

Alluvial alder forests of the Greater Caucasus, Georgia: ecology, habitats and variability

Alluviale Erlenwälder des Großen Kaukasus, Georgien: Ökologie, Lebensräume und Variabilität

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Abstract

The Caucasus Region belongs among the most remarkable biodiversity hotspots globally. Local mountain floodplain forests represent highly endangered ecosystems and possess the status of protective forests. However, they have not been extensively phytosociologically assessed using Braun-Blanquet methods to date. Here, we present a novel dataset of vegetation plots recorded in two remarkable areas of forest plant diversity in this region. They were Enguri (Black Sea watershed) and Aragvi (Caspian Sea watershed) River basins in the Western and Eastern Greater Caucasus, respectively. Based on 49 relevés, sampled on a broad elevation gradient (980–1830 m), we distinguished three vegetation types using unsupervised classification. Main gradients in their species composition reflect biogeographical and climatic differences. *Alnus incana* dominated two types. The Enguri type (*Brunnero macrophyllae-Alnetum incanae*) was characterized by numerous species typical of the western part of the Greater Caucasus, including tall forbs and mountain species. The Aragvi type (*Veronico filiformis-Alnetum incanae*) showed a diagnostic combination of common Caucasian species and relatively thermophilous forest species. The subdivision of this unit included three subtypes according to grazing intensity. The last type (*Sedo stoloniferi-Alnetum barbatae*) was significant by a putative Tertiary relict *Alnus glutinosa* subsp. *barbata* as a canopy dominant. It occupied lower elevations of the Enguri Region, significantly influenced by the nearby Colchic Region. To provide a regional context of the sampled vegetation, we compiled an expanded dataset of alluvial alder forests from the Caucasus and its surroundings. Their joint classification highlighted the uniqueness of the recorded communities with *A. incana* and clearly distinguished them from the Euxinian alliance *Alnion*

barbatae delimited by relict species typical of the Colchic refugium (e.g. *Diospyros lotus*, *Pterocarya fraxinifolia*). A comparison of the Caucasian *A. incana* forests with the alluvial forests of the boreo-nemoral alliance *Alnion incanae* supported the individuality of the Caucasian stands in terms of floristic composition and allowed us to describe them as a new alliance (*Veronico filiformis-Alnion incanae* all. nova). It is characterized by the dominance of *A. incana* accompanied by numerous geographically restricted species (e.g. *Senecio propinquus*, *Symphytum asperum*) coupled with boreo-montane forest species (e.g. *Oxalis acetosella*, *Polygonatum verticillatum*). Caucasian alluvial forests face many ongoing threats, including constructing of new water reservoirs and hydropower plants, overgrazing and illegal cutting.

Keywords: Alluvium, *Alno glutinosae-Populetea albae*, Caucasus, forest, phytosociology, riparian community, vegetation classification

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

The Caucasus is a mountain range with an extremely diverse landscape stretching the boundary between Europe and Asia. It is a crucial area of high biodiversity in western Eurasia and, as such, has been included among the 32 top biodiversity hotspots of global significance (MITTERMEIER et al. 2004, ZAZANASHVILI & MALLON 2009). This high mountain chain, exceeding 5000 m a.s.l., served as an essential refugium of biota during the Quaternary climatic oscillations (MILNE & ABBOT 2002, CONNOR 2006) as well as a remarkable migration corridor for numerous mountain taxa migrating between Asia and Europe in the past (NAKHUTSRISHVILI et al. 2017). Its species-rich flora (~6350 species) is well-known for its high endemism rate at both species (~20%) and genus levels (GAGNIDZE et al. 2002). It harbours extraordinarily diverse deciduous and coniferous forest vegetation (BOHN et al. 2000–2003, NAKHUTSRISHVILI 2013, GEGECHKORI 2020). While zonal woody communities have mostly been at least basically phytosociologically studied following the Braun-Blanquet approach (e.g. PASSARGE 1981a, b, KOROTKOV 1995, SHEVCHENKO & BRESLAVSKAYA 2021, NOVÁK et al. 2021), only little attention has been paid to azonal types (e.g. KALNÍKOVÁ et al. 2020, NOVÁK et al. 2021), including local floodplain forests (PEPER 2008, ATAMOV et al. 2018, ERMAKOV 2021), to date.

Floodplains are belong among important centres of biotic complexity, diversity and productivity across the landscape (WARD et al. 1999, TOCKNER & STANDFORD 2002, PETSCH et al. 2022). Floodplain forests are azonal riparian ecosystems influenced by long-term high water levels, either floodwater or slow-flowing groundwater. They are supposed to be one of the most dynamic forest ecosystems across western Eurasia since rivers deposit various materials and create systems of terraces of different ages and sediment grain sizes. They are associated with river corridors (LEUSCHNER & ELLENBERG 2017). The variability of floodplain forest vegetation at large spatial scales is driven by climatic gradients (DOUDA et al. 2016) and biogeography encompassing migrations and evolutionary processes (DOUDA et al. 2018). Within individual catchments, local ecological factors become predominant, including hydrological regime (PARKER & BENDIX 1996, KUGLEROVÁ et al. 2015), stream power (PIELECH 2015), site productivity (SLEZÁK et al. 2017) or soil properties (NAQINEZHAD et al. 2008). Temperate floodplain forests might be extraordinarily species-rich on a small scale (CHYTRÝ et al. 2015) due to specific environmental conditions enhancing the coexistence of various ecological species groups, e.g. forest species, wetland specialists or ruderal species (DOUDA et al. 2016, PIELECH 2021). They provide multiple ecosystem functions and

services, including erosion and flood control, improving water quality, carbon sequestration, protection of watercourses against pollution, and recreational and aesthetic functions (NAIMAN & DECAMPS 1997, TOCKNER & STANDFORD 2002).

