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Carpinus orientalis forests in Georgian Colchis: First insights

Carpinus orientalis-Wälder in der georgischen Kolchis: Erste Einblicke

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Abstract

Colchis (Caucasus Ecoregion, Euxinian Province) is a region with unique Tertiary relict biota and high species and vegetation diversity. However, its vegetation has been only little studied by Braun-Blanquet methods so far. Based on original field data (20 phytosociological relevés), we describe a novel vegetation type of calciphilous and thermophilous *Carpinus orientalis* forests in western Georgia (*Campanulo alliariifoliae-Carpinetum orientalis* ass. nova). This species-rich community inhabits sunny limestone slopes and is developed under a humid warm-temperate climate. We present the community in the context of relevés from the literature (n = 105 in total) of *Carpinus orientalis* dominated or co-dominated forests across the whole Euxinian Province (southern Black Sea coast). Ordination and unsupervised classification analyses revealed the main pattern in their species composition closely linked to biogeography backed up by macroclimatic gradients and vegetation history. Eastwards, Balkan and Mediterranean species decrease gradually, while Euxinian and Euxino-Caucasian species are more frequent. Although the analysed forest communities were highly variable in species composition, they all shared a subset of submediterranean and Euxinian species. Numerous Eastern Euxinian and Euxino-Caucasian endemics (e.g. *Campanula alliariifolia*, *Klasea quinquefolia*) are characteristic of the community recorded in Georgia. These are accompanied by evergreen species (e.g. *Smilax excelsa*, *Vinca major* subsp. *hirsuta*) and common forest mesophytes (e.g. *Campanula rapunculoides*, *Carex digitata*) both indicating a relatively mild and precipitation-rich climate. The association *Erico-Carpinetum* described in NE Turkey was identified as the most similar unit to the new community. As it is the type association of the alliance *Castaneo sativae-Carpinion orientalis*, we adopted this assignment for the new association from Georgia.

Keywords: biogeography, *Carpinus orientalis*, Caucasus, Colchis, ecology, Euxinia, forest vegetation, Georgia, phytosociology

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

Colchis is an area encompassing the south-eastern shore of the Black Sea in Turkey, Georgia and Russia. It covers the western slopes of the Greater and Lesser Caucasus, the northern slopes of the Pontic range and the Colchic Lowland. It is well-known for its unique

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relict biota (ZAZANASHVILI et al. 2000, NAKHUTSRISHVILI et al. 2015). It is one of the most important Tertiary refugia across the temperate zone of the northern hemisphere. The biological legacy of those times has survived in only a few warm-temperate regions with an exceptionally stable environment (MILNE & ABBOTT 2002). Colchis is a part of the Caucasus Ecoregion. The Caucasus is listed among the top 34 biologically richest and most endangered biodiversity hotspots globally (MITTERMEIER et al. 2004, ZAZANASHVILI & MALLON 2009). In terms of phytogeography, Colchis represents an eastern sector of the Euxinian Province encompassing the southern coast of the Black Sea between Bulgaria and Russia (TAKHTAJAN 1986). Euxinia has diverse flora and vegetation reflecting its position between the Balkans, the Mediterranean Basin, Anatolia and the Caucasus. Deciduous forests with evergreen Tertiary relict shrubs (e.g. *Ilex colchica*, *Prunus laurocerasus*, *Rhododendron ponticum*) are its unique feature (TAKHTAJAN 1986). They were identified as temperate rainforests by some authors (e.g. NAKHUTSRISHVILI et al. 2015). Recent phylogeographical and phylogenetic research on forest vascular plants confirmed the unique biogeographical position of the province within western Eurasia (e.g. GRIMM & DENK 2014, VOLKOVA et al. 2020). Euxinia is also a region of diverse climate regimes. Its Mediterranean character with dry summer periods gradually disappears eastwards and the easternmost part of the province is precipitation-rich throughout the year. The climate of Colchis is humid warm-temperate (WALTER 1970). With annual precipitation of around 1800–2000 mm (but locally exceeding 4000 mm), it is one of the most humid regions of western Eurasia. The absence of regular winter frosts at low elevations is another essential climatic feature of Colchis (DENK et al. 2001, NAKHUTSRISHVILI et al. 2015).

The forests of Euxinia have been a subject of phytosociological research mainly in Turkey (e.g. QUÉZEL et al. 1980, KORKMAZ et al. 2011, KAVGACI et al. 2012, ÇOBAN & WILLNER 2019) and Bulgaria (e.g. TZONEV et al. 2019). Studies from Georgia published to date have dealt with mesophilous forest types (e.g. FILIBECK et al. 2004, NOVÁK et al. 2019), while almost no attention has been paid to thermophilous types. The presented study is focused on *Carpinus orientalis* (hereafter "*C. orientalis*") forests of the limestone massifs of western Georgia. *Carpinus orientalis* is a submediterranean deciduous tree distributed in south-eastern Europe, Anatolia, Syria, Crimea, Caucasus and northern Iran. It is a thermophilous and xerophilous species preferring calcareous soils, well-known is its tolerance to various traditional management practices (SIKKEMA & CAUDULLO 2016). Forests dominated or co-dominated by *C. orientalis* occur across the entire Euxinia (QUÉZEL et al. 1980, ÇOBAN & WILLNER 2019, AKHALKATSI 2019). Generally, they prefer sunny slopes on various bedrock. However, they may represent a dominant forest type in coastal regions under the influence of the Mediterranean climate. They form both low and open, as well as tall and closed stands (QUÉZEL et al. 1980). Colchic *C. orientalis* forests are partly supposed to be a regeneration stage after the degradation of oak or mixed forests (DOLUKHANOV 2010, AKHALKATSI 2015). Locally, they served as coppices (AKHALKATSI 2015), similarly to the Balkans (STUPAR et al. 2016) or Italy (BLASI et al. 2001).

The vegetation of thermophilous deciduous forests is still relatively understudied in Euxinia and the Caucasus, at least by Braun-Blanquet methods (cf. ÇOBAN & WILLNER 2019, MUCINA et al. 2016). They have been investigated mainly in the western part of the area (see citations above). Despite their broad distribution in the eastern part (GULISASHVILI et al. 1975, NAKHUTSRISHVILI 2013), they have been studied only marginally so far, although some types are listed in national red lists of habitats (e.g. AKHALKATSI 2019). Within the Caucasus Ecoregion, dry-mesic forests of *C. orientalis* and *Zelkova carpinifolia* have recently been described phytosociologically in eastern Georgia (NOVÁK et al. 2020) and in Hyrcania in northern Iran (GHOLIZADEH et al. 2020).

Due to the lack of knowledge on the phytosociology of thermophilous Colchic forests and their position within the Euxinian forest vegetation, the goals of this study are (1) to describe the ecology and species composition of the newly recorded *C. orientalis* forests in western Georgia, and (2) to determine the ecological and floristic relationships between the community studied here and the *C. orientalis* stands documented so far in Euxinia.

2. Study region

The study region stretches between the cities of Chiatura (Imereti Region) and Jvari (Samegrelo Region) in western Georgia (42°17'–42°46' N, 42°02'–43°18' E). The sampling sites were located at low elevations (90–570 m a.s.l.) of the limestone massifs of Kvira, Senaki, Askhi, Tskaltubo-Kutaisi, Racha and Chiatura. Rendzic leptosol developed on Cretaceous limestones is the main soil type of the sampling sites (URUSHADZE & GHAMBASHIDZE 2013, ASANIDZE et al. 2019). The region represents a transition zone between the Colchic and Greater Caucasian climatic zones (BONDYREV et al. 2015). The sampling sites have mean annual temperature of 11.8–14.8 °C and annual precipitation of 999–2074 mm (KARGER et al. 2017). The temperature may drop slightly below freezing point in the winter. Rainfall is distributed almost evenly over the year (Fig. 1) and is accompanied by frequent horizontal precipitations brought by moist air masses from the Black Sea. However, the water-permeable limestone bedrock presumably weakens the effect of humid climate on vegetation (DENK et al. 2001, DOLUKHANOV 2010, BONDYREV et al. 2015).

The region is covered by extensive forests, generally deciduous (BOHN et al. 2000–2003, NAKHUTSRISHVILI 2013). They harbour a significant diversity of understorey species, including narrow endemics (KOLAKOVSKII 1961), both shrubs (e.g. *Corylus colchica*, *Staphylea colchica*) and herbs (e.g. *Cyclamen colchicum*, *Peucedanum adae*). It is an area with one of the highest concentrations of endemic plant species within Georgia (SLODOWICZ et al. 2018). In the study region, forests dominated or co-dominated by *Carpinus orientalis* are reported as a distinctive vegetation type of steep limestone slopes at low elevations (DOLUKHANOV 2010, NAKHUTSRISHVILI 2013). They generally occur up to 800 m, i.e. within the zone of mixed Colchic forests (e.g. *Carpinus betulus*, *Castanea sativa*, *Fagus orientalis*, *Quercus petraea* subsp. *iberica*) with evergreen shrubs.

The forests in the study region have been disturbed by human activities in many ways, especially since the middle of the 20th century. This includes overlogging, setting forest fires, building activities and overgrazing by domestic animals, all followed by soil erosion and landslides, tree pathogen outbreaks and general degradation of forest ecosystems (AKHALKATSI 2015). Only a negligible part of these forests lies within protected areas.

3. Methods

3.1 Field sampling

During the field survey (2016–2019), we recorded 20 square-shaped phytosociological relevés (100 m^2). The aim was to sample forests dominated or co-dominated by *Carpinus orientalis* (except for one relevé dominated by the ecologically similar *Zelkova carpinifolia*; DENK et al. 2001). In each relevé, we assessed the percentage covers of tree (E_3), shrub (E_2), herb (E_1) and moss (E_0) layers and covers of species of vascular plants in each layer using the nine-degree Braun-Blanquet scale (DENGLER et al. 2008). Furthermore, we estimated mean heights of the tree, shrub and herb layers. For each relevé, we determined slope inclination and aspect and cover of rocks. We collected soil samples from a depth of 5–10 cm for soil pH measuring done in a suspension of a dried soil sample (particles < 2 mm) with distilled water (2:5) by a portable Greisinger instrument. The geographical position (WGS 84) and elevation of the relevés were acquired by a portable GPS device. The relevés were stored in the Turboveg 2.1 database (HENNEKENS & SCHAMINÉE 2001) and processed in Juice 7.1 software (TICHÝ 2002). The vascular plant nomenclature was standardized following the Euro+Med PlantBase (http://ww2.bgbm.org/EuroPlusMed/; accessed 2020–10–01) except for one *ad hoc* aggregate (*Carex muricata* aggr. – *Carex divulsa*, *C. muricata*, *C. spicata*) and all *Rubus* taxa recorded during the field survey were merged as *Rubus* subgen. *Rubus* (SOCHOR & TRÁVNÍČEK 2016). The relevés were also stored in the AS-00–005 Transcaucasian Vegetation Database included in the European Vegetation Archive (CHYTRÝ et al. 2016).

3.2 Dataset and data analyses

We compiled a dataset of original relevés from Georgia and relevés from the literature to compare biogeographical and environmental aspects of the newly described community with previously described *C. orientalis* forests described to date from the rest of Euxinia. We included relevés of associations dominated or co-dominated by *C. orientalis*. These were extracted from the following sources: QUÉZEL et al. (1980) (*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), YARCI (2002) (*Querco cerridis-Carpinetum orientalis*, *n* = 10) and KORKMAZ et al. (2011) (*Corno mari-Quercetum cerridis*, *n* = 10). The dataset contained 105 relevés in total. Relevés from the literature were georeferenced based on descriptions of sampling sites. Climatic data were obtained from the CHELSA Bioclim dataset (KARGER et al. 2017). For each relevé, average values of essential climatic variables (mean annual temperature, annual precipitation, temperature seasonality, precipitation seasonality) were retrieved as a mean value from a circular buffer zone of 25 km^2. We applied classification (flexible beta clustering with parameter β = -0.2 and Bray-Curtis distance) and ordination (NMDS) analyses to show ecological and floristic patterns in the dataset. Taxa determined to only the genus level were omitted, records of same-name species were merged across the layers (FISCHER 2015) and percentage cover values of species were square-root transformed prior to the analyses (TICHÝ et al. 2020). The ordination analysis was computed using the package vegan 2.5-7 (OKSANEN et al. 2020) in the R 4.0.2 environment (R CORE TEAM 2020). Species-to-cluster fidelity was expressed as the phi coefficient (CHYTRÝ et al. 2002). Diagnostic ($\Phi \geq 0.25$) and highly diagnostic ($\Phi \geq 0.55$) species are provided for each cluster. Before its calculation, the number of plots per cluster was virtually equalized (TICHÝ & CHYTRÝ 2006). Fisher's exact test ($p \geq 0.05$) was applied to omit species with non-significance occurrence from the list of diagnostic species.

The new association was formally described following the 4th edition of the Code of Phytosociological Nomenclature (THEURILLAT et al. 2021). Due to the many unresolved issues in the syntaxonomy of the Euxinian forest vegetation, the first mention of a syntaxon is accompanied by an author citation, except for classes whose nomenclature follows MUCINA et al. (2016).

