.	45	.	35	.
Crataegus monogyna	.	44	3	.	80	**100**
Quercus cerris	.	.	37	94	85	100
Other frequent species						
Carpinus orientalis	100	56	89	100	100	100
Geum urbanum	.	38	29	29	.	40
Ligustrum vulgare	33	32	21	.	.	.
Trachystemon orientalis	29	.	32	.	35	.
Rubus subgen. *Rubus*	33	26	16	12	5	.
Teucrium chamaedrys	29	.	8	29	30	.
Fragaria vesca	10	18	16	24	5	.
Aegonychon purpurocaeruleum	.	3	21	18	10	.
Clematis vitalba	14	3	11	24	5	.
Luzula forsteri	19	.	13	18	.	.

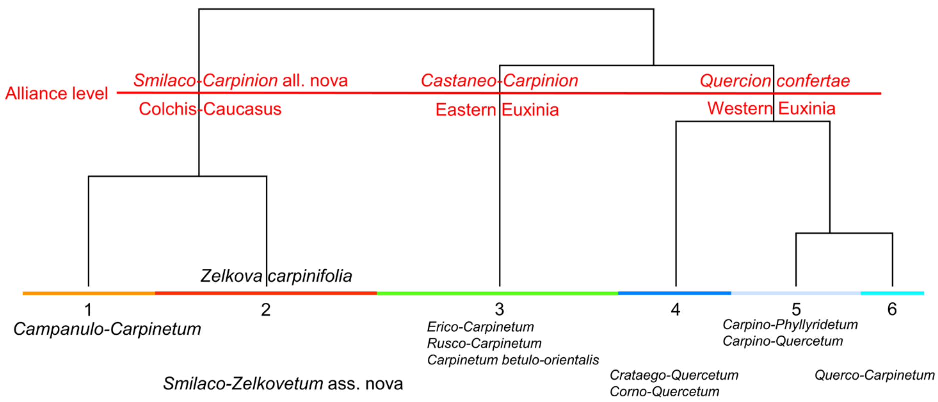

Fig. 5. Interpreted classification dendrogram (Modified TWINSPAN) of the Euxinian Dataset.

Abb. 5. Interpretiertes Klassifikationsdendrogramm (modifizierte TWINSPAN-Analyse) des Euxinischen Datensatzes.

the Balkans, including tree species (e.g. *Quercus cerris*). The syntaxonomic units corresponding to the second and third group are the alliances *Castaneo-Carpinion* and *Quercion confertae*, respectively. The first group represents an alliance that has not yet been described, for which we provide the formal description below.

The lower level of the classification revealed that the closest cluster to the Colchic *Z. carpinifolia* forests are the Colchic-Caucasian dry forests occurring in the limestone foothills of the Greater Caucasus in western Georgia (association *Campanulo-Carpinetum*; Novák et al 2021). Unlike the *Z. carpinifolia* forests, this community was richer in nemoral species slightly tolerant to drier substrates, both graminoids (e.g. *Carex digitata*, *Drymochloa drymeja*) and herbs (e.g. *Campanula rapunculoides*, *Potentilla micrantha*), as well as species of rock crevices (e.g. *Asplenium trichomanes*, *Sesleria alba*), as these forests often occur on exposed rocky slopes. Conversely, *Z. carpinifolia* forests were characterized by a higher abundance of nitrophilous shade-tolerant species with somewhat ruderal tendencies (e.g. *Geum urbanum*) and grasses (e.g. *Agrostis capillaris*, *Poa trivialis*), indicating an ongoing grazing pressure. Of the Colchic evergreen species, *Hypericum xylosteifolium* was recorded in plots of *Z. carpinifolia* forests. In addition to the species listed in the description of the Colchic-Caucasian group, these two subordinate clusters shared evergreen submediterranean species (e.g. *Hedera helix*, *Ruscus aculeatus*) and hemicryptophytes (e.g. *Asplenium adiantum-nigrum*, *Viola alba*), both species groups typical of deciduous dry forests of southeastern Europe (Stupar 2015). Regarding species richness, plots of *Campanulo-Carpinetum* were considerably richer compared to *Z. carpinifolia* stands, probably due to occurrence in areas with more rugged topography at various spatial scales. This supports a higher microhabitat diversity and generally higher gamma diversity.

The classification of the dry deciduous forests of northeastern Turkey has been recently conducted by Kavgacı et al. (2023). They provided a syntaxonomic scheme, aligned with the EuroVegChecklist (Mucina et al. 2016), placing these forests into the class *Quercetea pubescentis* and order *Quercetalia pubescenti-petraeae*. Within this framework, they recognized four subordinate alliances: *Quercion confertae* for the western part of the region, *Castaneo sativae-Carpinion orientalis* for the northeastern part, *Querco cerridis-Carpinion orientalis* for deciduous types with a strong Mediterranean influence and *Quercion crispatae* for subeuxine oak forests. The alliance *Castaneo sativae-Carpinion orientalis*, spatially closest to the Colchis Lowland, combines Colchic and Mediterranean evergreen species, both laurophyllous and sclerophyllous. However, this vegetation was found to be fundamentally different from dry forests common in western Georgia's low and middle elevations (Fig. 4 and 5). Based on the data from Georgian stands (clusters 1 and 2), we therefore designate this type of the Caucasian-Colchic dry deciduous forests as a new alliance, *Smilaco excelsae-Carpinion orientalis*. This alliance represents a connection between dry deciduous forests of the Euxinian Province and the Crimean Peninsula. The latter were described as an individual alliance, *Elytrigo nodosae-Quercion pubescentis* (Didukh 1996, Mucina et al. 2016). These forests elementally differ from the Georgian stands due to the common occurrence or dominance of *Quercus pubescens* and *Fraxinus ornus*, important European submediterranean tree species absent in the southern Caucasus. In their understory, Mediterranean and Crimean floral elements are well represented, whereas Caucasian and Colchic species are generally absent (Didukh 1996). Dry mixed forests of *Carpinus orientalis* and *Quercus pubescens* are reported from the Caucasian foothills on the Russian Black Sea coast (Grebenshikov et al. 1990, Bocharnikov et al. 2019) and their syntaxonomic position remains debatable owing to a combination of species typical for the Crimean and Colchic-Caucasian stands. However, a co-dominance of *Q. pubescens* suggests their affinity to the Crimean alliance. The vegetation typology traditionally applied within the Georgian

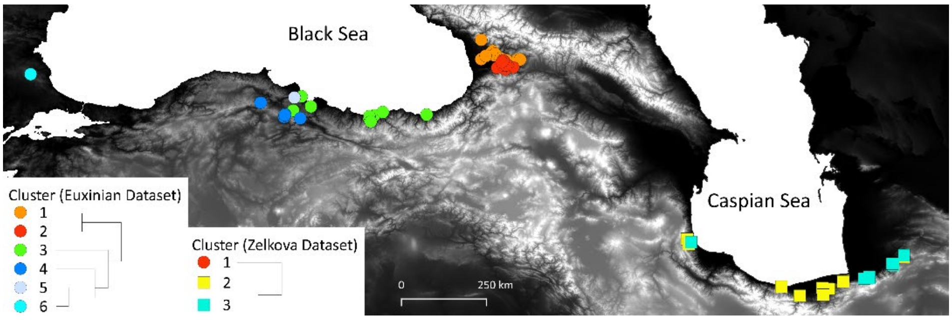

Fig. 6. Distribution of plots of the classified Zelkova and Euxianian Datasets.

Abb. 6. Verteilung der Plots der klassifizierten Zelkova- und Euxischen Datensätze.

territory recognizes only forests co-dominated by *Carpinus orientalis* and oaks (*Quercus petraea* subsp. *iberica*, *Q. robur* subsp. *imeretina*) or *Z. carpinifolia*, while pure stands of *C. orientalis* are not distinguished as an individual unit (Nakhutsrishvili 2013, Bebiya 2022).

3.4 Colchic *Zelkova carpinifolia* forests in the frame of the European habitat typology

Regarding the position of Colchic *Z. carpinifolia* stands within the EUNIS habitat typology applied in Europe and surrounding areas, we propose classifying them under the following upper units of the classification hierarchy, based on the habitat descriptions (https://eunis.eea.europa.eu/habitats) and characteristic species listed by Chytrý et al. (2020). The designed classification is as follows: T – Forest and other wooded land > T1 – Deciduous broadleaved forest > T19 – Temperate and submediterranean thermophilous deciduous forest > T19B – Mixed thermophilous forest. The classification at the lower levels needs further analyses on a broader set of plots. A provisional assignment would be: T19B2 – *Carpinus orientalis* forests > T19B23 – Anatolio-Caucasian oriental hornbeam forests. However, our analyses of the Euxinian Dataset revealed striking differences between Anatolian (Turkish) types and Colchic/Caucasian (Georgian) types. Georgian habitat classification recognizes the priority habitat 92ZC-GE Zelkova forest assigned to the unit 92. Mediterranean deciduous forests (Akhalkatsi & Tarkhnishvili 2012). However, this classification requires verification to ensure compliance with habitat classification systems applied in the European Union, as Georgia was granted EU candidate status in 2023.