The Caucasus is an area of relatively well-preserved river networks supporting the development of alluvial plant communities, including forests (BONDYREV et al. 2015). River floodplains represent remarkable centres of floristic diversity (KUGLEROVÁ et al. 2015, FAYVUSH & ALEKSANYAN 2021). They form an important part of the vegetation mosaic of the region (GROSSHEIM 1948, GULISASHVILI et al. 1975, DOLUKHANOV 2010, BEBIYA 2022). Alluvial forests with alders comprise 5.5% of forested areas of Georgia (AKHALKATSI 2015). Nevertheless, they are one of the most endangered ecosystems, exhibiting a sharp decline globally (TOCKNER & STANDFORD 2002). Caucasian alluvial forests have been under anthropogenic pressure for millennia (CONNOR 2006, AKHALKATSI & TIMERIDZE 2012). Numerous factors have contributed to their threat and decrease, counting river regulations, dam and water reservoir constructions, gravel mining, overgrazing by domestic animals, extensive tree cutting and biotic invasions (AKHALKATSI 2015, JANSSEN et al. 2016). Consequently, native floodplain ecosystems have been preserved in only 5–6% of their original area in Georgia (ZAZANASHVILI & MALLON 2009).

Two alders native to Georgia, *Alnus glutinosa* subsp. *barbata* and *A. incana* represent keystone taxa capable of becoming canopy dominants (DOLUKHANOV 2010, DOUDA 2016). The Caucasus is a putative glacial refugium for both, as indicated by phylogeographical analyses (HAVRDOVÁ et al. 2015, MANDÁK et al. 2016a), ecological niche modelling (MANDÁK et al. 2016b) and molecular investigation of their symbiotic actinomycetes (ROY et al. 2017). They share many environmental requirements, including high light demands of seedlings and young individuals, high water requirements, relative indifference to soil nutrient status, presence of nitrogen-fixing root actinomycetes and high regeneration ability, counting tolerance to coppicing (HOUSTON DURRANT et al. 2016a, b). After the dissolution of the Soviet Union in the early 1990s, alders often expanded on abandoned arable land across the Caucasus Region and beyond (AOSAAR et al. 2012, BEBIYA 2022). *Alnus incana* is a boreal-mountain and relatively short-living and shallow-rooting tree with a distribution centre in northern, central and eastern Europe, having an isolated outpost in the Caucasus (HOUSTON DURRANT et al. 2016b, LEUSCHNER & ELLENBERG 2017). It preferentially occurs in mountain river valleys with intermediate energy streams and on coarse mineral soils with permanently high groundwater levels (BROWN et al. 1997). In the Caucasus, *A. incana* usually dominates the tree layer of alluvial mountain forests, generally between 1200 m a.s.l. and 1900 m a.s.l. (GULISASHVILI 1961, DOLUKHANOV 2010). It is an unpalatable species avoided by cattle (LEUSCHNER & ELLENBERG 2017). In contrast, an alleged Euxino-Hyrcanian Tertiary relic *A. glutinosa* subsp. *barbata* (ROY et al. 2017) often assumes the canopy dominance at lower elevations within the mountain valleys under warmer conditions and in the Black and Caspian Sea coastal lowlands. It occupies wet soils influenced by flowing or stagnant water (GULISASHVILI 1961, DOLUKHANOV 2010, NAKHUTSRISHVILI 2013, GEGECHKORI 2020, GHOLIZADEH et al. 2020, BEBIYA 2022). EUNIS habitat typology classifies these alder-dominated forests to the unit G1.2a *Alnus* woodland on riparian and upland soils (CHYTRÝ et al. 2020), a least concern (LC) habitat for both EU28 and EU28+ (JANSSEN et al. 2016). Emerald habitat classification broadly applied in Georgia recognizes them as a separate unit G1.21 Riverine *Fraxinus* - *Alnus* woodland (COUNCIL OF EUROPE 2018). Moreover, they belong to the Annex I priority habitat 91E0 Alluvial forests with

Alnus glutinosa and *Fraxinus excelsior* (COUNCIL DIRECTIVE 92/43/EEC) and Georgia as a country with Association Agreement with EU adopted this assignment in its national NATURA 2000 habitat classification (AKHALKATSI & TARKHNISHVILI 2012).

In Georgia, these forests have been phytosociologically investigated applying the Braun-Blanquet approach only recently in the selected mountain regions of the western part of the country (NAKHUTSRISHVILI 2019) and the coastal lowland in Abkhazia (ERMAKOV et al. 2021). Generalized descriptions of alluvial forests using a dominant-based approach were provided in vegetation overviews of the national territory (e.g. BOHN et al. 2000–2003, DOLUKHANOV 2010, NAKHUTSRISHVILI 2013, BEBIYA 2022). Alder floodplain forests are also reported from other Caucasian countries (GULISASHVILI 1961), i.e. Armenia (FAYVUSH & ALEKSANYAN 2016), Azerbaijan (ATAMOV et al. 2018) and the northern part of the mountain range (SERGEEVA et al. 2004). However, detailed data on their floristic composition has been mostly missing.

Understanding vegetation and habitat diversity and its drivers is of key importance for adequate nature protection (RODWELL et al. 2018, CHYTRÝ et al. 2020). Hence, the main objectives of this study are to: (1) reveal patterns of species composition of the alluvial forests of the Southern Greater Caucasus on an example of two river valleys (Aragvi, Enguri) in Georgia, (2) identify distinct community types of this vegetation and characterize them in terms of ecology, distribution, vegetation structure, species composition and potential threats, (3) examine the position of the described communities in the context of floodplain forests of the Caucasus and the whole western Eurasia.

2. Methods

2.1 Study area

The field research took place in two regions with a remarkable occurrence of floodplain forests within Georgia (DOLUKHANOV 2010), i.e. valleys of Enguri and Aragvi rivers and their tributaries (hereafter Enguri and Aragvi Regions; Fig. 1). Both belong among Georgian rivers with the largest catchment areas (BONDYREV et al. 2015). These two study regions represent two contrasting areas of the Georgian Greater Caucasus in terms of biogeography (GAGNIDZE 1999), altitudinal vegetation zonation (ZAZANASHVILI et al. 2000), natural-historical regionalization (GEGECHKORI 2020) and national climatic division (BONDYREV et al. 2015) and thus served as representative areas for the purposes of this study. We focused on alluvial alder (*Alnus* spp.) forests inhabiting river valleys.