4. Results and discussion

4.1 *Carpinus orientalis* community in Georgian Colchis

In the study region, *Carpinus orientalis* forests inhabit various topographic positions, generally with soil water shortage. They favour steep slopes (mean inclination 30°) with rugged rock outcrops (Fig. 1). They also occur on hilltops and plateau edges. Stony topsoil

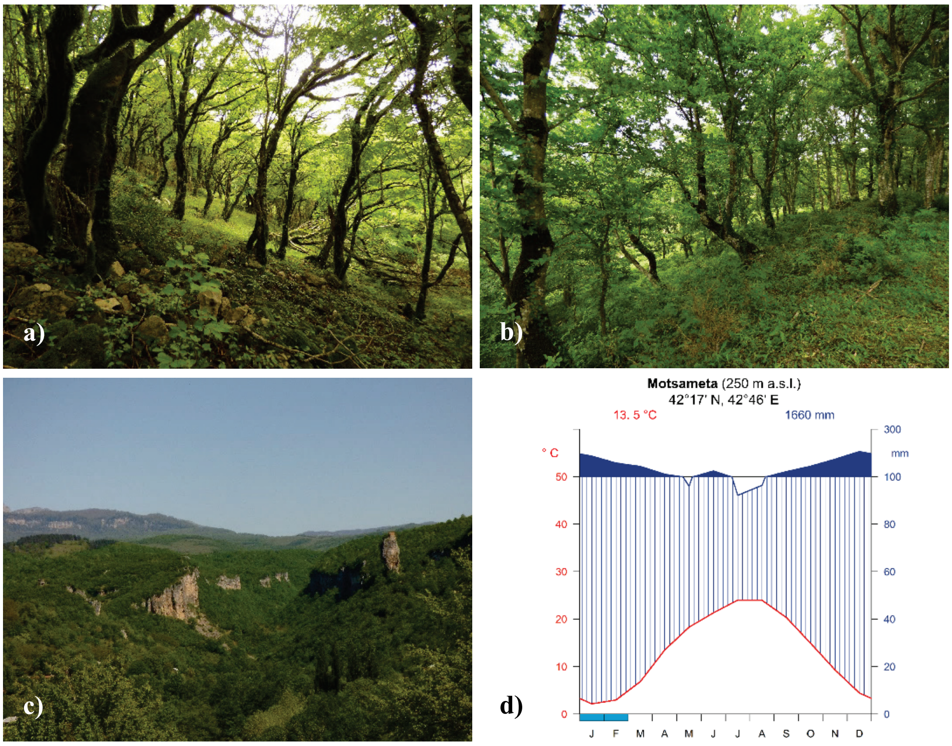

Fig. 1. a) *Carpinus orientalis* forests below the Motsameta Monastery near Kutaisi, site of the type relevé of the association *Campanulo alliariifoliae-Carpinetum orientalis* ass. nova. **b)** *Carpinus orientalis* forests near Tsutskhvati. **c)** Limestone landscape around Katski Pilar Monastery where *Carpinus orientalis* forests dominate (Photos: P. Novák, a) July 2019 b) July 2017 c) May 2018). **d)** Walter-type climadiagram for Motsameta (based on CHELSA Bioclim dataset; KARGER et al. 2017). Additional photos are provided in Supplement E4.

Abb. 1. a) *Carpinus orientalis-Wälder* unterhalb des Motsameta-Klosters bei Kutaisi, Lokalität der Typusaufnahme des *Campanulo alliariifoliae-Carpinetum orientalis* ass. nova. **b)** *Carpinus orientalis*-Wälder bei Tsutskhvati. **c)** Kalkgesteinslandschaft im Bereich des Klosters Katski Pilar, wo *Carpinus orientalis*-Wälder dominieren (Fotos: P. Novák, a) Juli 2019 b) Juli 2017 c) Mai 2019). **d)** Klimadiagram nach Walter für Motsameta (basierend auf dem CHELSA Bioclim Datensatz; KARGER et al. 2017). Zusätzliche Fotos sind in Anhang E4 zu finden.

of neutral to slightly alkaline reaction (pH 6.6–7.8) reflects the limestone bedrock. It is a relatively species-rich community (30–45 species per 100 m^2).

The tree canopy is rather closed (mean cover 83%), generally reaching around 10 m in height. The dominant tree *C. orientalis* is often accompanied by other deciduous trees (e.g. *Acer campestre*, *Carpinus betulus*, *Fraxinus excelsior*), and infrequently also endemic and subendemic ones (e.g. *Acer cappadocicum*, *Quercus hartwissiana* and *Zelkova carpinifolia*). Frequent multi-trunk *C. orientalis* trees indicate former coppice management. *Smilax excelsa*, a widespread evergreen liana in the community, is a characteristic species of regions with mild winters in Euxinia, the Caucasus and northern Iran (NAKHUTSRISHVILI 2013, GHOLIZADEH et al. 2020, NOVÁK et al. 2020). In contrast to mesophilous Colchic forests (NAKHUTSRISHVILI 2013, NOVÁK et al. 2019), endemic *Hedera colchica* is usually substituted by *H. helix* which has lower air humidity requirements (DOLUKHANOV 1980). The shrub layer is mostly developed (mean cover 14%). It consists of species of the canopy accompanied by deciduous shrubs (e.g. *Cornus mas*, *Corylus avellana*, *Staphylea colchica*). Evergreen Colchic shrubs are generally absent except for *Ilex colchica* which is remarkably tolerant to shallow calcareous soils (DOLUKHANOV 1980). *Buxus sempervirens* was previously common (cf. DOLUKHANOV 2010, Supplement E4). Its ongoing massive dieback induced by a co-invasion of alien fungus and insect pathogens has seriously damaged a large portion of Colchic *Buxus* population since 2009 when damages were firstly detected (MATSIAKH et al. 2018). That will presumably influence affected forest ecosystems by increasing slope erosion, modifying forest succession and loss of species obligate on *Buxus* (MITCHELL et al. 2018). The herb layer (mean cover 37%) usually lacks a clear dominant species. Evergreen species including *Ruscus aculeatus* and *Vinca major* subsp. *hirsuta* are frequent and co-dominate in places together with lianas. The community is rich in Caucasian endemic and subendemic forest mesophytes (e.g. *Campanula alliariifolia*, *Symphytum grandiflorum*, *Veronica peduncularis*). However, species diagnostic for the Colchic mesophilous forests (e.g. *Polystichum woronowii*, *Pteris cretica*, *Ruscus colchicus*; NOVÁK et al. 2019) are almost absent. A group of xerophilous species also shows rather high endemism (e.g. *Digitalis schischkinii*, *Peucedanum adae*, *Klasea quinquefolia*), alongside broadly distributed species (e.g. *Asplenium adiantum-nigrum*, *Teucrium chamaedrys*). A mixture of mesophilous and xerophilous species in the undergrowth of *C. orientalis* forests has also been reported in other regions of their common occurrence, e.g. the Balkans (STUPAR et al. 2015), Italy (BLASI et al. 2001) and Crimea (DIDUKH 1996). Submediterranean forest generalists are represented by *Dioscorea communis*, *Potentilla micrantha* and *Viola alba* for instance. Shade-tolerant species of rock crevices (e.g. *Asplenium ruta-muraria*, *A. trichomanes*) inhabit rock outcrops. The humid climate supports ferns (*Adiantum capillus-veneris*, *Asplenium scolopendrium*) which generally avoid *C. orientalis* forests in south-eastern Europe except for the bottoms of limestone canyons (STUPAR et al. 2020). Local populations of pasture weeds (e.g. *Leontodon hispidus*, *Plantago lanceolata*, *Pteridium aquilinum*) indicate occasional wood-pasture management. Alien species (sensu KIKODZE 2010) are mostly rare in the community. There are two exceptions – the stoloniferous grass *Oplismenus hirtellus* subsp. *undulatifolius* which is common across Colchic forests (DOLUKHANOV 2010) and *Robinia pseudoacacia* which used to be planted in Georgia and is now spreading spontaneously (AKHALKATSI 2015). The moss layer is mostly well-developed (mean cover 16%), preferentially colonizing rock outcrops. Moreover, epiphytic bryophytes often cover tree trunks, as a characteristic feature of Colchic forests, due to high rainfall and frequent fogs (KÜRSCHNER et al. 2012).

The community resembles the formerly described forest type "*Carpinuleto-Querceta ruscosa* (*Ruscus colchicus*)", and partly also "*Carpinuleto-Querceta seslerietosa*" inhabiting more rocky sites, both reported from the study region (DOLUKHANOV 2010, NAKHUTSRISHVILI 2013). In terms of nature protection, stands with *Buxus sempervirens* or *Zelkova carpinifolia* are particularly important as both are listed among the priority habitat types of Georgia (AKHALKATSI 2019).

It should be emphasized that the *C. orientalis* forests of Georgian Colchis require further phytosociological research, as their occurrence is also reported on well-drained soils of riverine terraces in the Colchic Lowland as well as on limestones and sands in the Black Sea coastal zone in the north-western part of the country (KOLAKOVSKII 1961, DOLUKHANOV 2010, NAKHUTSRISHVILI 2013).

4.2 Colchic *Carpinus orientalis* forests in the context of Euxinian forest vegetation

The comparison of the newly recorded community (Supplements E1–E2) with previously reported Euxinian communities dominated or co-dominated by *C. orientalis* (Fig. 2–3, Table 1) resulted in three biogeographically distinct main clusters recognized in the unsupervised classification. We interpreted them at the alliance level.

The first main cluster involved *C. orientalis* forests of the eastern part of Euxinia. Eastern Euxinian and Euxino-Caucasian endemics (e.g. *Campanula alliariifolia*, *Klasea quinquefolia*, *Vinca major* subsp. *hirsuta*) were among its highly diagnostic species. They were accompanied by Mediterranean evergreen shrubs with a scattered distribution across the whole of Euxinia (e.g. *Arbutus andrachne*, *Buxus sempervirens*, *Cistus salviifolius*, *Erica arborea*; cf. DONNER 1990, DENK et al. 2001, NAKHUTSRISHVILI 2013). Its syntaxonomic interpretation is discussed below. The second main cluster contained mainly *C. orientalis* forests of the central part of Euxinia. Mesophytes, mostly Euxinian endemics and subendemics (e.g. *Asperula cimulosa*, *Cirsium hypoleucum*), were diagnostic. Mesophilous tree species (e.g. *Carpinus betulus*, *Fagus orientalis*) often co-dominated with *C. orientalis*. Numerous mesophytes indicated its transitional position between thermophilous forests and mesophilous Euxinian oak-hornbeam forests of the alliance *Trachystemono orientalis-Carpinion betuli* Çoban & Willner 2019 (class *Carpino-Fagetea*). The third main cluster unified forests of *C. orientalis* and *Quercus cerris* recorded predominantly in western Euxinia. Mediterranean (e.g. *Phillyrea latifolia*, *Styrax officinalis*) and Balkan (e.g. *Quercus cerris*) species with a limited distribution in Euxinia (cf. DONNER 1990) and nitrophytes (e.g. *Alliaria petiolata*, *Viola odorata*) were diagnostic. Following the classification presented by ÇOBAN & WILLNER (2019), we assigned it under the alliance *Quercion confertae* Horvat 1958 (class *Quercetea pubescentis*).

The classification and ordination analyses revealed biogeography as the key factor determining the variability of the Euxinian *C. orientalis* forests. Species characteristic of the Balkan dry forests and partly also Mediterranean species gradually retreat eastwards while Eastern Euxinian and Euxino-Caucasian endemics become more frequent (see the examples above). Analogous patterns have been reported, for instance, for Euxinian oak-hornbeam forests (NOVÁK et al. 2019) and to some extent also for oriental beech forests (KAVGACI et al. 2012). This shift in species composition seems to be an essential pattern of the Euxinian flora (cf. DONNER 1990). Moreover, in Euxinia, the precipitation seasonality characteristic of

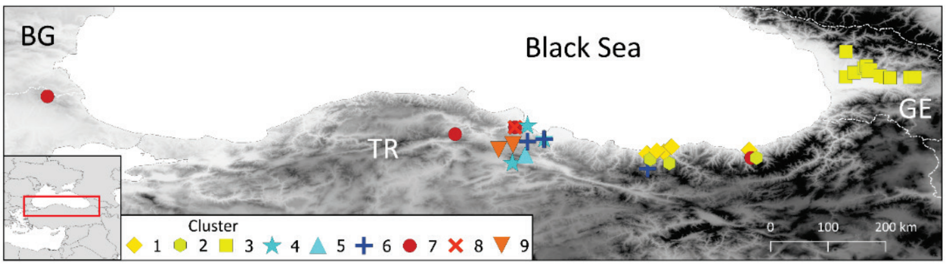

Fig. 2. Distribution of relevé sites of the dataset. Different symbols refer to their cluster assignment.

Abb. 2. Verteilung der Lokalitäten der Vegetationsaufnahmen des Datensatzes. Unterschiedliche Symbole beziehen sich auf ihre Cluster-Zuordnung.

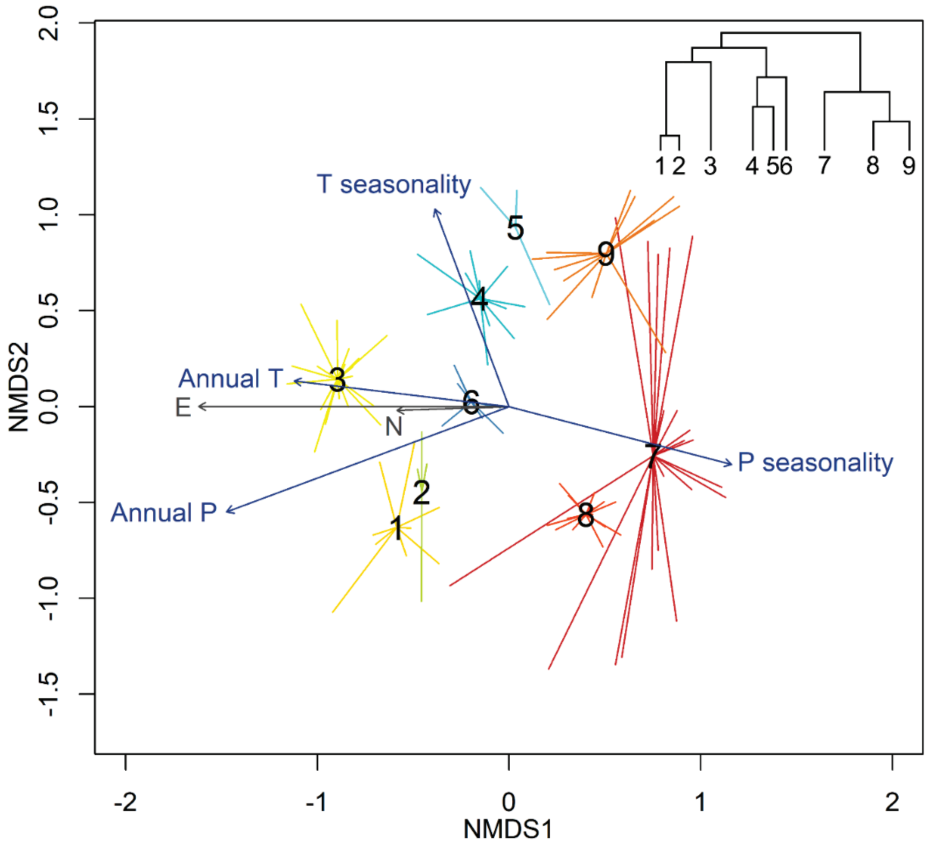

Fig. 3. NMDS analysis of the dataset with relevé-to-cluster assignment and centroids of the clusters based on the classification analysis (see dendrogram in the right upper part). Vectors of geographical position (in black) and climatic variables (in blue) were passively plotted. Stress value = 0.214.