3.5 *Zelkova carpinifolia* forests in Colchis and their conservation aspects

Although *Z. carpinifolia* is considered a flagship species of Georgian nature protection (Akhalkatsi 2019), its habitats face various ongoing threats. Over millennia, human activity in Colchis led to widespread deforestation for agricultural development, resulting in the persistence of only remnants of forests, with over 90% of its territory deforested. In the past, even during the last century, *Z. carpinifolia* was logged for valuable timber (Kozlowski et al. 2013). Another major threat is overgrazing. Although the number of cows bred in Georgia has decreased by about one-third in recent decades (Bondyrev et al. 2015), overgrazing remains a significant threat to the majority of Colchic *Z. carpinifolia* stands, suppressing tree regeneration, analogically to some other Mediterranean woodlands subjected to grazing intensification (Bergmeier et al. 2010). Currently, most recorded stands serve as cow forest pastures of various intensities, including those in the Ajameti Managed Reserve. Fortunately, some forest sections in the reserve have been recently fenced to prevent cattle from entering. Due to the lack of data on this crucial nature conservancy topic, observing the reaction of forest vegetation to the termination of cattle grazing would be beneficial. It could be carried out e.g. by establishing a network of regularly surveyed permanent plots, which is among the most important tools in current vegetation science (Chytrý et al. 2019). Although the effect of grazing on the herb and shrub understory is debatable, the frequent occurrence or even dominance of *Ruscus aculeatus*, a characteristic plant of grazed woodlands in southern Europe (Thomas & Mukassabi 2014), suggests its impact. Stands on hillslopes below roads are often subjected to illegal dumping, directly damaging *Z. carpinifolia* rejuvenation. Infrastructure development, including road construction, represents another significant threat, with some stands damaged during building activities associated with the S1 Highway near Kutaisi and BTC pipeline intersecting the Ajameti Managed Reserve, including the segments with *Z. carpinifolia*. The observed spread of invasive woody species further exacerbates the threats to Georgian lowland forests (Aleksidze et al. 2021, Kavtaradze et al 2023), although their seedlings are also largely reduced by grazing. *Z. carpinifolia*, like some other members of the *Ulmaceae* family, is susceptible to Dutch elm disease caused by *Ascomycota Ophiostoma novo-ulmi* (Akhalkatsi 2019), though we did not observe visibly infected trees during our fieldwork in Colchis. General conservation actions to be taken to support *Z. carpinifolia* were summarized by Bétrisey et al. (2018). To preserve the Colchic stands, we emphasize reducing grazing pressure (e.g. by fencing selected areas as mentioned above) and controlling alien species, at least within nature reserves.

4. Syntaxonomic outline

Cl.: *Quercetea pubescentis* Doing-Kraft ex Scamoni et Passarge 1959

Ord.: *Quercetalia pubescenti-petraeae* Klika 1933

***Smilaco excelsae-Carpinion orientalis* all. nov. hoc loco**

Diagnostic species of the alliance: *Asplenium adiantum-nigrum*, *Campanula alliariifolia*, *Carex michelii*, *Carpinus orientalis*, *Clinopodium umbrosum*, *Digitalis schischkinii*, *Hypericum xylosteifolium*, *Klasea quinquefolia*, *Lathyrus laxiflorus*, *Peucedanum adae*, *Polygonatum glaberrimum*, *Primula acaulis* subsp. *rubra*, *Quercus petraea* subsp. *iberica*, *Quercus robur* subsp. *imeretina*, *Ruscus aculeatus*, *Sedum stoloniferum*, *Smilax excelsa*, *Symphytum grandiflorum*, *Veronica peduncularis*, *Vinca major* subsp. *hirsuta*, *Viola alba*, *Zelkova carpinifolia*

Holotypus: *Smilaco excelsae-Zelkovetum carpinifoliae* ass. nov. hoc loco (see below)

Colchic-Caucasian dry and xeromesophilous deciduous forests of lower and mid-elevations. Subordinate associations: *Smilaco excelsae-Zelkovetum carpinifoliae* ass. nov. hoc loco and *Campanulo alliariifoliae-Carpinetum orientalis* Novák et al. 2021.

***Smilaco excelsae-Zelkovetum carpinifoliae* ass. nov. hoc loco**

Diagnostic species of the association: *Carex flacca* subsp. *serrulata*, *Carpinus orientalis*, *Hypericum xylosteifolium*, *Quercus robur* subsp. *imeretina*, *Ruscus aculeatus*, *Smilax excelsa*, *Veronica peduncularis*, *Vinca major* subsp. *hirsuta*, *Zelkova carpinifolia*

Holotypus: Relevé 4 (Supplements E1 and E2). Rokiti (distr. Baghadati), Ajameti Managed Reserve (western part), 27 Aug 2022, area 10 × 10 m^2, 180 m a.s.l., aspect 90°, slope 2°, 42.1115556° N, 42.7785556° E (±5 m), soil pH 5.33, authors P. Novák & M. Večeřa.

Tree layer (cover 80%, average height 22 m): *Zelkova carpinifolia* 4, *Quercus robur* subsp. *imeretina* 2b, *Carpinus orientalis* 2a, *Quercus petraea* subsp. *iberica* 1, *Sorbus torminalis* 1; Shrub layer (2%, 1 m): *Zelkova carpinifolia* 1, *Crataegus monogyna* +, *Prunus avium* +, *Smilax excelsa* +; Herb layer (20%, 0.35 m): *Ruscus aculeatus* 2a, *Hypericum xylosteifolium* 1, *Carex michelii* +, *C. muricata* aggr. +, *Hedera helix* +, *Lathyrus vernus* +, *Lonicera caprifolium* +, *Rubus* subgen. *Rubus* +, *Smilax excelsa* +, *Viola alba* +, *V. reichenbachiana* +, *Carex flacca* subsp. *serrulata* r, *Dioscorea communis* r, *Lathyrus laxiflorus* r, *Polygonatum glaberrimum* r; juveniles: *Zelkova carpinifolia* 1, *Crataegus monogyna* +, *Fraxinus excelsior* +, *Ligustrum vulgare* +, *Quercus robur* subsp. *imeretina* +, *Carpinus orientalis* r, *Prunus avium* r; Moss layer (1%).

Erweiterte deutsche Zusammenfassung

Einleitung – Der Kaukasus wird aufgrund seiner außerordentlich reichen Biota mit einer hohen Endemismusrate zu den 34 wichtigsten Biodiversitätshotspots der Welt gezählt und umfasst zwei Refugien tertiärer Biota von globaler Bedeutung – Kolchis (Westgeorgien, Nordosttürkei) und teilweise Hyrkanien (Südostaserbaidschan, Nordiran) (Mittermeier et al. 2004). *Zelkova carpinifolia* (im Folgenden *Z. carpinifolia*), ein hoher Laubbaum, ist eine bemerkenswerte Reliktart, die fast ausschließlich auf diese Refugien beschränkt ist. *Zelkova carpinifolia* ist eine gefährdete Art und wird als eine der Flaggschiffarten des georgischen Naturschutzes geführt. Ihre Bestände werden in der nationalen Lebensraumtypologie als prioritärer Lebensraum eingestuft (Akhalkatsi & Tarkhnishvili 2012). Obwohl *Z. carpinifolia* aus Naturschutzperspektive als bemerkenswerte Art gilt, fehlten bisher detaillierte Daten zur Ökologie, Verbreitung und Artenzusammensetzung ihrer Bestände in der Kolchis. Daher haben wir uns mit folgenden Fragen beschäftigt: (1) Wie ist die Artenzusammensetzung und Struktur der kolchischen *Z. carpinifolia*-Wälder? (2) Was sind ihre grundlegenden Umweltbedingungen? (3) Gibt es Unterschiede in der Artenzusammensetzung zwischen kolchischen und hyrkanischen *Z. carpinifolia*-Wäldern, und wenn ja, welche möglichen Determinanten sind für sie entscheidend und welche Arten differenzieren sie? (4) Welche Stellung haben die kolchischen *Z. carpinifolia*-Wälder im Kontext der trockenen Laubwaldvegetation Euxinischen Provinz?

Methoden – Vegetationsaufnahmen wurden auf 100 m^2 großen Flächen nach dem Braun-Blanquet-Verfahren in der Colchis, Westgeorgien, erhoben. Für jede Fläche wurden die Deckung (in Prozent) und die Höhe (m) der Vegetationsschichten ermittelt, während die einzelnen Arten auf einer 9-teiligen Skala (Dengler et al. 2008) geschätzt wurden. Darüber hinaus erfassten wir die geografische Position (WGS 84), die Neigung und Exposition des Hangs sowie den pH-Wert des Oberbodens. Wir haben drei relevante Datensätze zusammengestellt. Der Colchis-Datensatz umfasste 35 Flächen aus unseren Feldbeprobungen, die hauptsächlich im Sommer 2022 durchgeführt wurden, um kolchische *Z. carpinifolia*-Wälder zu charakterisieren. Der Zelkova-Datensatz (60 Flächen) enthielt den Colchis-Datensatz, der mit von *Z. carpinifolia* dominierten Flächen aus dem Nordiran (Gholizadeh et al. 2020) zusammengeführt wurde, um kolchische und hyrkanische *Z. carpinifolia*-Bestände zu vergleichen. Der Euxinische Datensatz (140 Flächen) kombinierte den Colchis-Datensatz mit Flächen, die von *Carpinus orientalis*, der häufigsten begleitenden Baumart von *Z. carpinifolia* in der Colchis, dominiert oder mitdominiert wurden, aus der Nordtürkei. Wir führten eine Reihe von unüberwachten Klassifikationen durch, um die Hauptgruppen der Flächen in den Datensätzen zu erkennen und ihre wesentlichen Merkmale und Unterschiede zu bestimmen.