The Enguri Region (Black Sea watershed) spans over a boundary between the Western and Central Greater Caucasus south of the highest section of the Greater Caucasian main ridge (Shkhara 5203 m a.s.l.). It encompasses the Enguri River and its tributaries (Adishchala, Dolra, Mestiachala, Mulkhura, Mushuri, Lasili, Nakra, Nenskra) between the municipalities of Davberi and Khaishi (1410–1830 m a.s.l.). Geologically, Mesozoic slates, turbidites and phyllites prevail in the area, accompanied by older migmatites and granitoids (ADAMIA 2010). In terms of geomorphology, the Enguri floodplain is often very limited as the river mostly flows in a narrow rocky ravine, forming a bedrock valley. Contrary, its tributaries within the study area often show relatively flat alluvia with meandering channels and gravel bars. Climatic conditions of this part of the study area can be characterized by data from the Mestia weather station (1441 m) with an annual mean temperature 5.7 °C and annual precipitation 992 mm (DOLUKHANOV 1989). In the national floristic division, the area stretches within the Svaneti Floristic Region, which harbours ~1100 vascular plant species (GAGNIDZE 2005). The territory is planned to be protected in the proposed Upper Svaneti National Park (GPAP 2008).

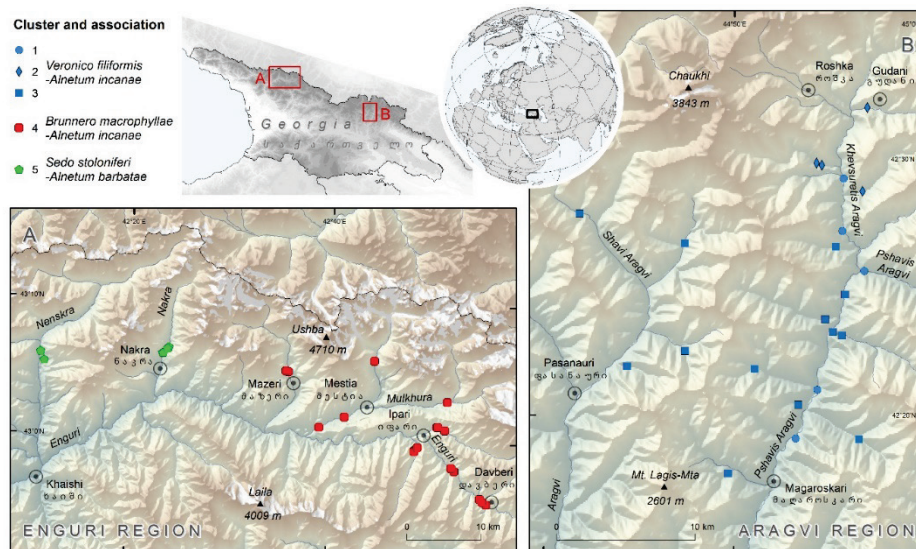


Fig. 1. Map of the study region with locations of relevés and their cluster and association affiliation.

Abb. 1. Karte der Untersuchungsregion mit Orten der Vegetationsaufnahmen sowie ihrer Cluster- und Assoziationszugehörigkeit.

The Aragvi Region (Caspian Sea watershed) is situated in the Eastern Greater Caucasus (NAKHUTSRISHVILI et al. 2017) and comprises the Aragvi River and its tributaries (Khevsureti Aragvi, Pshavi Aragvi, Shavi Aragvi) in an area between the municipalities of Zhinvali, Pasaunauri and Gudani (980–1560 m). It includes deeply incised river valleys in the rugged mountain landscape with peaks exceeding 3000 m a.s.l. The geological bedrock comprises erosion-prone Mesozoic slates and turbidites (ADAMIA 2010). Floodplains in the studied area are primarily flat with irregular gravel accumulations and a combination of straight, braided or wandering river channels. Data from the weather stations Barisakho (1325 m, 6.4 °C, 1044 mm) and Pasaunauri (1070 m, 7.8 °C, 932 mm) provide basic climatic characteristics of the region (DOLUKHANOV 1989). The area is a part of the Mtiuleti and Tusheti-Pshavi-Khevsureti Floristic Regions with ~1200 species of vascular plants (SHETEKauri 2017). The area mainly lies within the boundaries of the Aragvi Protected Landscape (998.02 km²; Georgia Law No. 7102-IS of 2020).

West Caucasian fir, spruce-fir and beech-fir and pine forests for the Enguri region and Caucasian Oriental beech and mixed oak-hornbeam forests for the Aragvi region represent dominant natural vegetation (BOHN et al. 2000–2003).

2.2 Field survey and environmental data

The field survey was conducted during the vegetation seasons of 2021 and 2022. Following the Braun-Blanquet approach, we sampled vegetation-plot records (relevés; DENGLER et al. 2008). The sampling aimed to capture a broad variability of alluvial alder forests. Prior to our fieldwork, potential locations of the target vegetation were identified based on relevant GIS layers, including landscape satellite and aerial imaginaries and SRTM digital elevation model data available in Google Earth Pro 7.3 (Google LLC, <https://earth.google.com/>). During the field survey, we visited those preselected sites and if the target vegetation was present, we sampled it by a randomly placed plot. The standard plot area was 200 m². However, in some cases, we sampled smaller plots due to the limited extent of the target habitat at a site. This strategy significantly increased the spatial evenness of plots across the study areas. Firstly, we assessed the percentage covers and average height of tree, shrub and herb layers and