Abb. 3. NMDS-Analyse des Datensatzes mit Zuordnung der Vegetationsaufnahmen zu Clustern und Zentroiden der Cluster basierend auf der Klassificationsanalyse (s. Dendrogramm rechts oben). Vektoren der geographischen Lage (in Schwarz) und der klimatischen Variablen (in Blau) wurden passiv geplottet. Stresswert = 0,214.

the Mediterranean and the southern Balkans is decreasing towards the humid Colchis (QUÉZEL et al. 1980, DENK et al. 2001). Therefore, we assume that the observed biogeographical pattern is driven by both vegetation history and macroclimatic gradients.

The finer division of the dataset into nine clusters (Fig. 2–3, Table 1) reproduced most of the analysed associations and communities relatively well, indicating their distinctive floristic composition (see Supplement E3). The Georgian community formed its own cluster within the first main cluster. Across the dataset, it possessed a unique combination of Eastern Euxinian and Caucasian species.

In the finer classification, the association *Erico-Carpinetum* Quézel et al. 1992 was identified as the association most similar to the Georgian community. *Erico-Carpinetum* is the type association of the alliance *Castaneo sativae-Carpinion orientalis* Quézel et al. 1992. In the EuroVegChecklist (MUCINA et al. 2016), the alliance was assigned to the order

Carpinetalia betuli P. Fukarek 1968, class *Carpino-Fagetea*. However, Çoban & Willner (2019) emphasized that this classification was in contradiction with its typification performed by QUÉZEL et al. (1992). As *Erico-Carpinetum* was identified as its type association, the alliance should unify thermophilous and xerophilous forests. Therefore, we classify the Georgian community under the alliance *Castaneo-Carpinion*. However, the position of the alliance itself deserves further study, as QUÉZEL et al. (1992) designated it as the type of the order *Rhododendro pontici-Fagetalia orientalis* Quézel et al. 1992, encompassing Euxinian deciduous forests, whose syntaxonomic concept is disputed (cf. MUCINA et al. 2016).

In the context of the Caucasian vegetation, there are many striking differences between the Colchic community and the *C. orientalis* stands of central and eastern Georgia (cf. DOLUKHANOV 2010, NAKHUTSRISHVILI 2013). The Colchic community harbours numerous Euxinian species, though it lacks characteristic flora of more arid regions of Transcaucasia (e.g. *Astragalus* spp., *Juniperus* spp., *Rhamnus pallasii*, *Spiraea hypericifolia*). Compared to *C. orientalis* forests reported in Hyrcania (GHOLIZADEH et al. 2020), there is a notable absence of the Hyrcanian floral element (e.g. *Centaurea hyrcanica*, *Digitalis nervosa*) and the presence of Euxinian and Euxino-Caucasian species. However, some species are shared (e.g. *Acer cappadocicum*, *Quercus petraea* subsp. *iberica*, *Sanicula europaea*).

4.3 Syntaxonomic outline

Based on the presented numerical comparison of Euxinian *C. orientalis* forests, we describe the Georgian community as a new association and classify it within the alliance *Castaneo sativae-Carpinion orientalis*.

Campanulo alliariifoliae-Carpinetum orientalis **ass. nova hoc loco**

Holotypus (hoc loco) of the association: Georgia, Motsameta (Imereti Region): a forest on a limestone slope ca 0.1 km N of the Motsameta Monastery, 42.28257° N, 42.75938° E, 10 × 10 m^2, 24 July 2019, elevation: 210 m, aspect: 40°, inclination: 30°, soil pH (H_2O): 7.33, cover of rocks: 10%, author: P. Novák. Relevé 19 in Supplements E1 and E2.

E_3 (85%, mean height = 9 m): *Carpinus orientalis* 5, *Fraxinus excelsior* 2b; E_2 (1%, mean height = 0.8 m): *Hedera helix* +, *Smilax excelsa* +, *Staphylea colchica* +; E_1 (30%, mean height = 0.2 m): *Hedera helix* 2a, *Brachypodium sylvaticum* 1, *Primula acaulis* 1, *Ruscus aculeatus* 1, *Sedum stoloniferum* 1, *Vinca major* subsp. *hirsuta* 1, *Viola alba* 1, *Acer campestre* +, *Asplenium adiantum-nigrum* +, *A. trichomanes* +, *Campanula alliariifolia* +, *Carex muricata* aggr. +, *C. sylvatica* +, *Clinopodium umbrosum* +, *Klasea quinquefolia* +, *Lamium galeobdolon* +, *Lapsana communis* +, *Lathyrus laxiflorus* +, *Orobanche laxissima* +, *Polypodium cambricum* +, *Quercus petraea* subsp. *iberica* +, *Sanicula europaea* +, *Silene balansae* +, *Smilax excelsa* +, *Teucrium chamaedrys* +, *Veronica peduncularis* +, *Gleditsia triacanthos* r, *Prunus avium* r, *Schedonorus giganteus* r, *Trachycarpus fortunei* r; E_0 (15%): indet.

Diagnostic species of the new association: *Asplenium adiantum-nigrum*, *Buxus sempervirens*, *Campanula alliariifolia*, *Carpinus orientalis*, *Hedera helix*, *Klasea quinquefolia*, *Lathyrus laxiflorus*, *Potentilla micrantha*, *Ruscus aculeatus*, *Smilax excelsa*, *Teucrium chamaedrys*, *Vinca major* subsp. *hirsuta*.

Table 1. Shortened synoptic table summarizing the classification results, species percentage frequencies are provided. Highly diagnostic species ($\Phi \geq 0.55$; grey shaded) for each cluster are shown. Highly diagnostic species for three main clusters are provided separately or marked by an asterisk if concurrently highly diagnostic for some of the clusters. Full version of the table is stored in Supplement E3.

Tabelle 1. Gekürzte Übersichtstabelle, die die Klassifikationsergebnisse zusammenfasst, prozentuale Stetigkeiten sind dargestellt. Hochdiagnostische Arten für die drei Hauptcluster werden separat dargestellt oder mit einem Sternchen gekennzeichnet, wenn sie gleichzeitig für einige der Cluster hochdiagnostisch sind. Die vollständige Version der Tabelle befindet sich in Anhang E3.

Cluster	1	2	3	4	5	6	7	8	9
Number of relevés	10	4	20	12	3	7	22	15	12
Main cluster 1									
Campanula alliariifolia	60	50	80	.	.	.	.	.	.
Oplismenus hirtellus subsp. *undulatifolius*	.	50	60	.	.	.	.	.	.
Cluster 1									
Arbutus andrachne	70	.	.	.	.	.	.	.	.
Cistus salviifolius	60	.	.	.	.	.	.	.	.
Laurus nobilis	60	.	5	.	.	14	.	.	.
Rhododendron ponticum	60	25	.	.	.	.	5	.	.
Cluster 2									
Buxus sempervirens	.	75	25	.	.	.	.	.	.
Vinca minor	.	50	.	.	.	.	.	.	.
Vincetoxicum nigrum	.	50	.	.	.	.	.	.	.
Datisca cannabina	10	50	.	.	.	.	.	.	.
Rhamnus imeretina	.	50	.	.	.	14	.	.	.
Hypericum xylosteifolium	10	50	.	.	.	.	5	.	.
Cluster 3									
Vinca major subsp. *hirsuta**	.	.	90	.	.	.	.	.	.
*Viola alba**	.	.	85	.	.	.	.	.	.
*Klasea quinquefolia**	.	.	75	.	.	.	.	.	.
Carex digitata	.	.	60	.	.	.	.	.	.
Clinopodium umbrosum	.	.	55	.	.	.	.	.	.
Veronica peduncularis	.	.	50	.	.	.	.	.	.
Diospyros lotus	.	.	40	.	.	.	.	.	.
Asplenium trichomanes	.	.	50	.	.	.	14	.	.
Viola reichenbachiana	.	.	35	.	.	.	.	.	.
Main cluster 2									
Epimedium pubigerum	20	25	.	83	67	57	.	13	8
Salvia forsskaolei	20	50	.	83	33	71	.	13	8
Asperula cimulosa	30	25	.	83	33	57	.	.	33
Carpinus betulus	.	.	35	58	100	86	9	.	8
Cirsium hypoleucum	30	25	.	75	33	57	5	.	17
Fagus orientalis	.	.	15	67	100	14	.	7	.
Cluster 4									
*Euphorbia oblongifolia**	.	.	.	75	.	14	.	.	.
Cluster 5									
Sesleria phleoides	.	.	.	.	100	.	.	.	.
Dictamnus albus	.	.	.	8	100	.	.	.	.
Cotinus coggygria	.	.	5	.	100	.	5	7	.
Tilia platyphyllos	.	.	.	8	100	14	.	.	.
Quercus pubescens	.	.	.	.	100	.	.	.	25
Frangula alnus	.	.	.	.	67	.	.	.	.
Pimpinella tripartita	.	.	5	.	67	.	.	.	.
Corylus avellana	20	.	20	17	100	14	27	.	.
Colutea cilicica	.	.	.	.	67	.	5	.	25
Campanula glomerata	.	.	.	17	67	.	.	.	17
Tanacetum poteriifolium	.	.	.	8	67	.	9	.	25

Cluster	1	2	3	4	5	6	7	8	9
Number of relevés	10	4	20	12	3	7	22	15	12
Fraxinus ornus	.	25	.	8	67	14	.	.	.
Cota tinctoria	.	.	.	.	33	.	.	.	.
Cluster 6									
Hedera colchica	.	.	20	8	.	57	.	.	.
Main cluster 3									
Crataegus monogyna	.	.	.	.	.	.	59	93	.
Quercus cerris	.	.	.	58	33	57	82	100	100
Cluster 7									
Potentilla reptans	.	.	.	.	.	.	36	.	.
Cluster 8									
Rubus ulmifolius	.	.	.	.	.	.	.	40	.
Cluster 9									
Vicia cracca	.	.	.	17	.	.	5	.	83
Crataegus rhipidophylla	.	.	.	.	.	.	.	.	42
Lathyrus roseus	.	.	.	.	.	.	.	.	42
Nepeta nuda subsp. *albiflora*	.	.	.	.	.	.	.	.	42
Sorbus umbellata	.	.	.	.	.	.	.	.	42
Cephalanthera rubra	.	.	.	17	.	.	9	.	58
Aristolochia pallida	.	.	.	.	.	.	.	.	33
Silene latifolia	.	.	.	.	.	.	.	.	33

Erweiterte deutsche Zusammenfassung

Einleitung – Die Wälder der Kolchis (Ökoregion Kaukasus, euxinische Provinz) stellen ein einzigartiges Refugium tertiärer Reliktbiota dar (NAKHUTSRISHVILI et al. 2015). Sie wurden jedoch hauptsächlich in Bulgarien und der Türkei pflanzensoziologisch untersucht (z. B. QUÉZEL et al. 1980), während in Georgien nur eine begrenzte Anzahl von Studien existiert (z. B. NOVÁK et al. 2019). Eine pflanzensoziologische Untersuchung mit Schwerpunkt auf thermophilen Laubwäldern der georgischen Kolchis fehlte bisher. Daher waren die Ziele dieser Studie (1) die Ökologie und Artenzusammensetzung der *Carpinus orientalis*-Wälder der georgischen Kolchis als ein Beispiel für kolchische thermophile Wälder zu beschreiben; (2) die ökologischen und floristischen Beziehungen zwischen der hier untersuchten Gesellschaft und analogen, bisher in der euxinischen Provinz erfassten Gesellschaften zu ermitteln.

Untersuchungsgebiet – Die Stichprobenerhebung konzentrierte sich auf mesozoische Kalksteingebiete in den Ausläufern des Großkaukasus im westlichen Georgien (BONDYREV et al. 2015). Das Untersuchungsgebiet hat ein feuchtes warm-gemäßigtes Klima, die Probenahmestellen hatten eine mittlere Jahrestemperatur von 11,8–14,8 °C und einen jährlichen Niederschlag von 999–2074 mm. Innerhalb Georgiens gilt es als das Gebiet, das außerordentlich reich an endemischen Gefäßpflanzenarten ist (SLODOWICZ et al. 2018).

Methoden – Wir erhoben 20 Vegetationsaufnahmen der Waldvegetation, die von Car*pinus orientalis* dominiert oder mitdominiert wurde. Anschließend haben wir einen Datensatz sowohl dieser Vegetationsaufnahmen, als auch der Aufnahmen analoger Assoziationen und Gesellschaften aus dem türkischen Teil der euxinischen Provinz (n = 105 Aufnahmen insgesamt) zusammengestellt. Wir haben flexibles Beta-Clustering (β = -0,2, Bray-Curtis-Distanz) und eine NMDS-Ordinationsanalyse angewendet, um Hauptmuster in ihrer Artenzusammensetzung zu erkennen.