Ergebnisse und Diskussion – Die kolchischen *Z. carpinifolia*-Bestände wiesen eine recht einheitliche Vegetationsstruktur und Artenzusammensetzung auf. Die Baumschicht (mittlere Deckung 78 %, mittlere Höhe 19 m) enthielt häufig *Carpinus orientalis* und *Quercus robur* subsp. *imeretina*. *Z. carpinifolia*, *Crataegus monogyna* und *Carpinus orientalis* waren die häufigsten Bestandteile der Strauchschicht (15 %, 1,8 m). Die Krautschicht (29 %, 0,36 m) wurde regelmäßig von *Ruscus aculeatus* dominiert. Wald-Xeromesophyten und -mesophyten waren häufig (z. B. *Carex muricata* aggr., *Viola* *alba*). Die euxinokaukasischen und euxinokaukasisch-hyrkanischen Florenelemente waren durch Kräuter (z. B. *Klasea quinquefolia*, *Sedum stoloniferum*) und immergrüne Arten (z. B. *Hypericum xylosteifolium*, *Smilax excelsa*) vertreten. Das häufige Auftreten von Sämlingen und jungen Individuen von *Z. carpinifolia* deutet auf eine kontinuierliche generative Vermehrung hin, die jedoch häufig durch das Vieh behindert wird. Der mittlere Artenreichtum pro Fläche lag bei 24,7 Gefäßpflanzenarten. Die kolchischen *Z. carpinifolia*-Wälder waren hinsichtlich der Geomorphologie und die Landnutzung in der Regel mit leicht sauren bis subneutralen Böden (durchschnittlicher pH-Wert 6,2) an spezifischen Standorten in der Landschaft assoziiert. Wir haben sie häufig an den Rändern großer Waldgebiete, an den oberen Rändern von Hochebenen und alten Flussterrassen sowie an Flusstalhängen gefunden. Die Bestände befinden sich in einem warm-gemäßigten Klima (mittlere Jahrestemperatur 14,0 °C, Spanne 13,0–14,5 °C), das reich an Niederschlägen ist (mittlere Jahresniederschlagsmenge 1431 mm, 1191–1681 mm). Die Beweidung mit Kühen ist in den untersuchten Waldbeständen nach wie vor weit verbreitet. Die hyrkanischen und kolchischen *Z. carpinifolia*-Wälder wiesen erhebliche Unterschiede auf. Im Gegensatz zum kolchischen Typus war der hyrkanische Typus mesophil; die häufigsten Begleiter von *Z. carpinifolia* im Kronendach waren *Carpinus betulus*, *Diospyros lotus* und die lokalen Endemiten *Parrotia persica* und *Quercus castaneifolia*, und der Unterwuchs zeigte dasselbe Muster. Die Gründe für diese ökologische Diskrepanz sind nach wie vor unbekannt und bedürfen weiterer Untersuchungen, die sowohl ökologische als auch genetische Aspekte umfassen. Analysen der Position der kolchischen *Z. carpinifolia*-Wälder im Waldvegetationsmosaik der Euxinischen Provinz ergaben, dass sie sich deutlich von den *Carpinus orientalis*-Wäldern in der Nordtürkei unterscheiden und einen festen Cluster mit Vegetationsaufnahmen des *Campanulo alliariifoliae-Carpinetum orientalis* bildeten, die in den Ausläufern des Großen Kaukasus in Westgeorgien beschrieben wurde. Daher haben wir einen neuen Verband *Smilaco excelsae-Carpinion orientalis* beschrieben, der kaukasisch-kolchische trockene Laubwälder vereinigt (s. u.). Im Rahmen der EUNIS-Lebensraumtypologie schlagen wir vor, die kolchischen *Z. carpinifolia*-Bestände wie folgt zu klassifizieren: T – Wald und andere bewaldete Flächen > T1 – Laubwälder > T19 – Temperierte und submediterrane thermophile Laubwälder > T19B – Thermophile Mischwälder. Die Klassifikation auf den unteren Ebenen bedarf weiterer Analysen. Überweidung stellt nach wie vor eine erhebliche Bedrohung für die meisten kolchischen *Z. carpinifolia*-Bestände dar und unterdrückt die Baumverjüngung analog zu einigen anderen mediterranen Wäldern, die einer intensiveren Beweidung ausgesetzt sind (Bergmeier et al. 2010). Gegenwärtig dienen die meisten erfassten Bestände als Rinderweiden unterschiedlicher Intensität, einschließlich der Bestände im Ajameti-Reservat. Die Entwicklung der Infrastruktur einschließlich Straßenbau und invasive gebietsfremde Arten (z. B. *Gleditsia triacanthos*, *Robinia pseudoacaccia*) stellen weitere bedeutende Gefährdungen dar. Allgemeine Erhaltungsmaßnahmen zur Unterstützung von *Z. carpinifolia* wurden von Bétrisey et al. (2018) zusammengefasst. Um die kolchischen Bestände zu erhalten, betonen wir die Verringerung des Weidedrucks und die Kontrolle gebietsfremder Arten, zumindest innerhalb der Reservate.

Syntaxonomisches Schema:

Kl.: *Quercetea pubescentis* Doing-Kraft ex Scamoni et Passarge 1959
- O.: *Quercetalia pubescenti-petraeae* Klika 1933
  - V.: *Smilaco excelsae-Carpinion orientalis* all. nov. hoc loco
    - Ass.: *Smilaco excelsae-Zelkovetum carpinifoliae* ass. nov. hoc loco
    - Ass.: *Campanulo alliariifoliae-Carpinetum orientalis* Novák et al. 2021

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Author contribution statement

P.N. conceived the research idea, led the writing, performed the numerical analyses and prepared the syntaxonomic scheme. P.N., Š.P., D.S., M.V. and V.K. participated in the field research. H.G. provided data from Iran and contributed to the interpretations of the classification analyses. M.V. processed spatial data. All the authors revised the drafts and agreed with the final manuscript for publication.

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Supplements

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. Relevés of the Colchic Dataset.

Anhang E1. Vegetationsaufnahmen des kolchischen Datensatzes.

Supplement E2. Header data of the relevés of the Colchic Dataset (Supplement E1).

Anhang E2. Kopfdaten der Vegetationsaufnahmen des kolchischen Datensatzes (Anhang 1).

Supplement E3 Full frequency table of the diagnostic species in the Zelkova Dataset.

Anhang E3. Vollständige Stetigkeitstabelle der diagnostischen Arten des Zelkova-Datensatzes.

Supplement E4. Full frequency table of the diagnostic species in the Euxinian Dataset.

Anhang E4. Vollständige Stetigkeitstabelle der diagnostischen Arten des euxinischen Datensatzes.

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Supplement E1. Relevés of the Colchic Dataset.

Anhang E1. Vegetationsaufnahmen des Kolchische Datensatzes.

Relevé number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
Tree layer																																			
Zelkova carpinifolia	5	4	4	4	4	4	3	5	4	5	5	3	3	5	4	4	5	4	5	4	4	4	4	5	4	4	4	4	4	4	5	4	5	3	5
Carpinus orientalis	.	2a	.	2a	2a	2a	.	2a	3	1	.	3	.	.	2b	1	.	3	2a	1	.	.	2a	.	.	.	.	2b	2b	2a	.	2b	2b	2b	.
Quercus robur subsp. *imeretina*	.	.	.	2b	2b	2a	3	.	.	.	.	.	.	.	.	.	+	.	.	+	.	.	.	.	1	2a	2b	.	.	+	3	.	2a	2a	.
Robinia pseudoacacia	.	1	.	.	.	.	.	2a	.	.	2a	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Quercus petraea subsp. *iberica*	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2b	.	.	.	.	.	.	1
Sorbus torminalis	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.
Shrub layer																																			
Zelkova carpinifolia	1	2b	1	1	3	1	+	4	1	+	2a	1	+	1	.	1	+	+	1	+	3	+	3	2b	3	2a	1	1	+	.	.	.	.	.	.
Crataegus monogyna	.	+	1	+	.	2a	1	.	.	1	+	.	.	.	.	.	.	.	.	.	.	1	.	.	2a	1	1	1	1	+	.	.	.	.	.
Carpinus orientalis	.	.	.	.	3	.	.	1	.	.	.	+	.	.	.	+	.	.	.	+	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.
Crataegus sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	1	1	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hedera helix	1	+	.	.	.	+	.	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ligustrum vulgare	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	+	+	.	.	.	.	.	.
Smilax excelsa	.	.	.	+	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	+	.	.	.	.	.	.	.
Crataegus pentagyna	.	.	+	.	.	.	.	.	+	.	.	1	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Crataegus germanica	.	+	.	.	.	.	.	.	.	+	.	.	.	.	.	2a	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
Robinia pseudoacacia	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.
Rosa sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Herb layer																																			
Ruscus aculeatus	2a	3	3	2a	1	2b	2a	1	1	+	2b	2b	3	2a	2a	2a	2a	1	2a	1	3	4	3	1	3	.	3	+	1	+	1	1	1	1	1
Carex muricata agg.	1	+	+	+	+	1	+	+	.	+	+	1	+	1	1	1	+	1	1	2a	2a	1	2a	+	2a	+	.	+	1	+	1	1	1	+	+
Hedera helix	+	+	+	+	+	+	+	2a	2a	+	+	1	1	.	+	+	+	+	r	+	.	+	+	1	.	1	+	+	+	+	+	+	+	+	+
Viola alba	1	+	+	+	.	+	+	r	+	1	+	1	+	r	+	+	+	+	+	+	.	2a	+	.	1	+	+	.	+	+	+	+	+	+	.
Viola reichenbachiana	.	+	.	+	.	+	+	.	+	+	r	.	+	.	+	+	+	1	+	+	+	+	+	.	+	.	.	2a	.	1	+	.	1	+	2a
Brachypodium sylvaticum	+	+	+	.	+	+	+	+	+	+	+	+	r	.	r	.	.	.	1	1	1	1	.	.	+	.	1	.	1	+	.	+	+	+	.
Veronica peduncularis	+	+	+	.	+	.	+	+	+	+	.	+	.	1	.	+	+	+	+	1	.	.	.	.	+	.	+	+	+	+	.	+	+	+	.
Vinca major subsp. *hirsuta*	+	1	.	.	1	+	.	.	+	+	+	+	r	+	+	.	.	+	+	+	1	+	.	.	1	.	.	1	+	+	.	.	+	r	1
Smilax excelsa	.	.	r	+	.	+	+	.	+	.	.	.	+	+	.	+	+	+	.	+	.	1	r	.	.	+	.	.	+	+	+	.	+	+	.
Poa trivialis	.	.	+	.	+	.	1	+	.	.	r	+	.	r	.	.	+	+	.	.	.	.	.	.	+	.	+	.	.	1	1	1	+	.	1
Carex sylvatica	.	.	.	.	.	+	.	.	+	1	.	.	1	.	+	+	2a	+	.	.	+	.	+	.	.	.	.	1	.	+	+	+	.	+	.
Primula acaulis subsp. *rubra*	r	+	.	.	+	+	+	.	1	.	r	.	+	.	.	.	.	.	+	.	+	.	.	.	.	.	+	+	+	.	.	.	.	+	.
Prunella vulgaris	.	.	.	.	.	+	+	.	+	+	.	.	.	.	+	+	.	+	.	.	.	.	+	.	+	.	.	1	+	2b	+	+	.	.	.
Geum urbanum	.	+	+	.	.	.	.	.	.	r	+	.	.	.	+	r	r	.	.	.	+	1	+	.	1	.	.	.	.	.	.	.	+	.	+
Hypericum xylosteifolium	.	+	.	1	1	+	.	+	.	+	.	.	+	+	+	+	.	.	.	+	.	.	+	.	.	.	.	.	.	.	.	.	.	r	.
Lapsana communis	.	r	.	.	.	+	r	.	+	+	.	.	.	.	r	.	.	+	r	.	.	.	.	.	.	+	.	+	.	+	+	.	.	.	.
Asplenium adiantum-nigrum	r	+	+	.	+	.	+	+	.	.	.	r	.	+	.	r	.	.	.	+	.	.	.	1	.	.	.	.	.	.	.	.	.	+	.
Carex flacca subsp. *serrulata*	.	.	.	r	.	.	+	+	2b	1	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	+	+	2b	1	3	.	.	.	.	+
Ajuga reptans	.	.	.	.	.	+	.	.	.	+	.	.	+	.	.	+	+	+	.	.	.	.	+	+	.	.	.	.	+	.	+	.	.	.	+
Lathyrus laxiflorus	.	.	.	r	.	+	+	.	.	r	.	.	.	.	.	.	.	.	.	r	.	.	.	.	+	.	+	.	+	.	.	+	+	+	.
Campanula rapunculoides	1	+	+	.	+	.	.	r	1	r	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.
Oenanthe pimpinelloides	.	.	+	.	.	+	+	.	.	.	.	.	.	.	.	+	r	+	+	.	.	.	.	.	.	.	.	.	r	.	+	.	.	.	+
Rubus subgen. *Rubus*	.	.	.	+	.	.	.	.	.	.	.	.	r	.	.	2m	r	.	.	+	+	.	.	+	.	+	.	.	+	.	.	.	.	.	.
Sedum stoloniferum	.	.	.	.	+	.	.	.	.	+	.	.	.	1	+	.	.	+	.	.	.	.	.	+	.	.	.	+	.	.	.	+	.	.	.
Agrostis capillaris	.	.	.	.	.	.	+	.	.	+	.	.	.	.	.	+	.	.	.	.	+	.	.	.	.	.	+	.	+	1	1	.	.	.	.
Klasea quinquefolia	.	.	.	.	+	.	.	.	+	.	.	.	.	.	r	.	.	.	r	.	.	.	.	.	.	.	.	.	r	.	.	.	.	r	.
Festuca drymeja	.	.	.	.	+	+	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+
Hypericum perforatum	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	r	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	+	.	.	+
Fragaria vesca	.	.	.	.	.	r	.	.	.	.	.	r	.	+	.	.	.	.	.	.	1	.	.	.	.	.	+	.	+	.	.	.	.	.	.
Lamium album	1	r	+	.	.	.	.	.	.	.	.	+	.	.	r	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.
Sanicula europaea	.	.	.	.	.	+	.	.	1	.	.	.	+	.	r	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.
Asplenium trichomanes	+	.	.	.	+	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	1	.	.	.	.	+	.	.	.	.	+	.
Allium saxatile	.	.	.	.	.	.	.	.	.	+	.	.	.	r	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.
Silene italica	.	r	.	.	.	.	.	.	.	.	.	+	.	r	.	.	.	.	+	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Helleborus orientalis	.	.	1	.	.	2a	.	.	.	+	.	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lonicera caprifolium	.	.	.	+	.	+	+	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.
Clinopodium umbrosum	.	.	.	.	.	+	.	.	+	.	.	.	.	.	+	.	.	+	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.
Leontodon hispidus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	r	+	+	.	.	.	.	.
Veronica serpyllifolia	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	+	.	.	.	+	.	.	.
Rumex obtusifolius subsp. *silvestris*	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	r	.	.
Symphytum grandiflorum	.	.	.	.	.	+	.	.	1	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.
Torilis japonica	.	.	.	.	.	.	.	.	.	.	.	+	.	.	r	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	+	.
Euphorbia sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	+	.	r	.	.	.	.	.	.	r	.
Campanula alliariifolia	.	.	+	.	.	.	.	.	+	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Clinopodium vulgare	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.
Jacobaea vulgaris	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	r	.	r	.	.	.	.
Vicia sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	r	.	.	.	.	.	.	r	.	.	.	.	.
Plantago major	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.	.
Catapodium rigidum	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	+	.
Dioscorea communis	+	.	.	r	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Trifolium pratense	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.
Oplismenus hirtellus subsp. *undulatifolius*	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	r	.	.
Poa nemoralis	.	.	.	.	+	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.
Glechoma hederacea	.	.	.	.	.	1	.	.	.	.	.	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Potentilla micrantha	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	+	.
Convallaria majalis	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.
Galium aparine	+	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.
Polystichum setiferum	.	r	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rumex sanguineus	.	.	.	.	.	.	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Hieracium sabaudum	.	.	.	.	.	.	r	.	r	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Stachys officinalis	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.
Carex sp.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2a	.	.	.	.	.	.	.	.	.	.
Daucus carota	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	r	.	.	.	.	.	.
Carex michelii	.	.	.	+	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Plantago lanceolata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.
Pteridium aquilinum	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.
Cyclamen coum	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sedum pallidum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.
Orobanche laxissima	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.
Seseli peucedanoides	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