covers of bryophytes. We estimated vascular plant species covers in particular vegetation layers using the nine-degree cover-abundance scale (DENGLER et al. 2008). A GPS receiver acquired geographical coordinates (WGS 84) and elevation. Moreover, we determined slope inclination and aspect. As soil acidity was indicated as an important environmental factor for variability of alluvial forests (NAQINEZHAD 2008), in each relevé, we took four subsamples of the uppermost 15 cm of soil and mixed them into one sample. Afterwards, we measured its pH in a suspension with deionized water (2:5) by a portable instrument Greisinger. In addition, for 11 plots in Aragvi Region, we made and described soil profiles and evaluated them following the current international soil classification system (IUSS WORKING GROUP WRB 2022). Since cattle grazing is widespread across the Caucasus, we assessed level of pasture pressure for each plot using the following ordinal scale: 1 – without grazing (without visible signs of cattle grazing), 2 – low and intermediate grazing levels (signs – detectable cattle paths), 3 – heavy grazing level (signs – marked cattle paths with sparse vegetation, visible browsing damages, cattle droppings). Coppicing and pollarding of alders are also broadly applied techniques in the southern Caucasus, supported by their high resprouting capacity (CLAESSENS et al. 2010, AOSAAR et al. 2012, HOUSTON DURRANT et al. 2016a,b). We recorded a binary variable of whether this kind of traditional forest management was noticeable in a focal stand.

In order to help to interpret the classification results, we additionally acquired the following climatic variables for each plot: annual mean temperature (BIO1), temperature seasonality (BIO4), annual precipitations (BIO12) and precipitation seasonality (BIO15), all obtained from the BIOCLIM+ dataset from the Chelsa database (BRUN et al. 2022). We have chosen these variables due to their relatively straightforward interpretability from an ecological perspective. Climatic data were processed in R 4.2.2 (R CORE TEAM 2022) using the packages *terra* (HIJMANS et al. 2022, <https://cran.r-project.org/web/packages/terra/index.html>) and *sf* (PEBESMA et al. 2023, <https://cran.r-project.org/web/packages/sf/index.html>). Other spatial data were managed in QGIS 3.8 environment (QGIS DEVELOPMENT TEAM 2021). We adopted data on the national distribution of species from the compendium Flora of Georgia, volumes 1–16 (e.g. KETSKHOVELI 1971, GAGNIDZE 2011).

2.3 Expanded datasets

To provide a regional context to the recorded communities, we compiled a regional dataset of vegetation-plot records of alluvial forests published from the Caucasus and its surroundings. It included plots from the following sources: Abkhazia Region of Georgia (16 plots; associations *Carici remotae-Pterocaryetum pterocarpae* and *Truello thurnbergii-Alnetum barbatae*; ERMAKOV et al. 2021), north-western Turkey (15; *Thelypteris limbospermae-Alnetum barbatae*; QUÉZEL et al. 1980), north-central Turkey (10; *Diospyros loti-Alnetum barbatae*; KORKMAZ et al. 2008). This plot collection was afterwards appended to our original dataset. To give a continental context of the recorded Caucasian plots with *Alnus incana*, we compared the proper relevés of the original dataset with the boreo-nemoral European alliance *Alnion incanae* using a synoptic table published by DOUDA et al. (2016). Moreover, we analyzed differential species between the Caucasian plots and the association *Alnetum incanae* encompassing mountain *A. incana* forests of the nemoral zone of Europe and provided in the synoptic table thereby (DOUDA et al. 2016). Within this European dataset, we analyzed diagnostic species of both units to determine their syntaxonomic position by applying the strategy described in the following subchapter. The phytosociological alliance definition was adopted from WILLNER (2020).

2.4 Data processing and analyses

Data from the original dataset (Supplements E1 and E2) were stored in the Transcaucasian Vegetation Database (GIVD code AS-00-005) using Turboveg 2.1 software (HENNEKENS & SCHAMINÉE 2001). In the original and regional datasets, vascular plant species nomenclature and concepts were harmonized according to the Euro+Med PlantBase (<http://ww2.bgbm.org/EuroPlusMed/>; accessed 2022–12–01), in addition, we defined several ad hoc species aggregates (Supplement E3). For the European dataset, we kept taxonomical concepts in the published synoptic table used for the comparisons (DOUDA et al. 2016). Bryophyte names in the original dataset were standardized according to the current European checklist (HODGETTS et al. 2020). Furthermore, data were processed and

analyzed mainly in Juice 7.1 software (TICHÝ 2002). In the regional and European datasets, we considered only vascular plants and same-name species were merged across the vegetation strata in these datasets using an approach by FISCHER (2015) based on a random overlap of species covers. This step was essential because data on layers were not available for all plots of these datasets. We applied OptimClass1 procedure (TICHÝ et al. 2010) to select the optimal classification method and number of clusters. It indicated *Beta flexible* algorithm and Bray-Curtis distance as a measure of sample species composition dissimilarity as the optimal clustering approach. Species percentage cover data were square-root transformed prior to the analyses (TICHÝ et al. 2020) and taxa determined at the genus level only were excluded. We applied the *phi* coefficient as a measure of species-to-cluster fidelity calculated on species presence-absence data (CHYTRÝ et al. 2002). Numbers of plots in clusters were virtually equalized prior to the fidelity calculations (TICHÝ & CHYTRÝ 2006). Species with the *phi* ≥ 0.25 were considered diagnostic and with the *phi* ≥ 0.5 as highly diagnostic. Species with non-significant *phi* values ($p = 0.05$) were excluded based on Fisher's exact test. Representativeness of the lists of diagnostic species was increased by Constancy Ratio ($CR \geq 2$; DENGLE 2003). Species with frequency $\geq 75\%$ were considered constant for a cluster while species reaching a cover $\geq 5\%$ at least in 25% of relevés of a cluster were determined dominant. Woody species in the lists of diagnostic, constant and dominant species are supplemented with a number of the respective vegetation layers (1 – tree, 4 – shrub, 7 – juvenile).