Ergebnisse und Diskussion – Die in Georgien erfassten *Carpinus orientalis*-Wälder besetzten normalerweise steile und oft felsige Hänge mit steinigem Oberboden mit neutraler bis schwach alkalischer Reaktion (pH 6,6–7,8). In der Baumschicht wurde *C. orientalis* häufig von anderen Laubbaumarten begleitet. Das Unterholz enthielt zahlreiche immergrüne Arten (z. B. *Hedera helix*, *Ruscus aculeatus*, *Smilax excelsa*, *Vinca major* subsp. *hirsuta*). Waldmesophyten (z. B. *Carex digitata*, *Veronica* *peduncularis*) waren in der Krautschicht häufig, begleitet von Xerophyten (z. B. *Klasea quinquefolia*, *Teucrium chamaedrys*). Chasmophyten waren ebenfalls vorhanden (z. B. *Asplenium scolopendrium*, *A. trichomanes*).

Die Clusteranalyse des Datensatzes ergab drei Hauptcluster, die eng mit der Biogeographie verknüpft sind. Bei dem ersten, dem östlichsten, handelte es sich um Typen mit signifikantem kaukasischem und ostauxinischem floristischem Einfluss. Er enthielt die georgische Gesellschaft und die Assoziation *Erico-Carpinetum*, Typusassoziation des Verbandes *Castaneo sativae-Carpinion orientalis*. Der zweite Hauptcluster war auf den zentralen Teil der euxinischen Provinz beschränkt. Aufgrund seines eher mesophilen Charakters, der oft von *Carpinus betulus* oder *Fagus orientalis* mitdominiert wird, scheint er einen Übergang zwischen thermophilen Wäldern und Eichen-Hainbuchen-Wäldern des Verbandes *Trachystemono orientalis-Carpinion betuli* darzustellen. Die dritte Hauptgruppe umfasste insbesondere Mischwälder aus *C. orientalis* und *Quercus cerris*. Sie wurden fast ausschließlich im westlichen Teil der Provinz nachgewiesen und enthielten mehr Balkan- oder Mittelmeerarten, die auf den westlichen Teil der euxinischen Provinz beschränkt sind. Diese Einheit wurde nach der Klassifizierung von ÇOBAN & WILLNER (2019) dem Verband *Quercion confertae* zugeordnet. In der feineren Unterteilung des Datensatzes waren die meisten beteiligten Assoziationen und Gesellschaften gut erkannt, was auf ihre charakteristische floristische Zusammensetzung hinweist. Diese zeigte auch viele einzigartige floristische Merkmale der georgischen Gesellschaft, die daher als neue Assoziation *Campanulo alliariifolae-Carpinetum orientalis* ass. nova hoc loco beschrieben wurde (Verband *Castaneo-Carpinion*). Die Ordinationsanalyse betonte auch die Bedeutung der Biogeographie für die Diversität der euxinischen *Carpinus orientalis*-Wälder, die vermutlich durch das Makroklima und die Vegetationsgeschichte bedingt wird.

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Author contributions

P.N. led the writing and performed analyses. P.N. and V.S. conceived the idea of the research. P.N and V.K. participated in the field sampling. All the authors critically revised the manuscript.

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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. Relevé table of the association *Campanulo alliariifoliae-Carpinetum orientalis*.

Anhang E1. Tabelle der Vegetationsaufnahmen des *Campanulo alliariifoliae-Carpinetum orientalis*.

Supplement E2. Header data for the original relevés of Supplement E1.

Anhang E2. Kopfdaten der Vegetationsaufnahmen von Anhang E1.

Supplement E3. Full synoptic table and correspondence between associations and clusters.

Anhang E3. Vollständige Übersichtstabelle und Übereinstimmung zwischen den Assoziationen und Clustern.

Supplement E4. Additional photos of the vegetation of the association *Campanulo alliariifoliae-Carpinetum orientalis*.

Anhang E4. Zusätzliche Fotos der Vegetation des *Campanulo alliariifoliae-Carpinetum orientalis.*

References

AKHALKATSI, M. (2015): Forest habitat restoration in Georgia, Caucasus Ecoregion. – Mtsignobari, Tbilisi: 102 pp.

AKHALKATSI, M. (2019): Plant species in NATURA 2000 habitats in Georgia. – Publisher of Plant Genetic Resources Division of Botany Institute, Tbilisi: 310 pp.

ASANIDZE, L., LEZHAVA, Z., TSIKARISHVILI, K., GAPRINDASHVILI, G., CHIKHRADZE, N. & POLK, J. (2019): Karst map of Georgia (Caucasus region) scale: 1:1 500 000. – Carbonates Evaporites 34: 1205–1212.

BLASI, C., DI PIETRO, R., FILESI, L. & FORTINI, P. (2001): Syntaxonomy, chorology and syndynamics of *Carpinus orientalis* communities in central Italy. – Phytocoenologia 31: 33–62.

BOHN, U., NEUHÄUSL, R., GOLLUB, G., HETTWER, C., NEUHÄUSLOVÁ, Z., RAUS, T., SCHLÜTER, H. & WEBER, H.E. (Eds.) (2000–2003): Karte der natürlichen Vegetation Europas / Map of the natural vegetation of Europe. Maßstab / Scale 1:2 500 000. – Landwirtschaftsverlag, Münster: 512 pp.

BONDYREV, I.V., DAVITASHVILI, Z.V. & SINGH, V.P. (2015): The geography of Georgia: problems and perspectives. – Springer, Cham: 228 pp.

CHYTRÝ, M., HENNEKENS, S.M., JIMÉNEZ-ALFARO, B. … YAMALOV, S. (2016): European Vegetation Archive (EVA): an integrated database of European vegetation plots. – Appl. Veg. Sci. 19: 173–180.

CHYTRÝ, M., TICHÝ, L., HOLT, J. & BOTTA-DUKÁT, Z. (2002): Determination of diagnostic species with statistical fidelity measures. – J. Veg. Sci. 13: 79–90.

ÇOBAN, S. & WILLNER, W. (2019): Numerical classification of the forest vegetation in the western Euxine region of Turkey. – Phytocoenologia 49: 71–106.

DENGLER, J., CHYTRÝ, M. & EWALD, J. (2008): Phytosociology. – In: JØRGENSE, S.E. & FATH, B.D. (Eds.): Encyclopedia of Ecology, Vol. 4: 2767–2779. Elsevier, Oxford.

DENK, T., FROTZLER, N. & DAVITASHVILI, N. (2001): Vegetational patterns and distribution of relict taxa in humid temperate forests and wetlands of Georgia (Transcaucasia). – Biol. J. Linn. Soc. 72: 287–332.

DIDUKH, Y.P. (1996): The communities of the class *Quercetea pubescenti-petraeae* at the Crimean Mountains. – Ukr. Fitotsenol. Zbirn., Ser. A, 1: 63–77.

DOLUKHANOV, A.G. (1980): Kolkhidskii podlesok (Colchic understorey) [in Russian]. – Metsniereba, Tbilisi: 261 pp.

DOLUKHANOV, A.G. (2010): Lesnaya rastitelnost Gruzii (Forest vegetation of Georgia) [in Russian]. – Universal, Tbilisi: 532 pp.

DONNER, J. (1990): Distribution maps to P.H. Davis, "Flora of Turkey, 1–10". – Linzer Biol. Beitr. 22: 385–515.

FILIBECK, G., ARRIGONI, P.V. & BLASI, C. (2004): Some phytogeographical remarks on the forest vegetation of Colchis (Western Georgia). – Webbia 59: 189–214.

FISCHER, H.S. (2015): On the combination of species cover values from different vegetation layers. – Appl. Veg. Sci. 18: 169–170.

GHOLIZADEH, H., NAQINEZHAD, A. & CHYTRÝ, M. (2020): Classification of the Hyrcanian forest vegetation, Northern Iran. – Appl. Veg. Sci. 23: 107–126.

GRIMM, G.W. & DENK, T. (2014): The Colchic region as refuge for relict tree lineages: cryptic speciation in field maples. – Turk J. Bot. 38: 1050–1066.

GULISASHVILI, V.Z., MAKHATADZE, L.B. & PRILIPKO, L.I. (1975): Rastitelnost Kavkaza (Vegetation of the Caucasus) [in Russian]. – Nauka, Moskva: 232 pp.
HENNEKENS, S.M. & SCHAMINÉE, J.H.J. (2001): TURBOVEG, a comprehensive database management system for vegetation data. – J. Veg. Sci. 12: 589–591.
KARGER, D.N., CONRAD, O., BÖHNER, J., KAWOHL, T., KREFT, H., SORIA-AUZA, R.W., ZIMMERMANN, N.E., LINDER, P. & KESSLER, M. (2017): Climatologies at high resolution for the Earth land surface areas. – Sci. Data 4: 170122.
KAVGACI, A., ARSLAN, M., BINGÖL, Ü., ERDOĞAN, N. & ČARNI, A. (2012): Classification and phytogeographical differentiation of oriental beech forests in Turkey and Bulgaria. – Biologia 67: 461–473.
KIKODZE, D., MEMIADZE, N., KHARAZISHVILI, D., MANVELIDZE, Z. & MUELLER-SCHAERER, H. (2010): The alien flora of Georgia. 2nd ed. – Joint SNSF SCOPES and FOEN publication, Ascona & Tbilisi: 36 pp.
KOLAKOVSKII, A.A. (1961): Rastitelnyi mir Kolkhidy (Plant World of Colchis) [in Russian]. – Izdatelstvo Moskovskogo universiteta, Moskva: 460 pp.
KORKMAZ, H., ENGIN, A., KUTBAY, H.G. & YALÇIN, E. (2011): A syntaxonomical study on the scrub, forest, and stepe vegetation of the Kızılırmak valley. – Turk. J. Bot. 35: 121–165.
KUTBAY, H.G. & KILINÇ, M. (1995): Bafra Nebyan Dağı (Samsun) ve çevresinin vejetasyonu üzerinde fitososyolojik ve ekolojik bir araştırma (A phytosociological and ecological investigation of Bafra Nebyan Mountains (Samsun) and its environs) [in Turkish with English summary]. – Turk. J. Bot. 19: 41–63.
KÜRSCHNER, H., KIRMACI, M., ERDAĞ, A., BATSATSASHVILI, K. & PAROLLY, G. (2012): Ecology and life strategies of epiphytic bryophyte communities from the Arcto-Tertiary relict forests of the Black and Caspian Sea areas. – Nova Hedwigia 94: 31–65.
MATSIAKH, I., KRAMARETS, V. & MAMADASHVILI, G. (2018): Box tree moth *Cydalima perspectalis* as a threat to the native populations of *Buxus colchica* in Republic of Georgia. – J. Entomol. Res. Soc. 20(2): 29–42.
MILNE, R.I. & ABBOTT, R.J. (2002): The origin and evolution of Tertiary relict floras. – Adv. Bot. Res. 38: 281–314.
MITCHELL, R., CHITANAVA, S., DBAR, R. ... KENIS, M. (2018): Identifying the ecological and societal consequences of a decline in Buxus forests in Europe and the Caucasus. – Biol. Inv. 20: 3605–3620.
MITTERMEIER, R.A., ROBLES GIL, P., HOFFMANN, M., PILGRIM, J., BROOKS, T., MITTERMEIER, C.G., LAMOREUX, J. & DA FONSECA, G.A.B. (2004): Hotspots revisited: Earth's biologically richest and most endangered terrestrial ecoregions. – CEMEX, Mexico City: 390 pp.
MUCINA, L, BÜLTMANN, H., DIERßEN, K. … TICHÝ, L. (2016): Vegetation of Europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. – Appl. Veg. Sci. 19: 3–264.
NAKHUTSRISHVILI, G. (2013): The Vegetation of Georgia (South Caucasus). – Springer, Berlin: 235 pp.
NAKHUTSRISHVILI, G., ZAZANASHVILI, N., BATSATSASHVILI, K. & MONTALVO MANCHENO, C.S. (2015): Colchic and Hyrcanian forests of the Caucasus: similarities, differences and conservation status. – Flora Medit. 25: 185–192.
NOVÁK, P., ZUKAL, D., HARÁSEK, M., VLČKOVÁ, P., ABDALADZE, O. & WILLNER, W. (2020): Ecology and vegetation types of oak-hornbeam and ravine forests of the Eastern Greater Caucasus, Georgia. – Folia Geobot. 55: 333–349.
NOVÁK, P., ZUKAL, D., KALNÍKOVÁ, V., CHYTRÝ, K. & KAVGACI, A. (2019): Ecology and syntaxonomy of Colchic forests in south-western Georgia (Caucasus region). – Phytocoenologia 49: 231–248.
OKSANEN, J., GUILLAUME BLANCHET, F., FRIENDLY, M. … WAGNER, H. (2020): vegan: Community Ecology Package. R package version 2.5-7. – URL: cran.r-project.org/web/packages/vegan/.
QUÉZEL, P., BARBÉRO, M. & AKMAN, Y. (1980): Contribution à l'étude de la végétation forestière d'Anatolie septentrionale (Contribution to study of the forest vegetation of northern Anatolia) [in French with English summary]. – Phytocoenologia 8: 365–519.
QUÉZEL, P., BARBERO, M. & AKMAN, Y. (1992): Typification de syntaxa décrits en région méditerranéenne orientale (Typification of syntaxa described in the eastern Mediterranean region) [in French with English summary]. – Ecol. Medit. 18: 81–87.
R Core Team (2020): R: A language and environment for statistical computing. Version 4.0.2. – R Foundation for Statistical Computing. – URL www.R-project.org.

SIKKEMA, R. & CAUDULLO, G. (2016): *Carpinus orientalis* in Europe: distribution, habitat, usage and threats. – In: SAN-MIGUEL-AYANZ, J., DE RIGO, D., CAUDULLO, G., HOUSTON DURRANT, T. & MAURI, A. (Eds.): European atlas of forest tree species: 73–75. Publication Office of the European Union, Luxembourg.