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Fortsetzung auf nächsten Seite

Relevé number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
Phleum pratense	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.
Veronica sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	+	.	.	.	.
Veronica officinalis	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.
Drymochloa drymeja	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	r	.
Hieracium sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.
Hedera colchica	.	.	.	.	1	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Galium album	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.
Festuca sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	1
Taraxacum sect. *Taraxacum*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	r	.	.	.
Tanacetum partheniifolium	.	.	.	.	.	.	.	.	+	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Juveniles																																			
Zelkova carpinifolia	1	+	1	1	1	1	1	2a	1	1	+	+	+	1	1	.	+	+	2b	1	.	+	.	3	.	2a	.	.	2a	1	1	1	1	+	1
Crataegus sp.	r	.	.	.	+	.	.	r	.	.	.	.	+	.	+	.	+	r	+	+	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.
Quercus robur subsp. *imeretina*	.	.	.	+	+	.	r	.	.	.	.	.	.	.	.	.	+	+	.	+	.	.	.	.	.	+	.	.	.	.	.	.	r	+	.
Ligustrum vulgare	.	.	.	+	.	.	+	.	+	.	.	.	.	.	.	.	r	r	.	r	.	+	.	.	.	.	.	.	+	.	.	.	.	r	.
Fraxinus excelsior	.	.	+	+	+	r	.	.	.	r	.	.	+	.	+	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.
Gleditsia triacanthos	.	.	.	.	.	+	.	.	.	r	.	.	.	.	.	r	.	.	.	.	.	.	.	.	r	.	.	+	.	.	.	r	+	.	+
Crataegus monogyna	.	.	.	+	.	+	+	.	.	+	r	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.	1	.	.	.	.	.
Carpinus orientalis	.	.	.	r	+	r	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	1	.	.	.	+	+	.
Acer campestre	.	.	.	.	r	r	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+	.	.	.	+	+	.
Quercus petraea subsp. *iberica*	.	.	.	.	.	.	.	+	.	r	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.
Citrus trifoliata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	r	.	.
Euonymus europaea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	r	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.
Rosa sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	+	.	.	.
Robinia pseudoacacia	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.
Laurus nobilis	.	.	r	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Records with a single occurence:

Tree layer: *Acer campestre* (34, 2b); *Carpinus betulus* (13, 3); *Fraxinus excelsior* (22, +); *Hedera helix* (25, 1); *Pyrus communis* subsp. *caucasica* (16, 2a); *Ulmus minor* (5, +)

Shrub layer: *Carpinus betulus* (13, +); *Citrus trifoliata* (11, +); *Cornus mas* (6, +); *C . sanguinea* (22, +); *Ficus carica* (5, +); *Fraxinus excelsior* (5, +); *Hypericum xylosteifolium* (5, 1); *Laurus nobilis* (8, 1); *Ligustrum japonicum* (8, 1); *Prunus avium* (4, +); *Rhododendron luteum* (26, 2b); *Sorbus torminalis* (16, +)

Herb layer: *Aegonychon purpurocaeruleum* (29, r); *Agrimonia eupatoria* (29, r); *Argyrolobium biebersteinii* (20, r); *Arum* sp. (1, +); *Bromus* sp. (30, +); *Calystegia sylvatica* (1, +); *Centaurium erythraea* (30, +); *Clematis vitalba* (22, +); *Clinopodium grandiflorum* (25, +); *Dactylis glomerata* (20, r); *Deschampsia cespitosa* (35, +); *Dianthus* sp. (20, r); *Doronicum orientale* (1, +); *Elymus caninus* (6, +); *Festuca rubra* (30, +); *Galium palustre* (31, +); *Geranium pusillum* (1, +); *G . Robertianum* (1, +); *Heracleum sphondylium* subsp. *cyclocarpum* (1, +); *Hieracium umbellatum* (30, +); *Inula conyzae* (8, +); *Juncus effusus* (16, +); *Juncus tenuis* (16, +); *Kickxia elatine* (16, r); *Lathyrus pratensis* (12, +); *L. rotundifolius* (35, +); *L.* sp. (28, +), *L. vernus* (4, +); *Leucanthemum vulgare* (29, +); *Limodorum abortivum* (20, r); *Lolium perenne* (29, +); *Medicago lupulina* (29, +); *M .* sp. (34, r); *Muscari* sp. (32, r); *Petrorhagia saxifraga* (30, +); *Peucedanum caucasicum* (9, +); *Phleum* sp. (30, +); *Pimpinella tripartita* (5, +); *Poa angustifolia* (1, 1); *P. compressa* (28, 1); *P .* sp. (2, +); *Polygonatum glaberrimum* (4, r); *Polygonum aviculare* (25, r); *Polypodium cambricum* (5, r); *Pulmonaria dacica* (9, +); *Ranunculus* sp. (1, 1); *Rubus sanctus* (23, +); *Ruscus colchicus* (9, +); *Sambucus ebulus* (24, +); *Satureja spicigera* (14, +); *Securigera varia* (29, +); *Schedonorus giganteus* (10, +); *Silene balansae* (1, 1); *Smyrnium perfoliatum* (25, +); *Solidago* sp. (30, +); *Trifolium medium* (30, +); *Veronica chamaedrys* (15, r); *Veronica magna* (33, +); *Vicia tetrasperma* (32, +); *Vincetoxicum* sp. (7, r)

Juveniles: *Acer* sp. (15, +); *Carpinus betulus* (1, r); *Crataegus pentagyna* (9, +); *Juglans regia* (15, +); *Ligustrum japonicum* (8, +); *Prunus avium* (4, r); *P. cerasifera* (7, +); *Pyrus communis* subsp. *caucasica* (23, r); *Rhododendron luteum* (16, +); *Sorbus torminalis* (16, r)

Supplement E2. Header data of the relevés of the Colchic Dataset (Supplement E1).