We applied non-metric multidimensional scaling (NMDS) with Bray-Curtis distance to visualize differences in species composition of the clusters resulting from the classification analysis of the original dataset. Environmental variables (climatic, soil pH and elevation) were passively projected onto the ordination space applying the function *envifit*. It was computed in R 4.2.2 environment (R CORE TEAM 2022) using the package *vegan* (OKSANEN et al. 2020). Percentage species covers were square-root transformed prior to the analysis. Boxplots provide an overview of selected environmental variables across the recognized clusters. Package *ggplot2* (WICKHAM 2016) was utilized to prepare boxplots depicting selected variables. We tested differences among the clusters in these variables by an analysis of variance and subsequent post-hoc Tukey's test using the R package *stats* (R CORE TEAM 2022).

3. Results and discussion

3.1 Alluvial forests of the southern Greater Caucasus

In the original dataset, we recorded 49 relevés of alluvial alder forests with 320 species of vascular plants and 60 species of bryophytes. The most frequent Caucasian endemics and subendemics included *Alnus glutinosa* subsp. *barbata*, *Aquilegia wittmanniana*, *Jacobaea othonnae*, *Lactuca racemosa*, *Paris incompleta*, *Sedum stoloniferum*, *Senecio propinquus*, *Valeriana alliariifolia* and *Veronica filiformis*. Species of this biogeographical group were recorded across all the plots with varying numbers and proportions of total richness. The species richness of the sampled communities was 53 species per 200 m² on average (and 46 for plots of the smaller size of 100 m²). Plot species richness of the studied alluvial forests appears to be considerably higher compared to the oak-hornbeam and ravine forests of the Greater Caucasus (cf. NOVÁK et al. 2020). It might be conditioned by more heterogeneous environmental conditions developed at a small spatial scale in the alluvial forests, e.g. slight variation in the surface level above the water table in alluvia might cause considerable differences in soil moisture availability. Therefore, alluvial forests harbour more diverse ecological species groups, including forest mesophytes, nutrient- and moisture-demanding species of various light requirements and species of pastures and meadows. Stony alluvial soils even support species of ravine and rock forests (DOUDA et al. 2016, PIELECH 2021). Moreover, river valleys are known as remarkable migration corridors with a large set of

abiotic conditions and linear connectivity enabling plant migrations both downstream and upstream. Hence, plant communities associated with river valleys often exhibit high species richness (ZELENÝ & CHYTRÝ 2007, HOLEŠTOVÁ & DOUDA 2022).

Alluvial forests are very restricted in the Enguri River valley since the river often flows in a deep rocky ravine. However, they locally occupy ravine slopes with lateral springs and alluvial fans. In places with flat floodplains, they often form a narrow strip lining the river banks. On the contrary, the plain and often a rather broad alluvium of the Pshavis Aragvi River support the development of larger complexes of alluvial forests. In this area, they locally inhabit moist slopes as well. Most of the stands served as cattle pastures of various intensities and as a source of firewood, indicated by coppice management.

In the original dataset, we applied unsupervised classification analysis (*Beta flexible*, $Beta = -0.2$) and recognized five clusters, afterwards we organized them as three individual vegetation types (Fig. 2 and 3). We give their overview below, including their syntaxonomic

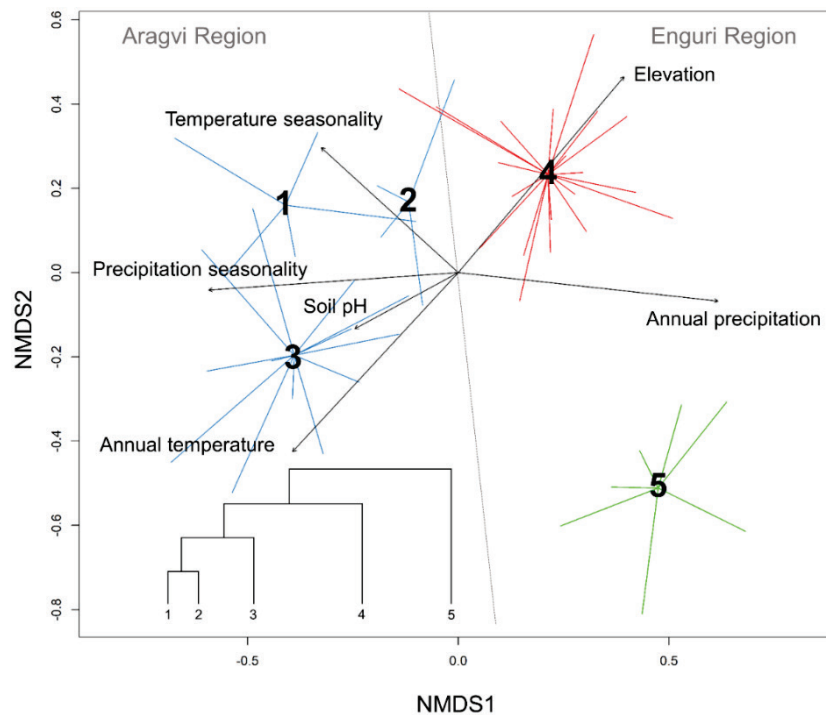


Fig. 2. Nonmetric multidimensional scaling analysis (stress 0.20) of the original dataset. Plots are assigned to five clusters resulting from the unsupervised classification, its classification dendrogram is located in the lower right corner. Centroids of each cluster are provided, while the line tips show the position of the individual plots. Selected environmental variables were passively projected onto the ordination space.