SLODOWICZ, D., DESCOMBES, P., KIKODZE, D., BROENNIMANN, O. & MÜLLER-SCHÄRER, H. (2018): Areas of high conservation value at risk by plant invaders in Georgia under climate change. – Ecol. Evol. 8: 4431–4442.

SOCHOR, M. & TRÁVNÍČEK, B. (2016): Melting pot of biodiversity: first insights into the evolutionary patterns of the Colchic bramble flora (*Rubus* subgenus *Rubus*, *Rosaceae*). – Bot. J. Linn. Soc. 181: 610–620.

STUPAR, V., BRUJIĆ, J. & LUKIĆ, O. (2020): Two new mesophilous oriental hornbeam communities from the northern Dinaric Alps (Bosnia and Herzegovina). – Hacquetia 19: 259–273.

STUPAR, V., BRUJIĆ, J., ŠKVORC, Ž. & ČARNI, A. (2016): Vegetation types of thermophilous deciduous forests (*Quercetea pubescentis*) in the Western Balkans. – Phytocoenologia 46: 49–68.

STUPAR, V., MILANOVIĆ, Đ., BRUJIĆ, J. & ČARNI, A. (2015): Formalized classification and nomenclatural revision of thermophilous deciduous forests (*Quercetalia pubescentis*) of Bosnia and Herzegovina. – Tuexenia 35: 85–130.

TAKHTAJAN, A.L. (1986): Floristic regions of the world. – University of California Press, Berkeley: 522 pp.

THEURILLAT, J.P., WILLNER, W., FERNÁNDEZ-GONZÁLEZ, F., BÜLTMANN, H., ČARNI, A., GIGANTE, D., MUCINA, L. & WEBER, H. (2021): International Code of Phytosociological Nomenclature. 4th edition. – Appl. Veg. Sci. 24: e12491.

TICHÝ, L. (2002): JUICE, software for vegetation classification. – J. Veg. Sci. 13: 451–453.

TICHÝ, L. & CHYTRÝ, M. (2006): Statistical determination of diagnostic species for site groups of unequal size. – J. Veg. Sci. 17: 809–818.

TICHÝ, L., HENNEKENS, S.M., NOVÁK, P., RODWELL, J.S., SCHAMINÉE, J.H. & CHYTRÝ, M. (2020): Optimal transformation of species cover for vegetation classification. – Appl. Veg. Sci. 23: 710–717.

TZONEV, R., DIMITROV, M., GUSSEV, C. … GLOGOV, P. (2019): Phytosociological classification of the thermophilous oak forests in Bulgaria: new interpretations and gaps in knowledge. – Phytocoenologia 49: 369–391.

URUSHADZE, T.F. & GHAMBASHIDZE, G.O. (2013): Soils of Georgia. – In: YIGINI, Y., PANAGOS, P. & MONTANARELLA, L. (Eds.): Soil resources of Mediterranean and Caucasus countries: 78–96. Office for Official Publications of the European Communities, Luxembourg.

VOLKOVA, P., LACZKÓ, L., DEMINA, O., SCHANZER, I. & SRAMKÓ, G. (2020): Out of Colchis: The colonization of Europe by *Primula vulgaris* Huds. (*Primulaceae*). – Acta Soc. Bot. Polon. 89: Art. 89313.

WALTER, H. (1970): Vegetationszonen und Klima. – Ulmer, Stuttgart: 309 pp.

YARCI, C. (2002): Istranca Dağları'ndan (Trakya Bölgesi) iki yeni birlik: *Carpino betuli-Fagetum orientalis* Yarcı ass. nov. ve *Querco cerridis-Carpinetum orientalis* Yarcı ass. nov. (Two new associations from the Istranca Mountains [Thrace Region]: *Carpino betuli-Fagetum orientalis* Yarcı ass. nov. and *Querco cerridis-Carpinetum orientalis* Yarcı ass. nov.) [in Turkish with English summary]. – Ekoloji Çevre Dergisi 11(42): 1–7.

ZAZANASHVILI, N., GAGNIDZE, R. & NAKHUTSRISHVILI, G. (2000): Main types of vegetation zonation on the mountains of the Caucasus. – Acta Phytogeogr. Suec. 85: 7–16.

ZAZANASHVILI, N. & MALLON, D. (Eds.) (2009): Status and protection of globally threatened species in the Caucasus. – CEPF & WWF, Tbilisi: 232 pp.

Supplement E1. Relevé table of the association *Campanulo alliariifoliae-Carpinetum orientalis* ass. nova hoc loco. Species are sorted according to vegetation layer and within layers according to decreasing frequency. Species recorded in one relevé are provided below the table. Header data are stored in Supplement E2.

Anhang E1. Tabelle der Vegetationsaufnahmen des Verbandes *Campanulo alliariifolae-Carpinetum* orientalis ass. nova hoc loco. Die Arten sind nach Vegetationsschichten und innerhalb der Schichten nach abnehmender Häufigkeit sortiert. Die in einer Vegetationsaufnahme erfassten Arten sind unter der Tabelle aufgeführt. Kopfdaten werden im Anhang E2 aufgeführt.

Relevé number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Tree layer cover (%)	95	90	90	90	85	85	70	70	85	70	80	80	90	70	85	80	90	80	85	85
Shrub layer cover (%)	8	7	20	3	20	12	15	20	35	25	10	30	8	3	1	30	5	15	1	2
Herb layer cover (%)	30	35	60	15	30	35	55	65	40	25	30	25	30	60	45	35	30	40	30	30
Moss layer cover (%)	4	2	5	6	5	20	20	10	10	40	30	0	5	12	6	2	30	40	15	50
Tree layer																				
Carpinus orientalis	3	3	5	4	3	4	3	5	3	4	4	4	5	4	5	.	5	5	5	5
Carpinus betulus	2b	3	.	4	2b	3	.	.	.	.	.	.	2a	.	2a	.	.	.	.	.
Acer campestre	1	2a	.	.	.	.	1	.	.	.	2a	.	2a	.	.	1	.	.	.	2a
Quercus petraea subsp. *iberica*	2b	.	.	.	.	.	.	.	.	.	2a	.	.	2b	.	.	.	.	.	.
Hedera helix	1	.	.	.	.	.	+	.	.	.	.	1	.	.	.	.	.	.	.	.
Fagus orientalis	.	.	.	.	2b	.	2a	.	2a	.	.	.	.	.	.	.	.	.	.	.
Fraxinus excelsior	.	.	.	.	.	.	1	.	.	.	1	.	.	.	.	.	.	.	2b	.
Acer cappadocicum	.	.	.	.	2a	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.
Robinia pseudoacacia	.	.	.	.	.	2m	.	.	.	.	.	.	.	.	.	2a	.	.	.	.
Ulmus glabra	.	.	.	.	.	.	.	1	.	.	.	2a	.	.	.	.	.	.	.	.
Zelkova carpinifolia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2b	5	.	.	.	.
Shrub layer																				
Smilax excelsa	.	+	2a	+	1	1	+	2a	1	1	.	.	2a	1	.	.	1	+	+	.
Carpinus orientalis	.	1	2a	.	1	+	+	.	2a	2a	1	.	+	.	.	2b	.	1	.	.
Crataegus sp.	.	+	.	.	1	1	+	1	.	.	1	.	.	.	.	.	.	.	.	.
Buxus sempervirens	1	.	.	.	1	.	.	.	.	.	.	2b	.	.	+	.	.	.	.	+
Cornus sanguinea	.	+	.	.	.	.	.	.	.	+	.	.	.	+	.	.	+	.	.	.
Quercus petraea subsp. *iberica*	.	.	.	.	1	.	.	.	+	+	.	.	.	1	.	.	.	.	.	.
Hedera helix	.	.	.	.	.	.	+	.	.	.	.	.	.	+	+	.	.	.	+	.
Corylus avellana	.	.	.	.	.	.	.	2a	2a	1	.	.	+	.	.	.	.	.	.	.
Ilex colchica	2m	+	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Crataegus pentagyna	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.
Ligustrum vulgare	.	.	.	.	.	.	+	.	.	.	+	.	.	.	.	.	.	+	.	.
Castanea sativa	+	.	.	.	.	.	.	.	2b	.	.	.	.	.	.	.	.	.	.	.
Rosa sp.	.	+	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.
Diospyros lotus	.	.	+	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.
Staphylea colchica	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	+	.
Ficus carica	.	.	.	.	.	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.
Pyrus communis	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	1	.	.
Philadelphus coronarius	.	.	.	.	.	.	.	.	.	1	+	.	.	.	.	.	.	.	.	.
Cornus mas	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	1	.	.
Herb layer																				
Vinca major subsp. *hirsuta*	1	+	1	+	+	1	+	2b	2a	2a	2m	+	1	+	.	+	+	.	1	+
Brachypodium sylvaticum	+	+	1	+	+	+	+	+	+	+	+	+	.	.	1	1	1	+	1	1
Hedera helix	1	1	2b	1	+	.	2b	1	+	1	.	1	r	.	1	2b	+	+	2a	1
Primula acaulis	1	1	2m	1	.	1	1	r	.	1	1	.	1	+	1	1	1	1	1	+
Viola alba	1	+	+	+	+	1	.	.	.	+	+	+	+	+	1	1	+	1	1	1
Smilax excelsa	+	+	2a	+	1	1	1	1	.	.	+	1	1	1	1	1	+	+	+	.
Campanula alliariifolia	+	+	.	+	.	+	+	2a	.	1	2m	.	+	+	+	+	1	1	+	+
Klasea quinquefolia	+	.	+	+	+	+	+	+	.	.	+	+	+	.	.	+	+	+	+	+
Ruscus aculeatus	.	.	2a	+	1	2a	+	r	.	+	+	+	.	.	2b	1	2b	3	1	1
Lathyrus laxiflorus	+	+	r	.	.	+	.	+	.	+	2a	.	.	+	+	+	+	1	+	+
Sanicula europaea	2a	1	+	+	+	.	1	+	.	+	+	+	+	.	.	.	.	.	+	.
Dioscorea communis	+	.	r	r	+	+	+	+	+	+	+	+	+	.	.	.	.	.	.	.
Potentilla micrantha	+	.	.	+	+	+	+	+	r	1	+	.	+	r	.	.	+	.	.	.
Oplismenus hirtellus subsp. *undulatifolius*	.	+	+	1	.	2a	+	2a	1	+	.	+	.	.	2a	+	+	.	.	.
Campanula rapunculoides	.	+	.	.	+	+	.	+	1	r	.	+	+	.	+	+	+	.	.	1
Carex digitata	.	.	+	+	+	.	1	1	1	1	+	.	+	.	+	.	1	1	.	.
Clinopodium umbrosum	+	+	+	+	.	+	.	.	.	.	+	+	.	.	+	+	.	+	+	.
Asplenium adiantum-nigrum	.	+	+	+	+	+	+	.	.	.	1	.	.	.	+	.	+	.	+	1
Veronica peduncularis	.	+	+	+	.	+	.	.	.	.	+	.	.	r	.	.	+	+	+	+
Drymochloa drymeja	.	.	+	+	2a	.	+	2b	2b	.	+	+	1	2a	.	.	.	.	.	.
Asplenium trichomanes	.	.	+	+	.	.	r	+	.	+	+	.	.	.	+	.	+	+	+	.
Carex sylvatica	1	.	.	+	.	1	1	.	.	+	.	+	.	.	+	.	.	.	+	+
Carex muricata aggr.	.	+	+	.	.	.	.	.	.	.	.	+	.	.	1	+	+	+	+	1
Viola reichenbachiana	+	.	.	.	.	+	+	+	r	+	.	+	.	.	.	.	.	.	.	.
Leontodon hispidus	.	.	1	+	.	.	.	r	.	.	.	.	.	.	+	1	1	1	.	.
Symphytum grandiflorum	2m	1	+	.	+	.	.	+	.	.	.	2m	.	.	.	.	.	.	.	.
Helleborus orientalis	+	+	.	.	.	.	.	.	.	.	.	+	.	.	.	1	1	+	.	.
Lathyrus vernus	+	.	.	+	.	.	.	.	r	.	.	+	+	.	.	.	+	.	.	.
Lapsana communis	.	+	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+
Asplenium scolopendrium	.	+	.	r	.	+	+	.	r	+	.	.	.	.	.	.	.	.	.	.
Teucrium chamaedrys	.	r	.	.	.	.	+	.	.	.	.	.	.	.	r	.	+	+	+	.
Trachystemon orientalis	.	.	+	.	+	.	+	1	1	+	.	.	.	.	.	.	.	.	.	.
Prunella vulgaris	.	.	+	.	.	+	+	.	.	.	+	r	.	.	.	.	+	.	.	.
Hieracium sabaudum	.	.	.	.	+	.	+	r	.	.	+	.	.	r	.	.	.	r	.	.
Rubus subgen. *Rubus*	.	.	+	.	.	+	.	.	.	1	.	.	+	.	.	.	+	.	.	.
Carpesium cernuum	.	.	.	+	.	+	.	.	.	.	.	.	.	.	+	+	+	.	.	.
Pteridium aquilinum	.	.	.	.	+	.	1	.	+	+	.	.	.	.	.	.	+	.	.	.
Digitalis schischkinii	.	.	.	.	+	.	.	r	1	+	+	.	.	.	.	.	.	.	.	.
Carex michelii	+	.	+	.	.	.	.	.	.	.	.	.	+	.	.	+	.	.	.	.
Luzula forsteri	+	.	.	.	+	+	.	.	.	r	.	.	.	.	.	.	.	.	.	.
Ajuga reptans	+	.	.	.	.	+	.	.	.	.	.	+	.	.	.	+	.	.	.	.
Euphorbia macroceras	.	1	.	.	+	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.
Calystegia silvatica	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.
Plantago lanceolata	.	.	+	.	.	r	.	.	.	.	.	.	.	.	.	.	r	+	.	.
Carex flacca subsp. *serrulata*	.	.	.	.	+	.	+	.	.	.	.	.	.	+	.	.	.	+	.	.
Physospermum cornubiense	.	.	.	.	+	.	.	.	.	.	+	.	+	+	.	.	.	.	.	.
Schedonorus giganteus	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	+	.	.	r	.
Sedum stoloniferum	.	.	.	.	.	+	.	.	.	.	+	.	.	.	.	.	.	.	1	1
Silene balansae	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	+	.	.	+	+
Salvia glutinosa	.	+	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.
Hedera colchica	.	+	.	.	.	.	.	.	.	.	1	.	.	2a	.	.	.	.	.	.
Trifolium repens	.	.	+	.	.	+	.	.	.	.	.	.	.	.	.	.	+	.	.	.
Epimedium pinnatum subsp. *colchicum*	.	.	.	.	1	.	.	.	.	.	.	.	2b	2a	.	.	.	.	.	.
Lonicera caprifolium	.	.	.	.	+	.	.	.	.	.	+	.	.	+	.	.	.	.	.	.
Peucedanum adae	.	.	.	.	+	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.
Ruscus colchicus	.	.	.	.	.	+	+	.	.	.	.	.	.	+	.	.	.	.	.	.
Medicago lupulina	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	+	+	.	.
Poa angustifolia	.	.	.	.	.	.	+	.	.	.	+	.	.	.	.	+	.	.	.	.
Securigera varia	.	.	.	.	.	.	r	.	.	+	.	.	.	.	.	.	.	r	.	.
Pimpinella saxifraga	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	+	.	+	.	.
Origanum vulgare	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+	+	.	.
Peucedanum caucasicum	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	+	.	.
Paeonia caucasica	+	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.
Carex sp.	.	+	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.
Potentilla indica	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Periploca graeca	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.
Fragaria vesca	.	.	.	.	+	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.
Hypericum androsaemum	.	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.
Solidago virgaurea	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.
Arabis nordmanniana	.	.	.	.	.	.	.	+	.	r	.	.	.	.	.	.	.	.	.	.
Galium valantioides	.	.	.	.	.	.	.	+	.	.	.	.	.	+	.	.	.	.	.	.
Euphorbia squamosa	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	+	.	.	.	.
Lamium galeobdolon	.	.	.	.	.	+	.	.	+	.	.	.	.	.	.	.	.	.	+	.
Clematis vitalba	.	.	.	.	.	.	.	.	.	r	.	.	+	.	.	.	.	.	.	.
Polypodium vulgare	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	r	.	.
Sesleria alba	.	.	.	.	.	.	.	.	.	.	.	.	+	2a	.	.	.	.	.	.
Brunnera macrophylla	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.
Cephalanthera longifolia	.	.	.	.	.	.	.	.	.	.	.	.	r	r	.	.	.	.	.	.
Trifolium pratense	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	.	.
Prunella ×intermedia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.
Cruciata glabra	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.
Polypodium cambricum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	1
Orobanche laxissima	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	r
Juveniles																				
Carpinus orientalis	.	+	+	+	.	.	+	.	1	+	.	+	.	+	.	.	+	1	.	.
Quercus petraea subsp. *iberica*	.	.	.	r	.	r	+	+	+	+	+	r	+	.	.	.	.	.	+	.
Crataegus sp.	r	.	+	.	+	+	+	+	.	r	+	.	.	+	.	.	.	.	.	.
Diospyros lotus	r	.	+	+	r	+	.	+	.	.	.	.	.	.	.	.	r	.	.	.
Ficus carica	.	.	.	r	.	+	.	r	r	+	.	.	.	.	.	+	.	+	.	.
Acer campestre	+	.	.	.	.	.	.	.	.	+	.	+	+	.	.	.	+	.	+	.
Cornus sanguinea	.	+	+	.	+	.	.	.	.	r	.	r	.	.	.	.	+	.	.	.
Carpinus betulus	+	+	.	.	+	+	.	.	.	.	.	.	.	.	+	.	.	.	.	.
Acer cappadocicum	+	+	.	.	+	.	.	.	1	.	.	+	.	.	.	.	.	.	.	.
Ligustrum vulgare	+	+	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.
Tilia begoniifolia	.	+	.	.	.	.	.	.	+	.	.	.	+	.	.	.	.	.	.	.
Crataegus pentagyna	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.
Fraxinus excelsior	.	.	.	r	.	.	+	.	.	.	.	.	+	.	.	.	.	.	.	.
Taxus baccata	.	.	.	.	+	.	.	.	.	r	.	.	.	r	.	.	.	.	.	.
Zelkova carpinifolia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	+	.	.	.
Castanea sativa	.	+	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.
Crataegus germanica	.	+	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
Ulmus glabra	.	r	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.
Robinia pseudoacacia	.	.	+	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Prunus avium	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.
Sorbus torminalis	.	.	.	.	+	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.
Staphylea colchica	.	.	.	.	.	+	.	.	.	.	.	.	.	+	.	.	.	.	.	.