Anhang E2. Kopfdaten der Vegetationsaufnahmen des Kolchischen Datensatzes. (Anhang E1).

#	Locality	N (°)	E (°)	Area (m^2)	Elevation (m a. s. l.)	Slope (°)	Aspect (°)	Cover (%)				Average height (m)			Soil pH	Date
								E_3	E_2	E_1	E_0	E_3	E2	E1		
1	Shorapani (distr. Zestaponi)	42.097167	43.083278	100	190	50	315	80	4	30	8	15	1,5	0.4	7.83	14.05.2019
2	Vani (distr. Vani)	42.083333	42.567667	100	110	40	80	75	20	35	3	14	2	0.4	6.29	27.08.2022
3	Vartsikhe (distr. Baghdati)	42.151000	42.714111	100	100	50	275	75	5	30	3	18	2	0.4	7.11	27.08.2022
4	Rokiti (distr. Baghdati)	42.111556	42.778556	100	180	2	90	80	2	20	1	22	1	0.35	5.33	27.08.2022
5	Baghdati (distr. Baghdati)	42.045444	42.826500	100	240	60	250	75	55	25	4	22	3,5	0.25	6.2	28.08.2022
6	Vartsikhe (distr. Baghdati)	42.150278	42.755278	100	130	0	-	60	10	45	1	30	3,5	0.3	5.35	28.08.2022
7	Sviri (distr. Zestaponi)	42.137389	42.903889	100	180	0	-	75	2	20	2	22	1,2	0.3	5.47	28.08.2022
8	Rionhesi (distr. Kutaisi)	42.199056	42.710778	100	120	65	190	85	70	15	4	20	2	0.25	7.75	29.08.2022
9	Sataplia (distr. Kutaisi)	42.309833	42.675167	100	430	15	175	80	3	55	4	15	3	0.3	6.33	29.08.2022
10	Kutaisi (distr. Kutaisi)	42.246389	42.760389	100	180	5	110	80	2	15	4	16	1,3	0.2	6.12	30.08.2022
11	Dikhashkho (distr. Vani)	42.083000	42.567556	100	120	15	110	85	15	20	5	17	1,5	0.5	6.33	27.08.2022
12	Vartsikhe (distr. Baghdati)	42.152278	42.716778	100	100	10	70	85	4	35	5	15	2	0.35	6.68	27.08.2022
13	Rokiti (distr. Baghdati)	42.112778	42.778611	100	160	3	360	90	2	40	5	20	1,5	0.5	5.49	27.08.2022
14	Baghdati (distr. Baghdati)	42.046167	42.826222	100	230	40	250	75	45	30	3	18	1,5	0.4	7.03	28.08.2022
15	Vartsikhe (distr. Baghdati)	42.148833	42.755500	100	120	1	360	80	1	30	2	25	2,5	0.4	5.71	28.08.2022
16	Tskhentaro (distr. Zestaponi)	42.147167	42.857333	100	160	0	-	70	20	25	8	15	2,2	0.4	5.18	28.08.2022
17	Sviri (distr. Zestaponi)	42.145833	42.902056	100	170	0	-	90	5	30	10	25	1,5	0.4	5.52	28.08.2022
18	Kutaisi (distr. Kutaisi)	42.257556	42.750611	100	280	8	210	90	1	20	3	10	1,5	0.3	5.9	28.08.2022
19	Rionhesi (distr. Kutaisi)	42.221278	42.715000	100	140	45	130	80	5	40	3	15	1,5	0.4	5.92	29.08.2022
20	Kutaisi (distr. Kutaisi)	42.246444	42.761444	100	180	12	215	70	2	25	10	17	1,7	0.4	6.22	30.08.2022
21	Dikhashkho (distr. Vani)	42.083000	42.567222	100	120	10	90	70	40	30	1	14	1,2	0.6	6.52	27.08.2022
22	Vartsikhe (distr. Baghdati)	42.152444	42.715389	100	100	10	70	70	2	80	-	17	3	0.5	6.63	27.08.2022
23	Rokiti (distr. Baghdati)	42.113556	42.779444	100	150	0	-	70	40	30	5	20	2	0.7	5.37	27.08.2022
24	Baghdati (distr. Baghdati)	42.046500	42.825611	100	220	35	225	90	20	30	8	15	1	0.3	6.87	28.08.2022
25	Vartsikhe (distr. Baghdati)	42.147889	42.754000	100	120	1	360	60	30	50	1	25	0.7	0.0	6.17	28.08.2022
26	Tskhentaro (distr. Zestaponi)	42..1442.22	42.858778	100	170	0	-	90	15	10	1	15	1,6	0.4	5.47	28.08.2022
27	Sviri (distr. Zestaponi)	42.145556	42.901611	100	170	0	-	90	10	5	1	25	4	0.4	6.67	28.08.2022
28	Kutaisi (distr. Kutaisi)	42.257667	42.753278	100	280	7	158	70	5	40	2	20	1,5	0.3	6.17	28.08.2022
29	Broliskedi (distr. Terjola)	42.227056	42.788944	100	140	7	90	70	4	30	6	15	1	0.25	6.6	29.08.2022
30	Kutaisi (distr. Kutaisi)	42.255278	42.771667	100	250	10	180	70	1	40	20	15	1	0.15	6.41	30.08.2022
31	Tskhentaro (distr. Zestaponi)	42.148000	42.857000	100	160	0	-	85	-	15	5	25	-	0.2	5.34	28.08.2022
32	Kutaisi (distr. Kutaisi)	42.258111	42.748889	100	270	25	215	60	-	15	2	15	-	0.25	5.85	28.08.2022
33	Rionhesi (distr. Kutaisi)	42.222111	42.715944	100	150	0	-	90	-	15	1	23	-	0.2	5.96	29.08.2022
34	Broliskedi (distr. Terjola)	42.226333	42.789944	100	140	7	360	90	-	15	7	25	-	0.3	6.74	29.08.2022
35	Rionhesi (distr. Kutaisi)	42.220722	42.714944	100	150	0	-	70	-	30	1	25	-	0.5	5.61	29.08.2022

Supplement E3. Full frequency table of the diagnostic species in the Zelkova Dataset. Species frequencies are provided. Highly diagnostic (*phi* ≥ 0.5, grey-shaded, in bold) and diagnostic species (*phi* ≥ 0.25, grey-shaded) of the clusters are sorted by decreasing *phi*. Species with non-significant phi values (*P* = 0.05) were excluded based on Fisher's exact test. Other species sorted by decreasing frequency are given at the bottom the table.

Anhang E3. Vollständige Stetigkeitstabelle der diagnostischen Arten des Zelkova-Datensatzes. Angegeben sind die prozentualen Frequenzen. Hoch diagnostische (*phi* ≥ 0.5, grau schattiert, in Fettdruck) und diagnostische Arten (*phi* ≥ 0.25, grau schattiert) der Cluster sind nach abnehmendem phi-Wert sortiert. Arten mit nicht signifikanten *phi*-Werten (*P* = 0.05) wurden basierend auf Fisher's exaktem Test ausgeschlossen. Die übrigen Arten sind nach abnehmener Frequenz sortiert am Ende der Tabelle zu finden.

Cluster number	1	2	3
Number of relevés	35	18	7
Ruscus aculeatus	**97**	.	.
Hedera helix	**94**	.	.
Viola reichenbachiana	**69**	.	.
Vinca major subsp. *hirsuta*	**66**	.	.
Veronica peduncularis	**66**	.	.
Viola alba	**86**	22	.
Smilax excelsa	**60**	11	.
Poa trivialis	**46**	.	.
Primula acaulis	**40**	.	.
Quercus robur subsp. *imeretina*	**40**	.	.
Prunella vulgaris	**40**	.	.
Hypericum xylosteifolium	**37**	.	.
Ligustrum vulgare	**34**	.	.
Lapsana communis	**34**	.	.
Carex flacca subsp. *serrulata*	**34**	.	.
Ajuga reptans	31	.	.
Carpinus orientalis	57	11	14
Campanula rapunculoides	29	.	.
Oenanthe pimpinelloides	29	.	.
Crataegus monogyna	43	.	14
Sedum stoloniferum	23	.	.
Robinia pseudoacacia	23	.	.
Agrostis capillaris	23	.	.
Gleditsia triacanthos	23	.	.
Carex muricata aggr.	94	39	71
Quercus petraea subsp. *iberica*	20	.	.
Acer campestre	20	.	.
Lathyrus laxiflorus	31	11	.
Fragaria vesca	17	.	.
Hypericum perforatum	17	.	.
Asplenium trichomanes	17	.	.
Crataegus microphylla	.	**61**	.
Viola caspia	.	50	14
Acer cappadocicum	.	50	14
Viola sintenisii	.	28	.
Alliaria petiolata	.	22	.
Viscum album	.	22	.
Vincetoxicum scandens	.	17	.
Buxus sempervirens subsp. *hyrcana*	.	17	.
Carpesium cernuum	.	17	.
Prunus cerasifera	3	33	14
Ruscus hyrcanus	.	28	14
Viola odorata	.	.	**86**
Euphorbia amygdaloides	.	17	**86**
Danae racemosa	.	.	**57**
Poa masenderana	.	.	**57**
Oplismenus hirtellus subsp. *undulatifolius*	9	17	**71**
Hypericum androsaemum	.	11	**57**
Galium odoratum	.	.	**43**
Vicia crocea	.	6	**43**
Circaea lutetiana	.	6	**43**
Crataegus ambigua	.	.	29
Scutellaria tournefortii	.	11	43
Hedera pastuchovii	.	11	43
Clinopodium umbrosum	14	17	57
Dactylis glomerata	3	.	29
Carpinus betulus	6	50	71
Ulmus glabra	.	6	29
Primula heterochroma	.	22	43
Diospyros lotus	.	22	43
Quercus castaneifolia	.	83	86
Parrotia persica	.	61	71
Acer velutinum	.	50	57