Abb. 2. Nichtmetrische mehrdimensionale Skalierungsanalyse (Stresswert 0,2) des Originaldatensatzes. Die Vegetationsaufnahmen werden fünf Clustern zugeordnet, die sich aus der unbeaufsichtigten Klassifizierung ergeben. Das Klassifizierungsdendrogramm befindet sich in der unteren rechten Ecke. Für jeden Cluster werden Schwerpunkte angegeben, während die Linienspitzen die Position der einzelnen Aufnahmen anzeigen. Ausgewählte Umgebungsvariablen wurden passiv auf den Ordinationsraum projiziert.

interpretation resulting from the comparison with previously described syntaxa. Highly diagnostic, constant and dominant species of the vegetation types were calculated in the context of the original dataset. Species names are accompanied by proper vegetation layer, except for the herb and moss layers. See Supplement E4 for complete lists of their diagnostic species. Ordination analysis (NMDS) was applied to visualize differences in the species composition of the clusters (Fig. 2). Boxplots of selected environmental variables are provided furthermore (Fig. 4). Details on soil characteristics of the selected relevés are given separately (Supplement E5).

Vegetation type 1 (association *Veronico filiformis*-*Alnetum incanae* ass. nova hoc loco)

Clusters 1–3 (22 relevés)

Highly diagnostic species: *Alliaria petiolata*, *Chrysosplenium alternifolium*, *Dipsacus pilosus*, *Fraxinus excelsior* (7), *Plagiomnium rostratum*, *Polygonatum glaberrimum*, *Primula veris* subsp. *macrocalyx*, *Salvia glutinosa*, *Sambucus nigra* (4), *Scutellaria altissima*

Constant species: *Alnus incana* (1), *Brachypodium sylvaticum*, *Brachythecium rivulare*, *Carex sylvatica*, *Dipsacus pilosus*, *Dryopteris caucasica* aggr., *Fragaria vesca*, *Fraxinus excelsior* (7), *Galium odoratum*

Dominant species: *Alnus incana* (1), *Brachypodium sylvaticum*, *Onoclea struthiopteris*, *Salvia glutinosa*, *Sambucus nigra* (4)

The first community includes alluvial alder forests of the Aragvi Region. They inhabit soils of various reaction (average pH 5.8), including strongly acidic as well as basic ones. Pedological research, led exclusively in the selected plots of the third cluster (ecological subtype; see below), showed that most of the investigated stands (73%) occupied Calcaric Skeletic Fluvisols while the rest occupied Calcaric Fluvic Skeletic Regosols (18%) and Dystric Fluvic Skeletic Regosols (9%). Regarding climate, these stands were recorded in comparably warm (average annual temperature 6.6 °C) and dry (annual precipitation 1096 mm) areas, showing significant seasonality in precipitation, in the context of the original dataset.

Alnus incana dominates in the tree layer (average cover 78%, average height 15 m), other species (*Alnus glutinosa* subsp. *barbata*, *Salix euxina*) are seldom admixed. All investigated stands were a subject of coppicing and forest grazing. The shrub layer (18%, 2.8 m) predominantly contains alder rejuvenation and deciduous shrubs (e.g. *Corylus avellana*, *Euonymus europaeus*, *Viburnum opulus*), including nitrophilous *Sambucus nigra*. Unpalatable herb *Salvia glutinosa* and nitrophilous grass *Brachypodium sylvaticum* mostly dominate the herb layer (74%, 0.76 m). In segments less affected by cattle, stoloniferous fern of humid forests *Onoclea struthiopteris* may attain dominance. The herb layer especially contains these ecological groups, nemoral herbs both common (e.g. *Galium odoratum*, *Impatiens noli-tangere*, *Oxalis acetosella*) or characteristic of lower and warmer areas of the Caucasus (e.g. *Clinopodium umbrosum*, *Dipsacus pilosus*, *Polygonatum glaberrimum*) as well as forest nutrient-demanding species (e.g. *Geranium robertianum*, *Schedonorus giganteus*, *Urtica dioica*). Occurrence of species characteristic of alluvial and ravine forests (e.g. *Aruncus dioicus*, *Pachyphragma macrophylla*) is also remarkable. Monocotyledonous geophytes (e.g. *Arum orientale*, *Dioscorea communis*) were recorded in most relevés, while tall forbs are rarer than in the following vegetation type. The other frequently occurring Caucasian species comprise *Aquilegia wittmanniana*, *Sedum stoloniferum*, *Valeriana alliariifolia* and *Veronica filiformis*. Some typical species exhibit a limited distribution in Georgia, common in the Aragvi region, while rare or missing in the Enguri Region

(e.g. *Chrysosplenium oppositifolium*). Juveniles involve particularly noble hardwood trees *Acer cappadocicum* and *Fraxinus excelsior*, indicating possible future successional trends in the canopy composition. Species of the moss layer (8%) reaching the highest frequency include *Brachythecium rivulare*, *Plagiomnium undulatum* and *Sciuro-hypnum populeum*, all generalists of wet habitats, and *Plagiomnium rostratum* that requires bare soil surface and prefers basic substrates.

The classification analysis revealed a considerable inner heterogeneity within this type and recognized three ecological subtypes. The first encompasses community with a higher concentration of ruderal and non-forest species (e.g. *Glechoma hederacea*, *Torilis japonica*), including annuals (e.g. *Euphorbia stricta*, *Sigesbeckia orientalis*), supported by intensive grazing. The second includes stands with broad-leaved nemoral herbs sensitive to grazing disturbances (e.g. *Pachyphragma macrophylla*, *Petasites albus*, *Silene multifida*) and represents well-preserved sections of alluvial alder forests under low grazing management. The last subtype is the dominant one, associated with intermediate grazing pressure. The level of anthropogenic influence is, therefore, presumably the driving factor distinguishing these subtypes.