Species recorded in one relevé: **Tree layer**: *Pyrus communis* 5: 1; *Hedera colchica* 6: 2a; *Corylus avellana* 8: 2a; *Tilia begoniifolia* 9: 3; *Pinus sylvestris* 12: 2m; *Prunus avium* 13: 2a; *Smilax excelsa* 13: 1; *Quercus hartwissiana* 20: 2a; *Diospyros lotus* 20: 1. **Shrub layer**: *Carpinus betulus* 2: +; *Prunus avium* 2: +; *Punica granatum* 3: +; *Rhododendron luteum* 5: 2a; *Sorbus torminalis* 5: 1; *Robinia pseudoacacia* 6: +; *Sambucus nigra* 8: 1; *Tilia begoniifolia* 9: 1; *Acer cappadocicum* 9: +; *Euonymus latifolius* 10: +; *Fraxinus excelsior* 13: +; *Acer campestre* 13: +; *Hedera colchica* 14: +; *Zelkova carpinifolia* 16: 2a; *Laurus nobilis* 16: 1; *Rosa canina* 17: +. **Herb layer**: *Pulmonaria mollis* 1: r; *Arum* sp. 2: +; *Geranium robertianum* 2: +; *Poa nemoralis* 2: +; *Sison amomum* 2: +; *Torilis japonica* 2: +; *Medicago* sp. 2: r; *Trifolium diffusum* 2: r; *Cirsium vulgare* 3: +; *Dactylis glomerata* 5: +; *Euphorbia amygdaloides* 5: 1; *Viola* sp. 5: r; *Aristolochia pontica* 6: +; *Euphorbia stricta* 6: +; *Plantago major* 6: +; *Lotus corniculatus* 7: +; *Ranunculus polyanthemos* 7: +; *Mercurialis perennis* 8: +; *Vicia sepium* 8: +; *Hypericum perforatum* 9: +; *Pachyphragma macrophyllum* 10: 1; *Taraxacum* sect. *Taraxacum* 10: +; *Silene* sp. 10: r; *Campanula raddeana* 11: 1; *Cardamine parviflora* 11: +; *Galium album* 11: +; *Hieracium murorum* 11: +; *Laser trilobum* 11: +; *Polygonatum glaberrimum* 11: +; *Ranunculus bulbosus* 11: +; *Cyclamen coum* 11: r; *Pimpinella tripartita* 11: r; *Primula veris* subsp. *macrocalyx* 12: 1; *Epipactis* sp. 12: r; *Brachypodium pinnatum* 14: 2a; *Carex humilis* 14: 2m; *Melampyrum elatius* 14: +; *Asplenium ruta-muraria* 14: r; *Jacobaea vulgaris* 15: +; *Erigeron annuus* 16: +; *Adiantum capillus-veneris* 17: +; *Lactuca muralis* 17: +; *Petrorhagia saxifraga* 17: r; *Scabiosa sosnowskyi* 18: +; *Leptopus chinensis* 20: +; *Tanacetum partheniifolium* 20: r. **Juveniles**: *Clematis vitalba* 2: +; *Cotinus coggygria* 2: +; *Malus sylvestris* 2: r; *Morus alba* 3: +; *Fagus orientalis* 7: r; *Lonicera caucasica* 9: +; *Euonymus latifolius* 10: +; *Corylus avellana* 10: +; *Rosa* sp. 11: +; *Euonymus latifolius* 14: r; *Pyrus* sp. 14: r; *Laurus nobilis* 16: r; *Cornus mas* 18: r; *Ulmus minor* 18: r; *Gleditsia triacanthos* 19: r; *Trachycarpus fortunei* 19: r.

Supplement E2. Header data (location, area, site conditions, vegetation height and date) for the original relevés of Supplement E1.

Anhang E2. Kopfdaten (Ort, Region, Standortsbedingungen, Vegetationshöhe und Datum) der Vegetationsaufnahmen von Anhang E1.

#	Municipality	Region	N (°)	E (°)	area (m^2)	Soil pH	Elevation (m)	Aspect (°)	Slope (°)	Cover of rocks (%)	Mean height E_3 (m)	Mean height E_2 (m)	Mean height E_1 (m)	Date
1	Banoja	Imereti	42.30944	42.67333	100	7.02	450	170	10	0	12	2	0.3	2016-07-22
2	Chiatura	Imereti	42.28556	43.30944	100	7.14	490	240	15	1	15	2	0.9	2017-07-03
3	Khidi	Imereti	42.42111	42.49528	100	7.57	250	140	35	3	11	3	0.75	2017-07-09
4	Martvili	Imereti	42.45361	42.37472	100	7.61	220	35	10	3	15	1	0.5	2017-07-09
5	Nokalakevi	Samegrelo	42.36528	42.19417	100	6.53	110	180	35	1	8	3	0.7	2017-07-10
6	Senaki	Samegrelo	42.29222	42.04139	100	6.83	90	250	25	7	13	3	0.5	2017-07-10
7	Tsutskhvati	Imereti	42.27333	42.85417	100	7.5	410	315	30	30	19	6	0.35	2017-07-04
8	Khidi	Imereti	42.42222	42.495	100	7.76	250	270	30	20	10	4	0.35	2017-07-09
9	Nokalakevi	Samegrelo	42.49	42.41806	100	7.67	130	10	30	5	8	2	0.4	2017-07-10
10	Nokalakevi	Samegrelo	42.37194	42.18778	100	7.71	145	360	35	30	10	4	0.6	2017-07-10
11	Katskhi	Imereti	42.28444	43.21556	100	7.2	570	280	35	25	8	2	0.5	2018-05-02
12	Banoja	Imereti	42.30972	42.67417	100	6.59	461	180	5	0	10	2	0.2	2016-07-22
13	Jvari	Samegrelo	42.75639	42.04361	100	6.75	510	135	30	3	8	1.5	0.25	2019-07-20
14	Jvari	Samegrelo	42.75417	42.04333	100	6.87	490	200	30	3	8	1.2	0.35	2019-07-20
15	Martvili	Imereti	42.45306	42.37639	100	7.09	220	225	35	1	12	1.5	0.35	2019-07-22
16	Matkhoji	Imereti	42.38944	42.44722	100	7.71	220	180	40	0	22	2.5	0.2	2019-07-23
17	Matkhoji	Imereti	42.39111	42.45083	100	7.16	270	180	35	8	7	1.2	0.2	2019-07-23
18	Matkhoji	Imereti	42.39167	42.44889	100	7.33	270	180	40	2	7	1.5	0.3	2019-07-23
19	Motsameta	Imereti	42.28257	42.75938	100	7.33	210	40	30	10	9	0.8	0.2	2019-07-24
20	Motsameta	Imereti	42.28194	42.76	100	7.41	240	80	55	5	10	1.5	0.25	2019-07-24

Supplement E3. Full synoptic table. Species percentage frequencies in the clusters are provided. Diagnostic (Φ ≥ 0.2, grey shaded) and highly diagnostic (Φ ≥ 0.55, grey shaded, in bold) species for each cluster are in the upper part of the table, sorted by decreasing fidelity. Other species are provided below, sorted by decreasing frequency in the dataset. Correspondence between associations and clusters is at the bottom of the table.

Anhangt E3. Vollständige Übersichtstabelle und Übereinstimmung zwischen den Assoziationen und Clustern. Diagnostische (Φ ≥ 0.2, grau schattiert) and hoch diagnostische (Φ ≥ 0.55, grau schattiert, in Fettdruck) Arten für jeden Cluster sind im oberen Teil der Tabelle, sortiert nach abnehmender Treue. Andere Arten sind darunter aufgeführt, nach abnehmender Frequenz im Datensatz sortiert. Die Übereinstimmung zwischen Assoziationen und Clustern findet sich am Fuß der Tabelle.