Cluster number	1	2	3
Number of relevés	35	18	7
Other species			
Zelkova carpinifolia	100	100	100
Brachypodium sylvaticum	69	39	57
Carex sylvatica	43	39	71
Geum urbanum	37	11	43
Asplenium adiantum-nigrum	34	28	.
Lamium album	17	33	.
Sanicula europaea	17	17	43
Fraxinus excelsior	26	11	14
Poa nemoralis	9	28	43
Crataegus germanica	11	22	14
Klasea quinquefolia	17	11	.
Drymochloa drymeja	17	.	14
Crataegus pentagyna	11	17	.
Dioscorea communis	9	17	.
Lonicera caprifolium	14	.	.
Rubus subgen. *Rubus*	9	11	.
Silene italica	14	.	.
Allium saxatile	14	.	.
Ficus carica	9	11	.
Helleborus orientalis	14	.	.
Torilis japonica	11	6	.
Clinopodium vulgare	11	.	14
Cyclamen coum	6	11	.
Trifolium pratense	9	.	14
Rumex sanguineus	9	6	.
Veronica serpyllifolia	11	.	.
Sorbus torminalis	9	6	.
Rumex obtusifolius subsp. *silvestris*	11	.	.
Campanula alliariifolia	11	.	.
Citrus trifoliata	11	.	.
Symphytum grandiflorum	11	.	.
Cornus sanguinea	3	11	14
Leontodon hispidus	11	.	.
Tilia begoniifolia	.	11	29
Galium aparine	9	.	.
Euonymus europaea	9	.	.
Jacobaea vulgaris	9	.	.
Hieracium sabaudum	9	.	.
Convallaria majalis	9	.	.
Polystichum setiferum	9	.	.
Potentilla micrantha	9	.	.
Glechoma hederacea	9	.	.
Catapodium rigidum	9	.	.
Plantago major	9	.	.
Cephalanthera longifolia	.	11	14
Calystegia silvatica	3	6	.
Phleum pratense	6	.	.
Stachys officinalis	6	.	.
Rhododendron luteum	6	.	.
Pteridium aquilinum	6	.	.
Veronica officinalis	6	.	.
Pyrus communis	6	.	.
Tanacetum partheniifolium	6	.	.
Sambucus ebulus	3	6	.
Hedera colchica	6	.	.
Prunus avium	3	6	.
Carex michelii	6	.	.
Orobanche laxissima	6	.	.
Laurus nobilis	6	.	.
Taraxacum sect. *Taraxacum*	6	.	.
Sedum pallidum	6	.	.
Galium album	6	.	.
Daucus carota	6	.	.
Seseli peucedanoides	6	.	.
Plantago lanceolata	6	.	.
Celtis australis	.	11	.
Vitis sylvestris	.	11	.
Stellaria media	.	11	.
Fagus orientalis	.	11	.
Erigeron bonariensis	.	11	.
Gleditsia caspia	.	11	.
Galanthus transcaucasicus	.	11	.
Albizia julibrissin	.	11	.
Centaurea hyrcanica	.	6	14
Allium paradoxum	.	11	.
Asplenium scolopendrium	.	6	14
Poa angustifolia	3	.	.
Silene balansae	3	.	.
Doronicum orientale	3	.	.
Heracleum sphondylium subsp. *cyclocarpum*	3	.	.
Geranium robertianum	3	.	.
Geranium pusillum	3	.	.

Cluster number	1	2	3
Number of relevés	35	18	7
Galium palustre	3	.	.
Juncus effusus	3	.	.
Juncus tenuis	3	.	.
Kickxia elatine	3	.	.
Satureja spicigera	3	.	.
Ulmus minor	3	.	.
Pimpinella tripartita	3	.	.
Polypodium cambricum	3	.	.
Lathyrus vernus	3	.	.
Polygonatum glaberrimum	3	.	.
Rubus sanctus	3	.	.
Clinopodium grandiflorum	3	.	.
Smyrnium perfoliatum	3	.	.
Polygonum aviculare	3	.	.
Juglans regia	3	.	.
Veronica chamaedrys	3	.	.
Lathyrus pratensis	3	.	.
Cornus mas	3	.	.
Elymus caninus	3	.	.
Clematis vitalba	3	.	.
Ligustrum japonicum	3	.	.
Inula conyzae	3	.	.
Leucanthemum vulgare	3	.	.
Medicago lupulina	3	.	.
Lolium perenne	3	.	.
Securigera varia	3	.	.
Aegonychon purpurocaeruleum	3	.	.
Agrimonia eupatoria	3	.	.
Veronica magna	3	.	.
Lathyrus rotundifolius	3	.	.
Deschampsia cespitosa	3	.	.
Schedonorus giganteus	3	.	.
Limodorum abortivum	3	.	.
Argyrolobium biebersteinii	3	.	.
Vicia tetrasperma	3	.	.
Hieracium umbellatum	3	.	.
Centaurium erythraea	3	.	.
Trifolium medium	3	.	.
Festuca rubra	3	.	.
Petrorhagia saxifraga	3	.	.
Poa compressa	3	.	.
Peucedanum caucasicum	3	.	.
Pulmonaria dacica	3	.	.
Ruscus colchicus	3	.	.
Euonymus velutinus	.	6	.
Hesperis hyrcana	.	6	.
Tanacetum parthenium	.	6	.
Stellaria holostea	.	6	.
Sonchus oleraceus	.	6	.
Torilis arvensis	.	6	.
Achnatherum bromoides	.	6	.
Microstegium vimineum	.	6	.
Persicaria hydropiper	.	6	.
Pteris cretica	.	6	.
Periploca graeca	.	6	.
Hieracium prenanthoides	.	6	.
Polystichum aculeatum	.	6	.
Teucrium hyrcanicum	.	6	.
Arum maculatum	.	6	.
Epimedium pinnatum	.	6	.
Laser trilobum	.	6	.
Digitalis nervosa	.	6	.
Polypodium vulgare	.	6	.
Artemisia annua	.	6	.
Rubus caesius	.	6	.
Chelidonium majus	.	6	.
Paliurus spina-christi	.	.	14
Pyrus boissieriana	.	.	14
Juniperus sabina	.	.	14
Cotoneaster nummularius	.	.	14
Lonicera floribunda	.	.	14
Melica uniflora	.	.	14
Allium lenkoranicum	.	.	14
Acer ibericum	.	.	14
Rhamnus cathartica	.	.	14
Populus caspica	.	.	14
Eupatorium cannabinum	.	.	14
Chenopodium album	.	.	14
Artemisia campestris	.	.	14
Fallopia convolvulus	.	.	14
Alnus glutinosa subsp. *barbata*	.	.	14
Oxalis corniculata	.	.	14
Medicago sativa	.	.	14
Bromopsis tomentella	.	.	14

Supplement E4. Full frequency table of the diagnostic species in the Euxinian Dataset. Species frequencies are provided. Highly diagnostic (*phi* ≥ 0.5, grey-shaded, in bold) and diagnostic species (*phi* ≥ 0.25, grey-shaded) of the clusters are sorted by decreasing *phi*. Species with non-significant *phi* values (*P* = 0.05) were excluded based on Fisher's exact test. Other species sorted by decreasing frequency are given at the bottom the table.

Anhang E1. Vollständige Stetigkeitstabelle der diagnostischen Arten des euxinischen Datensatzes. Angegeben sind die prozentualen Frequenzen. Hoch diagnostische (*phi* ≥ 0.5, grau schattiert, in Fettdruck) und diagnostische Arten (*phi* ≥ 0.25, grau schattiert) der Cluster sind nach abnehmendem phi-Wert sortiert. Arten mit nicht signifikanten *phi*-Werten (*P* = 0.05) wurden basierend auf Fisher's exaktem Test ausgeschlossen. Die übrigen Arten sind nach abnehmener Frequenz sortiert am Ende der Tabelle zu finden.