Vegetation type 2 (*Brunnero macrophyllae-Alnetum incanae* ass. nova hoc loco)

Cluster 4 (20 relevés)

Highly diagnostic species: *Alchemilla vulgaris* aggr., *Dactylorhiza urvilleana*, *Plagiothecium cavifolium*, *Ribes biebersteinii* (4), *Senecio propinquus*

Constant species: *Alnus incana* (1), *Athyrium filix-femina*, *Dryopteris caucasica* aggr., *Epilobium montanum*, *Fragaria vesca*, *Geranium robertianum*, *Geum urbanum*, *Oxalis acetosella*, *Rubus idaeus*, *Schedonorus giganteus*

Dominant species: *Alnus incana* (1), *Athyrium filix-femina*, *Brachypodium sylvaticum*, *Oxalis acetosella*, *Rubus idaeus* (7), *Viola odorata*

Forests of this vegetation type inhabit stony alluvial soils of various reaction (average pH 5.8). Regarding climate, they were recorded in comparatively cold (4.3 °C) and humid (1317 mm) sections of the Enguri Region, which additionally show high temperature seasonality unlike the last vegetation type, but similarly low precipitation seasonality.

This type encompasses forests dominated merely by *Alnus incana* in the tree layer (average cover 86%, average height 13 m). Most of the stands serve as coppices, but some remain intact in this respect. The majority of frequent species of the shrub layer (6 %, 1.9 m) involve Caucasian endemics and subendemics (e.g. *Lonicera steveniana*, *Ribes biebersteinii*), including conifers (*Abies nordmanniana*, *Picea orientalis*), accompanied by broadly distributed species (e.g. *Corylus avellana*, *Sorbus aucuparia*) and alder rejuvenation. The herb layer (70%, 0.55 m) was co-dominated by common forest mesophytes and nitrophytes, including especially herbs (e.g. *Athyrium filix-femina*, *Oxalis acetosella*, *Viola odorata*) and less frequently grasses (*Brachypodium sylvaticum*, *Schedonorus giganteus*). Many tall forbs (e.g. *Senecio propinquus*, *Symphytum asperum*, *Valeriana alliariifolia*), inclusive of species diagnostic to the cluster (e.g. *Caucasalia macrophylla*, *Swertia iberica*), represent Caucasian endemics and subendemics.

Species with their Georgian distribution restricted to the Western Caucasus (e.g. *Caucasoseris abietina*, *Cirsium uliginosum*, *Pulmonaria dacica*) are also diagnostic. *Gymnocarpium dryopteris* and *Polygonatum verticillatum* represent the boreo-montane floral element. Frequent pasture weeds include Western Caucasian endemic *Cirsium uliginosum* or



Fig. 3. **a)** Alluvial alder forest (association *Veronico filiformis-Alnetum incanae*) in the Khevsuretis Aragvi River valley near Datvisi Village. **b)** Pshavis Aragvi River valley near Sharakhevi Village. **c)** Alluvial alder forest (association *Brunnero macrophyllae-Alnetum incanae*) in the Enguri River valley near Vichnashi village. **d)** Enguri River valley below Mestia City. **e)** Coppiced alluvial alder forest (association *Sedo stoloniferi-Alnetum barbatae*) in the Nakra River valley near Nakra Village. **f)** Nakra River valley, ibidem (Photos: V. Kalníková a) August 2021, P. Novák b) August 2021, c)-f) August 2022). See Supplement E6 for further photos.

Abb. 3. **a)** Alluvialer Erleneald (*Veronico filiformis-Alnetum incanae*) im Tal des Khevsuretis Aragvi-Flusses beim Dorf Datvisi. **b)** Tal des Pshavis Aragvi-Flusses nahe dem Dorf Sharakhevi. **c)** Alluvialer Erlenwald (*Brunnero macrophyllae-Alnetum incanae*) im Tal des Enguri-Flusses beim Dorf Vichnashi. **d)** Tal des Enguri-Flusses unterhalb der Stadt Mestia. **e)** Als Niederwald genutzter alluvialer Erlenwald (*Sedo stoloniferi-Alnetum barbatae*) im Tal des Nakra-Flusses beim Dorf Nakra. **f)** Nakra-Flusstal, ebendort (Fotos: V. Kalníková a) August 2021, P. Novák b) August 2021, c)-f) August 2022). Siehe Anhang E6 für weitere Fotos.

common herb *Prunella vulgaris*. The majority of the sites served as at least occasional cattle pastures. However, they were generally slightly less grazed compared to the previous type, particularly in sparsely inhabited lateral valleys. *Brachythecium rivulare* was the most common dominant of the moss layer (4%). Other species were primarily low in cover; of the more frequent, for example, *Plagiomnium elatum*, *P. medium* and *Sciuro-hypnum populeum*.

Vegetation type 3 (*Sedo stoloniferi-Alnetum barbatae* ass. nova hoc loco)

Cluster 5 (7 relevés)

Highly diagnostic species: *Alnus glutinosa* subsp. *barbata* (1), *Alnus glutinosa* subsp. *barbata* (4), *Carex remota*, *Circaea lutetiana*, *Clinopodium grandiflorum*, *Erigeron annuus*, *Lycopus europaeus*, *Persicaria hydropiper*, *Picea orientalis* (7), *Tussilago farfara*

Constant species: *Alnus glutinosa* subsp. *barbata* (1), *Athyrium filix-femina*, *Carex sylvatica*, *Circaea lutetiana*, *Galium odoratum*, *Geranium robertianum*, *Rubus idaeus* (7), *Schedonorus giganteus*, *Sedum stoloniferum*, *Urtica dioica*

Dominant species: *Alnus glutinosa* subsp. *barbata* (1), *A. incana* (1), *Brachythecium rivulare*, *Corylus avellana* (4), *Onoclea struthiopteris*, *Persicaria hydropiper*, *Picea orientalis* (4), *Salvia glutinosa*, *Sedum stoloniferum*

This vegetation type includes stands primarily developed on soils of strongly to moderately acidic reaction (average pH 5.6). Climatically, forests belonging to this cluster are characteristic of relatively warm (6.3 °C) and humid (1588 mm) lower segments of the Enguri Region. In comparison with the alluvial forests of the Aragvi Region, precipitation seasonality is significantly lower, indicating a relatively balanced precipitation regime.