Cluster	1	2	3	4	5	6	7	8	9
Number of relevés	10	4	20	12	3	7	22	15	12
Cluster 1									
Arbutus andrachne	**70**	.	.	.	.	.	.	.	.
Cistus salviifolius	**60**	.	.	.	.	.	.	.	.
Laurus nobilis	**60**	.	5	.	.	14	.	.	.
Rhododendron ponticum	**60**	25	.	.	.	.	5	.	.
Bituminaria bituminosa	40	.	.	.	.	.	9	.	.
Trifolium campestre	30	.	.	.	.	.	.	.	.
Castanea sativa	70	25	20	17	.	14	.	.	.
Paliurus spina-christi	20	.	.	.	.	.	.	.	.
Ligustrum vulgare	50	.	30	17	.	14	.	.	.
Cornus sanguinea	50	50	35	.	.	14	.	7	.
Rubia tinctorium	20	.	.	.	.	14	.	.	.
Hypericum calycinum	30	25	.	.	.	14	.	.	.
Vaccinium arctostaphylos	50	50	.	33	.	29	.	7	.
Tilia begoniifolia	30	25	15	.	.	14	.	.	.
Dorycnium pentaphyllum	30	25	.	25	.	.	5	.	8
Brachypodium pinnatum	60	50	5	42	33	43	18	.	42
Cluster 2									
Buxus sempervirens	.	**75**	25	.	.	.	.	.	.
Vinca minor	.	**50**	.	.	.	.	.	.	.
Vincetoxicum nigrum	.	**50**	.	.	.	.	.	.	.
Datisca cannabina	10	**50**	.	.	.	.	.	.	.
Rhamnus imeretina	.	**50**	.	.	.	14	.	.	.
Hypericum xylosteifolium	10	**50**	.	.	.	.	5	.	.
Briza media	10	50	.	.	.	14	.	.	.
Pyrus communis	.	50	15	.	.	.	.	.	17
Arbutus unedo	.	25	.	.	.	.	.	.	.
Calluna vulgaris	.	25	.	.	.	.	.	.	.
Drymochloa drymeja	50	100	50	50	33	43	.	.	.
Cluster 3									
Vinca major subsp. *hirsuta*	.	.	**90**	.	.	.	.	.	.
Viola alba	.	.	**85**	.	.	.	.	.	.
Klasea quinquefolia	.	.	**75**	.	.	.	.	.	.
Carex digitata	.	.	**60**	.	.	.	.	.	.
Clinopodium umbrosum	.	.	**55**	.	.	.	.	.	.
Veronica peduncularis	.	.	**50**	.	.	.	.	.	.
Diospyros lotus	.	.	**40**	.	.	.	.	.	.
Asplenium trichomanes	.	.	**50**	.	.	.	14	.	.
Viola reichenbachiana	.	.	**35**	.	.	.	.	.	.
Carex muricata aggr.	.	.	45	.	.	.	.	.	17
Asplenium scolopendrium	.	.	30	.	.	.	.	.	.
Hieracium sabaudum	.	.	30	.	.	.	.	.	.
Lathyrus vernus	.	.	30	.	.	.	.	.	.
Symphytum grandiflorum	.	.	30	.	.	.	.	.	.
Oplismenus hirtellus subsp. *undulatifolius*	.	50	60	.	.	.	.	.	.
Carpesium cernuum	.	.	25	.	.	.	.	.	.
Digitalis schischkinii	.	.	25	.	.	.	.	.	.
Campanula rapunculoides	.	.	60	.	.	14	.	20	42
Brachypodium sylvaticum	30	25	90	42	.	43	27	20	17
Carex sylvatica	.	25	45	.	.	14	.	.	.
Prunella vulgaris	.	.	30	.	.	.	5	7	.
Calystegia silvatica	.	.	20	.	.	.	.	.	.
Carex flacca subsp. *serrulata*	.	.	20	.	.	.	.	.	.
Carex michelii	.	.	20	.	.	.	.	.	.
Euphorbia macroceras	.	.	20	.	.	.	.	.	.
Plantago lanceolata	.	.	20	.	.	.	.	.	.
Robinia pseudoacacia	.	.	20	.	.	.	.	.	.
Sedum stoloniferum	.	.	20	.	.	.	.	.	.
Schedonorus giganteus	.	.	20	.	.	.	.	.	.
Silene balansae	.	.	20	.	.	.	.	.	.
Ulmus glabra	.	.	20	.	.	.	.	.	.
Primula acaulis	10	25	85	42	.	57	9	27	17
Leontodon hispidus	.	.	35	.	.	.	5	.	17
Fraxinus excelsior	10	.	25	.	.	.	.	.	.
Epimedium pinnatum subsp. *colchicum*	.	.	15	.	.	.	.	.	.
Lamium galeobdolon	.	.	15	.	.	.	.	.	.
Lonicera caprifolium	.	.	15	.	.	.	.	.	.
Medicago lupulina	.	.	15	.	.	.	.	.	.
Peucedanum adae	.	.	15	.	.	.	.	.	.
Peucedanum caucasicum	.	.	15	.	.	.	.	.	.
Pimpinella saxifraga	.	.	15	.	.	.	.	.	.
Poa angustifolia	.	.	15	.	.	.	.	.	.
Ruscus colchicus	.	.	15	.	.	.	.	.	.
Staphylea colchica	.	.	15	.	.	.	.	.	.
Taxus baccata	.	.	15	.	.	.	.	.	.
Trifolium repens	.	.	15	.	.	.	.	.	.
Zelkova carpinifolia	.	.	15	.	.	.	.	.	.
Ajuga reptans	.	.	20	.	.	.	.	7	.
Origanum vulgare	.	.	15	.	.	.	5	.	.
Arabis nordmanniana	.	.	10	.	.	.	.	.	.
Brunnera macrophylla	.	.	10	.	.	.	.	.	.
Cephalanthera longifolia	.	.	10	.	.	.	.	.	.
Cruciata glabra	.	.	10	.	.	.	.	.	.
Euonymus latifolius	.	.	10	.	.	.	.	.	.
Euphorbia squamosa	.	.	10	.	.	.	.	.	.
Galium valantioides	.	.	10	.	.	.	.	.	.
Hypericum androsaemum	.	.	10	.	.	.	.	.	.
Orobanche laxissima	.	.	10	.	.	.	.	.	.
Paeonia caucasica	.	.	10	.	.	.	.	.	.
Periploca graeca	.	.	10	.	.	.	.	.	.
Philadelphus coronarius	.	.	10	.	.	.	.	.	.
Polypodium cambricum	.	.	10	.	.	.	.	.	.
Potentilla indica	.	.	10	.	.	.	.	.	.
Prunella ×intermedia	.	.	10	.	.	.	.	.	.
Sesleria alba	.	.	10	.	.	.	.	.	.
Solidago virgaurea	.	.	10	.	.	.	.	.	.
Prunus avium	.	.	20	17	.	.	.	.	.
Ficus carica	30	25	35	.	.	.	9	.	.
Cluster 4									
Euphorbia oblongifolia	.	.	.	**75**	.	14	.	.	.
Crataegus pentagyna	20	25	15	92	.	43	.	.	33
Rhododendron luteum	10	50	5	67	.	29	.	.	.
Aegonychon purpurocaeruleum	.	.	.	58	33	.	.	13	25
Acer cappadocicum	10	25	25	58	.	14	.	.	.
Lysimachia punctata	.	.	.	25	.	.	.	.	8
Galium rotundifolium	.	.	.	17	.	.	.	.	.
Phlomis samia	.	.	.	17	.	.	.	.	.
Viola sieheana	.	50	.	92	33	71	41	33	33
Bromopsis benekenii	.	.	.	17	.	.	.	.	8
Luzula forsteri	.	.	20	33	.	14	.	.	25
Silene compacta	.	.	.	17	.	14	.	.	.
Asyneuma rigidum	40	.	.	58	67	29	9	.	42
Daphne pontica	40	25	.	58	33	43	.	53	.
Cluster 5									
Sesleria phleoides	.	.	.	.	**100**	.	.	.	.
Dictamnus albus	.	.	.	8	**100**	.	.	.	.
Cotinus coggygria	.	.	5	.	**100**	.	5	7	.
Tilia platyphyllos	.	.	.	8	**100**	14	.	.	.
Quercus pubescens	.	.	.	.	**100**	.	.	.	25
Frangula alnus	.	.	.	.	**67**	.	.	.	.
Pimpinella tripartita	.	.	5	.	**67**	.	.	.	.
Corylus avellana	20	.	20	17	**100**	14	27	.	.
Colutea cilicica	.	.	.	.	**67**	.	5	.	25
Campanula glomerata	.	.	.	17	**67**	.	.	.	17
Tanacetum poteriifolium	.	.	.	8	**67**	.	9	.	25
Fraxinus ornus	.	25	.	8	**67**	14	.	.	.
Cota tinctoria	.	.	.	.	**33**	.	.	.	.
Milium vernale	.	.	.	33	67	29	.	.	8
Cluster 6									
Hedera colchica	.	.	20	8	.	**57**	.	.	.
Oenanthe pimpinelloides	30	25	.	33	.	86	.	40	8
Trachystemon orientalis	20	50	30	8	.	86	5	47	.
Asplenium adiantum-nigrum	50	75	55	.	.	86	5	27	.
Staphylea pinnata	.	25	.	.	.	29	.	.	.
Galium paschale	.	25	.	17	33	43	.	.	.
Ruscus hypoglossum	.	25	.	.	.	29	.	7	.
Cluster 7									
Potentilla reptans	.	.	.	.	.	.	**36**	.	.
Agrimonia eupatoria	.	.	.	.	.	.	27	.	.
Festuca jeanpertii	.	.	.	.	.	.	27	.	.
Hypericum perforatum	.	.	5	.	.	.	32	.	.
Geranium purpureum	.	.	.	.	.	.	23	.	.
Lonicera etrusca	.	.	.	.	.	.	23	.	.
Styrax officinalis	.	.	.	.	.	.	23	.	.
Arum maculatum	.	.	.	.	.	.	18	.	.
Chaerophyllum nodosum	.	.	.	.	.	.	18	.	.
Rostraria cristata	.	.	.	.	.	.	18	.	.
Teucrium polium	.	.	.	.	.	.	18	.	.
Doronicum orientale	.	.	.	.	.	.	23	.	8
Epipactis helleborine	.	.	.	.	.	.	14	.	.
Alliaria petiolata	.	.	.	.	.	.	23	.	17
Scutellaria albida	.	.	.	.	.	.	23	.	17
Viola odorata	.	.	.	.	.	.	23	.	17
Phillyrea latifolia	.	.	.	.	.	.	23	20	.
Rosa canina	.	.	5	.	.	.	23	.	17
Carlina corymbosa	.	.	.	.	.	.	9	.	.
Cynosurus echinatus	.	.	.	.	.	.	9	.	.
Daucus carota	.	.	.	.	.	.	9	.	.
Erysimum cuspidatum	.	.	.	.	.	.	9	.	.
Geranium dissectum	.	.	.	.	.	.	9	.	.
Neottia nidus-avis	.	.	.	.	.	.	9	.	.
Piptatherum coerulescens	.	.	.	.	.	.	9	.	.
Rubus sanctus	.	.	.	.	.	.	9	.	.
Tilia tomentosa	.	.	.	.	.	.	9	.	.
Torilis arvensis	.	.	.	.	.	.	9	.	.
Trifolium pannonicum	.	.	.	.	.	.	9	.	.
Vicia tenuifolia subsp. *dalmatica*	.	.	.	.	.	.	9	.	.
Juniperus oxycedrus	10	.	.	.	.	.	27	.	25
Stachys officinalis	.	.	.	8	.	.	18	7	.
Galium aparine	.	.	.	.	.	.	18	.	17
Campanula rapunculus	.	.	.	.	.	.	14	.	8
Digitalis lamarckii	.	.	.	.	.	.	14	.	8
Galium verum	.	.	.	.	.	.	14	.	8
Teucrium chamaedrys	10	50	30	.	.	.	41	.	17
Cluster 8									
Rubus ulmifolius	.	.	.	.	.	.	.	**40**	.
Cirsium pseudopersonata	.	.	.	.	.	.	.	20	.
Arum italicum	.	.	.	.	.	.	.	13	.
Veronica serpyllifolia	.	.	.	.	.	.	.	13	.
Cluster 9									
Vicia cracca	.	.	.	17	.	.	5	.	**83**
Crataegus rhipidophylla	.	.	.	.	.	.	.	.	**42**
Lathyrus roseus	.	.	.	.	.	.	.	.	**42**
Nepeta nuda subsp. *albiflora*	.	.	.	.	.	.	.	.	**42**
Sorbus umbellata	.	.	.	.	.	.	.	.	**42**
Cephalanthera rubra	.	.	.	17	.	.	9	.	**58**
Aristolochia pallida	.	.	.	.	.	.	.	.	**33**
Silene latifolia	.	.	.	.	.	.	.	.	**33**
Asperula involucrata	.	.	.	.	.	.	14	.	42
Cephalanthera damasonium	.	.	.	.	.	.	.	.	25
Vicia abbreviata	.	.	.	.	.	.	.	.	25
Silene italica	.	.	.	.	.	.	9	.	33
Trifolium medium	.	.	.	8	.	.	5	.	33
Poa nemoralis	.	.	5	33	67	.	.	.	67
Astragalus ornithopodioides	.	.	.	.	.	.	.	.	17
Astragalus ponticus	.	.	.	.	.	.	.	.	17
Hippocrepis emerus	.	.	.	.	.	.	.	.	17
Moehringia trinervia	.	.	.	.	.	.	.	.	17
Onobrychis arenaria subsp. *cana*	.	.	.	.	.	.	.	.	17
Prunus mahaleb	.	.	.	.	.	.	.	.	17
Tanacetum parthenium	20	25	.	.	.	.	27	.	50
Astragalus glycyphylloides	.	25	.	8	.	14	.	.	42
Cornus mas	10	25	10	75	100	57	50	7	100
Dianthus calocephalus	.	.	.	.	.	.	5	.	17
Geranium molle	.	.	.	.	.	.	5	.	17
Hedysarum varium	.	.	.	.	.	.	5	.	17
Salvia verticillata	.	.	.	.	.	.	5	.	17
Clematis vitalba	10	25	15	8	.	.	5	7	33
Securigera varia	20	50	15	8	33	.	5	.	42
Species diagnostic for two or more clusters									
Erica arborea	**100**	**100**	.	.	.	14	5	.	.
Cistus creticus	60	75	.	.	.	14	9	7	.
Campanula alliariifolia	60	50	80	.	.	.	.	.	.
Vitis vinifera	50	50	.	8	.	43	5	.	.
Iris lazica	40	**75**	.	.	.	.	.	.	.
Pteridium aquilinum	70	50	25	42	.	71	5	33	8
Rubus subgen. *Rubus*	40	25	35	8	.	.	5	7	8
Ilex colchica	40	.	15	25	.	57	5	.	.
Hedera helix	90	75	90	50	67	14	9	87	50
Genista tinctoria	10	75	.	67	.	.	.	.	.
Verbascum lagurus subsp. *ponticum*	.	50	.	.	.	43	.	.	.
Potentilla micrantha	30	.	60	50	.	43	.	.	8
Sanicula europaea	10	.	60	42	.	86	.	.	.
Acer campestre	.	.	55	.	.	71	45	40	.
Dioscorea communis	20	50	60	58	.	57	.	.	17
Festuca heterophylla	.	.	.	58	.	.	.	53	.
Sorbus torminalis	10	.	10	83	.	29	32	.	83
Asperula cimulosa	30	25	.	83	33	57	.	.	33
Epimedium pubigerum	20	25	.	83	67	57	.	13	8
Salvia forsskaolei	20	50	.	83	33	71	.	13	8
Prunus domestica subsp. *insititia*	.	.	.	33	.	.	.	.	25
Digitalis lanata	.	.	.	33	.	.	.	.	25
Cirsium hypoleucum	30	25	.	75	33	57	5	.	17
Fagus orientalis	.	.	15	67	**100**	14	.	7	.
Lathyrus aureus	20	50	.	58	.	43	.	.	.
Lathyrus laxiflorus	20	.	70	92	67	100	32	.	75
Stellaria holostea	.	.	.	50	33	.	41	.	50
Cardamine bulbifera	.	.	.	33	**67**	.	5	.	.
Helleborus orientalis	10	50	30	75	33	86	5	40	50
Geranium asphodeloides	.	.	.	33	.	43	.	13	25
Lathyrus tukhtensis	.	.	.	.	**67**	.	.	.	42
Carpinus betulus	.	.	35	58	100	86	9	.	8
Clinopodium vulgare	10	.	.	.	67	.	18	.	50
Physospermum cornubiense	.	.	20	8	67	.	.	.	50
Cyclamen coum	.	.	5	42	100	71	14	33	50
Laser trilobum	.	.	5	17	67	43	.	.	17
Lapsana communis	30	25	30	58	100	43	27	.	75
Euonymus europaeus	.	25	.	17	67	71	.	.	25
Quercus hartwissiana	.	.	5	.	.	**57**	27	.	.
Crataegus monogyna	.	.	.	.	.	.	59	93	.
Euphorbia amygdaloides	.	.	5	.	.	.	36	60	8
Quercus petraea	80	25	65	75	.	29	.	7	8
Ruscus aculeatus	90	100	75	8	.	100	36	100	.
Smilax excelsa	80	75	95	25	.	100	5	47	.
Quercus cerris	.	.	.	58	33	57	82	100	100
Other species									
Carpinus orientalis	80	100	100	83	100	100	100	100	100
Crataegus germanica	40	50	10	25	33	43	5	27	8
Geum urbanum	20	50	.	33	.	29	32	.	25
Dactylis glomerata	.	.	5	33	.	.	27	7	25
Fragaria vesca	20	.	10	25	33	.	5	7	25
Melica uniflora	.	.	.	25	33	29	.	.	.
Pyracantha coccinea	20	.	.	8	.	14	5	.	.
Salvia glutinosa	.	25	15	.	.	14	.	.	.
Salvia tomentosa	.	.	.	.	33	.	18	.	.
Trifolium pratense	.	.	10	.	.	.	5	.	17
Geranium lucidum	.	.	.	.	.	.	9	.	17
Geranium robertianum	10	.	5	8	.	14	.	.	.
Veronica chamaedrys	.	.	.	.	.	.	9	7	8
Athyrium filix-femina	.	.	.	.	.	.	9	.	8
Campanula involucrata	.	.	.	.	.	.	9	.	8
Lactuca muralis	.	.	5	.	.	.	9	.	.
Petrorhagia saxifraga	.	.	5	.	.	.	9	.	.
Polypodium vulgare	.	.	10	.	.	.	.	7	.
Vicia hirsuta	.	.	.	.	.	.	9	.	8
Achillea biserrata	.	25	.	.	.	.	5	.	.
Anthemis kotschyana	.	.	.	.	.	.	5	.	8
Anthemis tinctoria	.	.	.	.	.	.	5	.	8
Astragalus leucothrix	.	.	.	.	.	.	5	.	8
Calystegia sepium	.	.	.	8	.	14	.	.	.
Celtis australis	10	.	.	.	.	.	5	.	.
Circaea lutetiana	10	25	.	.	.	.	.	.	.
Epipactis condensata	.	.	.	.	.	.	5	.	8
Epipactis pontica	.	.	.	.	.	.	5	.	8
Hieracium murorum	.	.	5	.	.	.	.	.	8
Lathyrus nissolia	.	.	.	.	.	.	5	.	8
Ochlopoa annua	.	.	.	.	.	.	5	.	8
Ononis pusilla	.	.	.	.	.	.	5	.	8
Pimpinella tragium	.	.	.	8	.	14	.	.	.
Poa bulbosa	.	.	.	.	.	.	5	.	8
Securigera cretica	.	.	.	.	33	.	.	.	8
Sideritis montana	.	.	.	.	.	.	5	.	8
Ulmus minor	.	.	5	.	.	14	.	.	.
Vicia sativa subsp. *nigra*	.	.	.	.	.	.	5	.	8
Acer trautvetteri	10	.	.	.	.	.	.	.	.
Adiantum capillus-veneris	.	.	5	.	.	.	.	.	.
Alnus glutinosa subsp. *barbata*	10	.	.	.	.	.	.	.	.
Argyrolobium biebersteinii	.	.	.	.	.	.	.	7	.
Aristolochia parvifolia	.	.	.	.	.	.	.	.	8
Aristolochia pontica	.	.	5	.	.	.	.	.	.
Asplenium ruta-muraria	.	.	5	.	.	.	.	.	.
Blackstonia perfoliata	.	.	.	.	.	.	5	.	.
Campanula raddeana	.	.	5	.	.	.	.	.	.
Cardamine parviflora	.	.	5	.	.	.	.	.	.
Carex humilis	.	.	5	.	.	.	.	.	.
Cirsium vulgare	.	.	5	.	.	.	.	.	.
Cleistogenes serotina	10	.	.	.	.	.	.	.	.
Crepis reuteriana	.	.	.	.	.	.	5	.	.
Cyanus depressus	.	.	.	.	.	.	.	.	8
Echinops spinosissimus	.	.	.	.	.	.	5	.	.
Epilobium montanum	.	.	.	.	.	.	.	7	.
Epilobium parviflorum	.	.	.	.	.	.	.	7	.
Erigeron annuus	.	.	5	.	.	.	.	.	.
Erysimum pulchellum	.	.	.	.	.	.	5	.	.
Euphorbia orientalis	.	.	.	.	.	.	5	.	.
Euphorbia stricta	.	.	5	.	.	.	.	.	.
Fallopia convolvulus	.	.	.	.	.	.	5	.	.
Filago pyramidata	.	.	.	.	.	.	.	7	.
Galium album	.	.	5	.	.	.	.	.	.
Geranium sanguineum	.	.	.	.	.	.	.	7	.
Gleditsia triacanthos	.	.	5	.	.	.	.	.	.
Hordeum bulbosum	.	.	.	.	.	.	.	.	8
Jacobaea vulgaris	.	.	5	.	.	.	.	.	.
Jasminum fruticans	.	.	.	.	.	.	5	.	.
Legousia speculum-veneris	.	.	.	.	.	.	5	.	.
Leptopus chinensis	.	.	5	.	.	.	.	.	.
Lonicera caucasica	.	.	5	.	.	.	.	.	.
Lotus corniculatus	.	.	5	.	.	.	.	.	.
Malus sylvestris	.	.	5	.	.	.	.	.	.
Medicago ×varia	.	.	.	.	.	.	5	.	.
Melampyrum elatius	.	.	5	.	.	.	.	.	.
Melilotus officinalis	.	.	.	.	.	.	5	.	.
Mercurialis perennis	.	.	5	.	.	.	.	.	.
Morus alba	.	.	5	.	.	.	.	.	.
Myosotis sylvatica	.	.	.	.	.	.	.	.	8
Ornithogalum sigmoideum	.	.	.	.	.	.	.	7	.
Paeonia mascula	.	.	.	.	.	.	.	7	.
Pachyphragma macrophylla	.	.	5	.	.	.	.	.	.
Pinus sylvestris	.	.	5	.	.	.	.	.	.
Plantago major	.	.	5	.	.	.	.	.	.
Polygonatum glaberrimum	.	.	5	.	.	.	.	.	.
Primula veris subsp. *macrocalyx*	.	.	5	.	.	.	.	.	.
Pulmonaria dacica	.	.	5	.	.	.	.	.	.
Punica granatum	.	.	5	.	.	.	.	.	.
Ranunculus bulbosus	.	.	5	.	.	.	.	.	.
Ranunculus polyanthemos	.	.	5	.	.	.	.	.	.
Rhagadiolus stellatus	.	.	.	.	.	.	.	.	8
Rhamnus alaternus	.	.	.	.	.	14	.	.	.
Sambucus nigra	.	.	5	.	.	.	.	.	.
Scabiosa sosnowskyi	.	.	5	.	.	.	.	.	.
Sison amomum	.	.	5	.	.	.	.	.	.
Smilax aspera	.	.	.	.	.	14	.	.	.
Sonchus asper	.	.	.	.	.	.	5	.	.
Sorbaria tomentosa	.	.	.	8	.	.	.	.	.
Sorbus aucuparia	.	.	.	8	.	.	.	.	.
Tanacetum partheniifolium	.	.	5	.	.	.	.	.	.
Taraxacum sect. *Taraxacum*	.	.	5	.	.	.	.	.	.
Thalictrum minus	.	.	.	.	.	.	5	.	.
Torilis japonica	.	.	5	.	.	.	.	.	.
Trachycarpus fortunei	.	.	5	.	.	.	.	.	.
Trachynia distachya	.	.	.	.	.	.	5	.	.
Trifolium diffusum	.	.	5	.	.	.	.	.	.
Trifolium ochroleucon	.	.	.	.	.	.	5	.	.
Veronica officinalis	.	.	.	.	.	14	.	.	.
Veronica orientalis	.	.	.	.	.	.	5	.	.
Vicia sepium	.	.	5	.	.	.	.	.	.
Number of relevés per association									
Campanulo alliariifoliae-Carpinetum orientalis	.	.	20	.	.	.	.	.	.
Carpino betulo-orientalis	.	.	.	11	.	.	.	.	.
Carpino orientalis-Phillyrietum latifoliae	.	.	.	.	.	.	6	.	.
Carpino orientalis-Quercetum cerridis	.	.	.	.	.	.	.	15	.
Corno maris-Quercetum cerridis	.	.	.	.	.	.	5	.	5
Crataego curvisepalae-Quercetum cerridis	.	.	.	.	.	.	.	.	7
Erico arboreae-Carpinetum orientalis	10	4	.	.	.	1	1	.	.
missing association assignment	.	.	.	.	3	.	.	.	.
Querco cerridis-Carpinetum orientalis	.	.	.	.	.	.	10	.	.
Rusco aculeate-Carpinetum orientalis	.	.	.	1	.	6	.	.	.