Cluster number	1	2	3	4	5	6
Number of relevés	21	34	38	17	20	10
Klasea quinquefolia	**76**	15	.	.	.	.
Carex digitata	**57**	.	.	.	.	.
Campanula alliariifolia	**81**	9	21	.	.	.
Clinopodium umbrosum	**57**	12	.	.	.	.
Oplismenus hirtellus subsp. *undulatifolius*	**57**	9	5	.	.	.
Diospyros lotus	**38**	.	.	.	.	.
Sanicula europaea	**62**	15	32	.	.	.
Asplenium scolopendrium	**29**	.	.	.	.	.
Smilax excelsa	95	59	61	.	30	.
Primula acaulis	86	38	32	12	15	20
Hieracium sabaudum	33	6	.	.	.	.
Potentilla micrantha	57	9	32	6	.	.
Lathyrus vernus	29	3	.	.	.	.
Symphytum grandiflorum	33	9	.	.	.	.
Carpesium cernuum	24	.	.	.	.	.
Digitalis schischkinii	24	.	.	.	.	.
Asplenium trichomanes	48	18	.	18	.	.
Campanula rapunculoides	62	26	3	29	15	.
Carex michelii	24	3	.	.	.	.
Peucedanum caucasicum	19	.	.	.	.	.
Ulmus glabra	19	.	.	.	.	.
Euphorbia macroceras	19	.	.	.	.	.
Ruscus colchicus	19	.	.	.	.	.
Brachypodium sylvaticum	90	68	32	12	15	60
Buxus sempervirens	24	.	8	.	.	.
Schedonorus giganteus	19	3	.	.	.	.
Calystegia silvatica	19	3	.	.	.	.
Silene balansae	19	3	.	.	.	.
Taxus baccata	14	.	.	.	.	.
Epimedium pinnatum subsp. *colchicum*	14	.	.	.	.	.
Pimpinella saxifraga	14	.	.	.	.	.
Lamium galeobdolon	14	.	.	.	.	.
Staphylea colchica	14	.	.	.	.	.
Peucedanum adae	14	.	.	.	.	.
Trifolium repens	14	.	.	.	.	.
Cornus sanguinea	33	3	21	.	5	.
Ficus carica	33	9	11	.	10	.
Leontodon hispidus	33	12	.	18	.	.
Plantago lanceolata	19	6	.	.	.	.
Prunus avium	19	3	5	.	.	.
Hedera colchica	24	3	13	.	.	.
Medicago lupulina	14	3	.	.	.	.
Poa angustifolia	14	3	.	.	.	.
Asplenium adiantum-nigrum	52	35	39	.	20	.
Pulmonaria dacica	10	.	.	.	.	.
Philadelphus coronarius	10	.	.	.	.	.
Euphorbia squamosa	10	.	.	.	.	.
Cephalanthera longifolia	10	.	.	.	.	.
Arabis nordmanniana	10	.	.	.	.	.
Paeonia caucasica	10	.	.	.	.	.
Sesleria alba	10	.	.	.	.	.
Cruciata glabra	10	.	.	.	.	.
Euonymus latifolius	10	.	.	.	.	.
Prunella ×intermedia	10	.	.	.	.	.
Galium valantioides	10	.	.	.	.	.
Solidago virgaurea	10	.	.	.	.	.
Potentilla indica	10	.	.	.	.	.
Hypericum androsaemum	10	.	.	.	.	.
Periploca graeca	10	.	.	.	.	.
Brunnera macrophylla	10	.	.	.	.	.
Origanum vulgare	14	.	.	.	5	.
Salvia glutinosa	14	.	5	.	.	.
Zelkova carpinifolia	19	**100**	.	.	.	.
Carex muricata aggr.	43	**97**	.	12	.	.
Poa trivialis	.	**47**	.	.	.	.
Quercus robur	.	**41**	.	.	.	.
Viola reichenbachiana	38	**68**	.	.	.	.
Hypericum xylosteifolium	.	38	11	.	.	.
Agrostis capillaris	.	24	.	.	.	.
Gleditsia triacanthos	5	24	.	.	.	.
Lamium album	.	18	.	.	.	.
Ruscus aculeatus	76	97	61	29	80	.
Allium saxatile	.	15	.	.	.	.
Carex flacca subsp. *serrulata*	24	32	.	.	.	.
Ajuga reptans	19	32	.	.	5	.
Rumex obtusifolius subsp. *silvestris*	.	12	.	.	.	.
Citrus trifoliata	.	12	.	.	.	.
Sedum stoloniferum	19	24	.	.	.	.
Robinia pseudoacacia	19	24	.	.	.	.
Fraxinus excelsior	24	26	3	.	.	.
Polystichum setiferum	.	9	.	.	.	.
Potentilla reptans	.	.	.	.	.	**80**
Festuca jeanpertii	.	.	.	.	.	**60**
Agrimonia eupatoria	.	3	.	.	.	**60**
Quercus hartwissiana	5	.	11	.	.	**60**
Euphorbia amygdaloides	5	.	5	.	40	**80**
Stellaria holostea	.	.	21	35	.	**80**
Rostraria cristata	.	.	.	.	.	**40**
Chaerophyllum nodosum	.	.	.	.	.	**40**
Arum maculatum	.	.	.	.	.	**40**
Corylus avellana	19	.	18	6	.	**60**
Galium aparine	.	9	.	12	.	40
Rosa canina	5	.	.	18	.	40
Acer campestre	52	21	13	.	40	80
Neottia nidus-avis	.	.	.	.	.	20
Torilis arvensis	.	.	.	.	.	20
Vicia tenuifolia subsp. *dalmatica*	.	.	.	.	.	20
Cynosurus echinatus	.	.	.	.	.	20
Carlina corymbosa	.	.	.	.	.	20
Piptatherum coerulescens	.	.	.	.	.	20
Geranium dissectum	.	.	.	.	.	20
Tilia tomentosa	.	.	.	.	.	20
Hypericum perforatum	5	18	.	.	15	40
Lactuca muralis	5	.	.	.	.	20
Dactylis glomerata	5	3	11	18	15	40
Veronica chamaedrys	.	3	.	6	5	20
Species diagnostic for more clusters						
Vinca major subsp. *hirsuta*	**90**	65	.	.	.	.
Viola alba	**86**	**85**	.	.	.	.
Dioscorea communis	57	9	39	12	.	.
Quercus petraea	62	21	55	.	5	.
Carex sylvatica	48	41	5	.	.	.
Veronica peduncularis	52	**65**	.	.	.	.
Drymochloa drymeja	48	18	50	.	.	.
Hedera helix	90	94	61	35	65	.
Prunella vulgaris	33	38	.	.	10	.
Lathyrus laxiflorus	67	32	58	82	.	20
Daphne pontica	.	.	45	.	35	.
Brachypodium pinnatum	5	.	47	47	.	.
Asyneuma rigidum	.	.	37	47	.	.
Viola sieheana	.	.	53	29	20	80
Crataegus monogyna	.	44	3	.	80	**100**
Quercus cerris	.	.	37	94	85	100
Other species						
Carpinus orientalis	100	56	89	100	100	100
Geum urbanum	.	38	29	29	.	40
Ligustrum vulgare	33	32	21	.	.	.
Trachystemon orientalis	29	.	32	.	35	.
Rubus subgen. *Rubus*	33	26	16	12	5	.
Teucrium chamaedrys	29	.	8	29	30	.
Fragaria vesca	10	18	16	24	5	.
Aegonychon purpurocaeruleum	.	3	21	18	10	.
Clematis vitalba	14	3	11	24	5	.
Luzula forsteri	19	.	13	18	.	.
Geranium asphodeloides	.	.	21	12	10	.
Laser trilobum	5	.	16	18	.	.
Pyrus communis	14	6	5	12	.	.
Tilia begoniifolia	14	.	13	.	.	.
Lonicera caprifolium	14	15	.	.	.	.
Trifolium pratense	10	9	.	18	.	.
Digitalis lanata	.	.	13	12	.	.
Cardamine bulbifera	.	.	13	12	.	.
Cotinus coggygria	5	.	5	6	10	.
Veronica serpyllifolia	.	12	.	.	10	.
Geranium robertianum	5	3	8	.	.	.
Torilis japonica	5	12	.	.	.	.
Tilia platyphyllos	.	.	11	6	.	.
Petrorhagia saxifraga	5	3	.	.	10	.
Jacobaea vulgaris	5	9	.	.	.	.
Pimpinella tripartita	5	3	3	6	.	.
Orobanche laxissima	10	6	.	.	.	.
Plantago major	5	9	.	.	.	.
Daucus carota	.	6	.	.	10	.
Ruscus hypoglossum	.	.	8	.	5	.
Lysimachia punctata	.	.	8	6	.	.
Dictamnus albus	.	.	8	6	.	.
Taraxacum sect. *Taraxacum*	5	6	.	.	.	.
Polypodium vulgare	10	.	.	.	5	.
Ulmus minor	5	3	3	.	.	.
Tanacetum partheniifolium	10	3	.	.	.	.
Galium album	5	6	.	.	.	.
Polypodium cambricum	10	3	.	.	.	.

Continued on next page

Fortsetzung auf nächsten Seite

Cluster number	1	2	3	4	5	6
Number of relevés	21	34	38	17	20	10
Euonymus europaea	.	9	.	.	.	.
Glechoma hederacea	.	9	.	.	.	.
Rumex sanguineus	.	9	.	.	.	.
Convallaria majalis	.	9	.	.	.	.
Catapodium rigidum	.	9	.	.	.	.
Epimedium pubigerum	.	.	**55**	.	5	.
Salvia forsskaolei	.	.	**55**	.	10	.
Erica arborea	.	.	**42**	.	.	.
Lathyrus aureus	.	.	**37**	.	.	.
Genista tinctoria	.	.	**32**	.	.	.
Vitis vinifera	.	.	**32**	.	.	.
Cirsium hypoleucum	.	.	**47**	18	.	.
Asperula cimulosa	.	.	**50**	24	.	.
Vaccinium arctostaphylos	.	.	**34**	.	5	.
Euphorbia oblongifolia	.	.	26	.	.	.
Rhododendron luteum	5	6	34	.	.	.
Rhododendron ponticum	.	.	21	.	.	.
Ilex colchica	14	.	32	.	.	.
Galium paschale	.	.	18	.	.	.
Iris lazica	.	.	18	.	.	.
Arbutus andrachne	.	.	18	.	.	.
Crataegus pentagyna	19	9	47	18	.	.
Pteridium aquilinum	24	6	53	.	30	.
Melica uniflora	.	.	16	.	.	.
Cistus salviifolius	.	.	16	.	.	.
Fagus orientalis	14	.	32	6	.	.
Milium vernale	.	.	21	6	.	.
Castanea sativa	19	.	29	.	.	.
Cistus creticus	.	.	26	.	15	.
Crataegus germanica	10	12	39	6	15	.
Verbascum lagurus subsp. *ponticum*	.	.	13	.	.	.
Hypericum calycinum	.	.	13	.	.	.
Pyracantha coccinea	.	.	13	.	.	.
Fraxinus ornus	.	.	13	.	.	.
Euonymus europaeus	.	.	26	18	.	.
Oenanthe pimpinelloides	.	29	42	.	25	.
Briza media	.	.	11	.	.	.
Acer cappadocicum	24	.	26	.	.	.
Carpinus betulus	33	6	42	6	.	20
Laurus nobilis	5	6	18	.	.	.
Dorycnium pentaphyllum	.	.	18	6	5	.
Bituminaria bituminosa	.	.	13	.	5	.
Helleborus orientalis	29	15	53	29	35	.
Rubia tinctorium	.	.	8	.	.	.
Staphylea pinnata	.	.	8	.	.	.
Silene compacta	.	.	8	.	.	.
Bromopsis benekenii	.	.	8	.	.	.
Trifolium campestre	.	.	8	.	.	.
Rhamnus imeretina	.	.	8	.	.	.
Datisca cannabina	.	.	8	.	.	.
Tanacetum parthenium	.	.	11	**65**	.	.
Vicia cracca	.	.	8	**59**	.	.
Cephalanthera rubra	.	.	5	**53**	.	.
Asperula involucrata	.	.	.	**47**	.	.
Viola odorata	.	.	.	**41**	.	.
Alliaria petiolata	.	.	.	**41**	.	.
Clinopodium vulgare	.	12	8	**59**	.	.
Cornus mas	10	3	47	**100**	5	60
Lathyrus tukhtensis	.	.	3	**35**	.	.
Doronicum orientale	.	3	.	**35**	.	.
Poa nemoralis	5	9	13	**53**	.	.
Lonicera etrusca	.	.	.	**29**	.	.
Lathyrus roseus	.	.	.	**29**	.	.
Nepeta nuda subsp. *albiflora*	.	.	.	**29**	.	.
Sorbus umbellata	.	.	.	**29**	.	.
Geranium purpureum	.	.	.	**29**	.	.
Colutea cilicica	.	.	3	29	.	.
Digitalis lamarckii	.	.	.	24	.	.
Geranium lucidum	.	.	.	24	.	.
Silene latifolia	.	.	.	24	.	.
Campanula rapunculus	.	.	.	24	.	.
Galium verum	.	.	.	24	.	.
Aristolochia pallida	.	.	.	24	.	.
Trifolium medium	.	3	3	29	.	.
Silene italica	.	15	.	35	.	.
Sorbus torminalis	10	9	37	71	.	40
Tanacetum poteriifolium	.	.	8	29	.	.
Crataegus rhipidophylla	.	.	3	24	.	.
Juniperus oxycedrus	.	.	3	35	15	.
Securigera varia	14	3	13	41	.	.
Lapsana communis	33	32	45	76	.	20
Quercus pubescens	.	.	5	24	.	.
Hedysarum varium	.	.	.	18	.	.
Vicia hirsuta	.	.	.	18	.	.
Epipactis helleborine	.	.	.	18	.	.
Vicia abbreviata	.	.	.	18	.	.
Cephalanthera damasonium	.	.	.	18	.	.
Campanula involucrata	.	.	.	18	.	.
Geranium molle	.	.	.	18	.	.
Salvia verticillata	.	.	.	18	.	.
Athyrium filix-femina	.	.	.	18	.	.
Dianthus calocephalus	.	.	.	18	.	.