Supplement E4. Additional photos of the vegetation of the association *Campanulo alliariifoliae-Carpinetum orientalis* ass. nova hoc loco and its sites in western Georgia. **a)** Forested landscape of the southern macroslope of the Racha Massif. *Carpinus orientalis* forests occupy mainly limestone rock outcrops here, while mixed forests of *Carpinus betulus*, *Castanea sativa* and *Fagus orientalis* dominate on zonal sites (July 2017). **b)** River Tskaltsitela limestone canyon above the Motsameta Monastery with extensive *Carpinus orientalis* forests (July 2019). **c)** Forests of *Carpinus orientalis* colonizing the upper part of a sunny limestone rock near the city Tkibuli (July 2017). **d)** Mixed *Carpinus betulus* and *C. orientalis* forests on a limestone ridge near the Sataplia Cave above the city Tskaltubo (July 2016). **e)** *Carpinus orientalis* forest below the Motsameta Monastery near the city Kutaisi. Recent massive dieback of *Buxus sempervirens* shrubs is apparent (July 2019). **f)** Undergrowth of an open *Carpinus orientalis* forest near the city Martvili. *Festuca drymeja*, *Laser trilobum* and *Leptopus chinensis* are visible in the understorey (July 2017). All photos by P. Novák.

Anhang E4. Zusätzliche Fotos der Vegetation des *Campanulo alliariifolae-Carpinetum orientalis* ass. nova hoc loco und ihrer Standorte in Westgeorgien. **a)** Waldlandschaft des südlichen Abhangs des Racha-Massivs. *Carpinus orientalis*-Wälder besetzen hier hauptsächlich Kalksteinfel-sen, während Mischwälder aus *Carpinus betulus*, *Castanea sativa* und *Fagus orientalis* an zonalen Standorten dominieren (Juli 2017). **b)** Kalksteinschlucht des Flusses Tskaltsitela oberhalb des Klosters Motsameta mit ausgedehnten *Carpinus orientalis*-Wäldern (Juli 2019). **c)** *Carpinus orientalis*-Wälder, die den oberen Teil eines sonnigen Kalksteinfelsens in der Nähe der Stadt Tkibuli besiedeln (Juli 2017). **d)** Mischwälder aus *Carpinus betulus* und *C. orientalis* auf einem Kalksteinrücken in der Nähe der Sataplia-Höhle oberhalb der Stadt Tskaltubo (Juli 2016). **e)** *Carpinus orientalis*-Wald unterhalb des Klosters Motsameta in der Nähe der Stadt Kutaisi. Das kürzliche massive Absterben von *Buxus sempervirens*-Sträuchern ist offensichtlich (Juli 2019). **f)** Unterholz eines offenen *Carpinus orientalis*-Waldes in der Nähe der Stadt Martvili. *Festuca drymeja*, *Laser trilobum* und *Leptopus chinensis* sind im Unterwuchs sichtbar (Juli 2017). Alle Fotos von P. Novák.