Cluster number	1	2	3	4	5	6
Number of relevés	21	34	38	17	20	10
Rubus sanctus	.	3	.	.	10	.
Veronica officinalis	.	6	3	.	.	.
Sesleria phleoides	.	.	5	6	.	.
Polygonatum glaberrimum	5	3	.	.	.	.
Hieracium murorum	5	.	.	6	.	.
Seseli peucedanoides	.	6	.	.	.	.
Argyrolobium biebersteinii	.	3	.	.	5	.
Phleum pratense	.	6	.	.	.	.
Sedum pallidum	.	6	.	.	.	.
Paliurus spina-christi	.	.	5	.	.	.
Achillea biserrata	.	.	5	.	.	.
Vincetoxicum nigrum	.	.	5	.	.	.
Circaea lutetiana	.	.	5	.	.	.
Celtis australis	.	.	5	.	.	.
Vinca minor	.	.	5	.	.	.
Pimpinella tragium	.	.	5	.	.	.
Calystegia sepium	.	.	5	.	.	.
Phlomis samia	.	.	5	.	.	.
Securigera cretica	.	.	3	6	.	.
Frangula alnus	.	.	3	6	.	.
Galium rotundifolium	.	.	5	.	.	.
Anthemis tinctoria	.	.	.	6	5	.
Lonicera caucasica	5	.	.	.	.	.
Sambucus nigra	5	.	.	.	.	.
Mercurialis perennis	5	.	.	.	.	.
Vicia sepium	5	.	.	.	.	.
Carex humilis	5	.	.	.	.	.
Melampyrum elatius	5	.	.	.	.	.
Asplenium ruta-muraria	5	.	.	.	.	.
Ranunculus polyanthemos	5	.	.	.	.	.
Lotus corniculatus	5	.	.	.	.	.
Pachyphragma macrophylla	5	.	.	.	.	.
Scabiosa sosnowskyi	5	.	.	.	.	.
Adiantum capillus-veneris	5	.	.	.	.	.
Erigeron annuus	5	.	.	.	.	.
Pinus sylvestris	5	.	.	.	.	.
Primula veris subsp. *macrocalyx*	5	.	.	.	.	.
Campanula raddeana	5	.	.	.	.	.
Ranunculus bulbosus	5	.	.	.	.	.
Cardamine parviflora	5	.	.	.	.	.
Sison amomum	5	.	.	.	.	.
Trifolium diffusum	5	.	.	.	.	.
Malus sylvestris	5	.	.	.	.	.
Trachycarpus fortunei	5	.	.	.	.	.
Punica granatum	5	.	.	.	.	.
Cirsium vulgare	5	.	.	.	.	.
Morus alba	5	.	.	.	.	.
Euphorbia stricta	5	.	.	.	.	.
Aristolochia pontica	5	.	.	.	.	.
Leptopus chinensis	5	.	.	.	.	.
Ligustrum japonicum	.	3	.	.	.	.
Inula conyzae	.	3	.	.	.	.
Geranium pusillum	.	3	.	.	.	.
Heracleum sphondylium subsp. *cyclocarpum*	.	3	.	.	.	.
Satureja spicigera	.	3	.	.	.	.
Sambucus ebulus	.	3	.	.	.	.
Lathyrus pratensis	.	3	.	.	.	.
Juglans regia	.	3	.	.	.	.
Clinopodium grandiflorum	.	3	.	.	.	.
Smyrnium perfoliatum	.	3	.	.	.	.
Polygonum aviculare	.	3	.	.	.	.
Limodorum abortivum	.	3	.	.	.	.
Centaurium erythraea	.	3	.	.	.	.
Festuca rubra	.	3	.	.	.	.
Hieracium umbellatum	.	3	.	.	.	.
Poa compressa	.	3	.	.	.	.
Elymus caninus	.	3	.	.	.	.
Leucanthemum vulgare	.	3	.	.	.	.
Lolium perenne	.	3	.	.	.	.
Prunus cerasifera	.	3	.	.	.	.
Veronica magna	.	3	.	.	.	.
Juncus tenuis	.	3	.	.	.	.
Juncus effusus	.	3	.	.	.	.
Kickxia elatine	.	3	.	.	.	.
Deschampsia cespitosa	.	3	.	.	.	.
Lathyrus rotundifolius	.	3	.	.	.	.
Galium palustre	.	3	.	.	.	.
Vicia tetrasperma	.	3	.	.	.	.
Cleistogenes serotina	.	.	3	.	.	.
Arbutus unedo	.	.	3	.	.	.
Acer trautvetteri	.	.	3	.	.	.
Alnus glutinosa subsp. *barbata*	.	.	3	.	.	.
Calluna vulgaris	.	.	3	.	.	.
Smilax aspera	.	.	3	.	.	.
Ornithogalum sigmoideum	.	.	3	.	.	.
Rhamnus alaternus	.	.	3	.	.	.
Sorbus aucuparia	.	.	3	.	.	.
Sorbaria tomentosa	.	.	3	.	.	.
Myosotis sylvatica	.	.	.	6	.	.
Hordeum bulbosum	.	.	.	6	.	.
Cota tinctoria	.	.	.	6	.	.
Erysimum pulchellum	.	.	.	6	.	.

Continued on next page

Fortsetzung auf nächsten Seite

Cluster number	1	2	3	4	5	6
Number of relevés	21	34	38	17	20	10
Physospermum cornubiense	19	.	8	35	.	.
Cyclamen coum	5	6	34	53	25	.
Astragalus glycyphylloides	.	.	11	24	.	.
Scutellaria albida	.	.	.	29	.	20
Stachys officinalis	.	6	3	24	5	.
Poa bulbosa	.	.	.	12	.	.
Ochlopoa annua	.	.	.	12	.	.
Prunus mahaleb	.	.	.	12	.	.
Hippocrepis emerus	.	.	.	12	.	.
Vicia sativa subsp. *nigra*	.	.	.	12	.	.
Epipactis pontica	.	.	.	12	.	.
Epipactis condensata	.	.	.	12	.	.
Trifolium pannonicum	.	.	.	12	.	.
Astragalus ornithopodioides	.	.	.	12	.	.
Lathyrus nissolia	.	.	.	12	.	.
Moehringia trinervia	.	.	.	12	.	.
Erysimum cuspidatum	.	.	.	12	.	.
Onobrychis arenaria subsp. *cana*	.	.	.	12	.	.
Sideritis montana	.	.	.	12	.	.
Anthemis kotschyana	.	.	.	12	.	.
Astragalus ponticus	.	.	.	12	.	.
Astragalus leucothrix	.	.	.	12	.	.
Ononis pusilla	.	.	.	12	.	.
Campanula glomerata	.	.	8	18	.	.
Prunus domestica subsp. *insititia*	.	.	11	18	.	.
Phillyrea latifolia	.	.	3	.	**35**	.
Rubus ulmifolius	.	.	.	.	**30**	.
Styrax officinalis	.	.	.	.	25	.
Teucrium polium	.	.	.	.	20	.
Festuca heterophylla	.	.	21	.	35	.
Cirsium pseudopersonata	.	.	.	.	15	.
Salvia tomentosa	.	.	.	6	20	.
Arum italicum	.	.	.	.	10	.

Cluster number	1	2	3	4	5	6
Number of relevés	21	34	38	17	20	10
Legousia speculum-veneris	.	.	.	6	.	.
Thalictrum minus	.	.	.	6	.	.
Fallopia convolvulus	.	.	.	6	.	.
Melilotus officinalis	.	.	.	6	.	.
Aristolochia parvifolia	.	.	.	6	.	.
Medicago ×varia	.	.	.	6	.	.
Trifolium ochroleucon	.	.	.	6	.	.
Jasminum fruticans	.	.	.	6	.	.
Veronica orientalis	.	.	.	6	.	.
Crepis reuteriana	.	.	.	6	.	.
Trachynia distachya	.	.	.	6	.	.
Cyanus depressus	.	.	.	6	.	.
Rhagadiolus stellatus	.	.	.	6	.	.
Euphorbia orientalis	.	.	.	.	5	.
Sonchus asper	.	.	.	.	5	.
Echinops spinosissimus	.	.	.	.	5	.
Blackstonia perfoliata	.	.	.	.	5	.
Geranium sanguineum	.	.	.	.	5	.
Paeonia mascula	.	.	.	.	5	.
Epilobium montanum	.	.	.	.	5	.
Filago pyramidata	.	.	.	.	5	.
Epilobium parviflorum	.	.	.	.	5	.