This vegetation type encompasses alluvial alder forests recorded in the Nakra and Nenskra River valleys in the Enguri Region's lowest parts. They represent a transition between the Caucasian mountain and Colchic Lowland alder forests. *Alnus glutinosa* subsp. *barbata* predominates the tree layer (average cover 89%, average height 12 m) while *A. incana* is merely admixed. The shrub layer (14%, 2.8 m) is constituted mainly of the rejuvenation of *A. glutinosa* subsp. *barbata* and coppiced shrubs of *Corylus avellana*, while coniferous species (*Abies nordmanniana*, *Picea orientalis*) occur only sporadically. The herb layer (38%, 0.33 m) is generally low and sparse compared to the previous vegetation type. Various species prevail, including ferns (e.g. *Athyrium filix-femina*, *Onoclea struthiopteris*). Shade-tolerant nitrophytes are frequent (e.g. *Geranium robertianum*, *Schedonorus giganteus*, *Urtica dioica*), accompanied by nemoral elements (e.g. *Dryopteris caucasica* aggr., *Galium odoratum*). In the context of the Enguri Region, this type appears comparatively more thermophilous, as indicated by *Clinopodium grandiflorum*, *Circaea lutetiana* and *Symphytum grandiflorum*, whereas many mountain tall herbs (e.g. *Jacobaea othonnae*, *Valeriana alliariifolia*) are scarce or even absent. These forests are under the most severe grazing treatment of the recorded communities, occurring in relatively warm and more inhabited segments of the Enguri Region. *Prunella vulgaris* and *Ranunculus repens* represent common pasture weeds. Moreover, several alien species accompany them. *Brachythecium rivulare*, a common bryophyte of humid sites, mostly dominates the moss layer (9%).

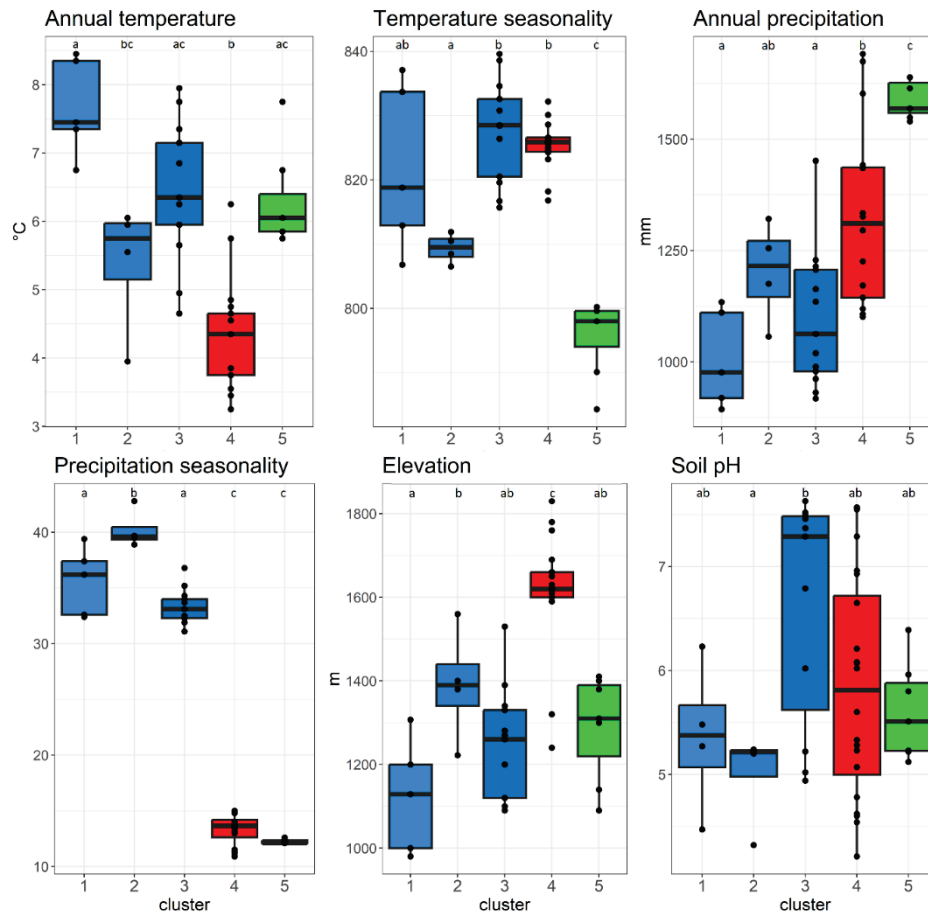


Fig. 4. Boxplots of selected environmental variables in the clusters of the original dataset, box colors indicate their association assignment (blue – *Veronico-Alnetum*, red – *Brunnero-Alnetum*, green – *Sedo-Alnetum*). Horizontal lines in the boxes show medians, while black dots indicate the positions of individual plots. The letters above the boxes identify homogeneous groups (Tukey's test, $p < 0.05$).

Abb. 4. Boxplots ausgewählter Umweltvariablen in den Clustern des Originaldatensatzes, die Farben der Boxen zeigen ihre Assoziationszuordnung an (blau – *Veronico-Alnetum*, rot – *Brunnero-Alnetum*, grün – *Sedo-Alnetum*). Horizontale Linien in den Kästchen zeigen Mediane an, während schwarze Punkte die Positionen einzelner Vegetationsaufnahmen anzeigen. Die Buchstaben über den Kästchen kennzeichnen homogene Gruppen (Tukey-Test, $p < 0,05$).

3.2 Regional dataset – Caucasian and Colchic alder forests

To investigate the position of the Caucasian alluvial alder forests in the regional context, we led an unsupervised classification analysis (*Beta flexible*, $Beta = -0.5$) of a broader dataset. It encompassed alder-dominated relevés from the following sources: the original dataset, relevés from the Colchic Lowland in Georgia and relevés from northeastern segment of Anatolia, including those of the type association of the alliance *Alnion barbatae*. The results of the analysis are summarized in the classification dendrogram (Fig. 5) and frequency synoptic table of the recognized clusters (Supplement E7).

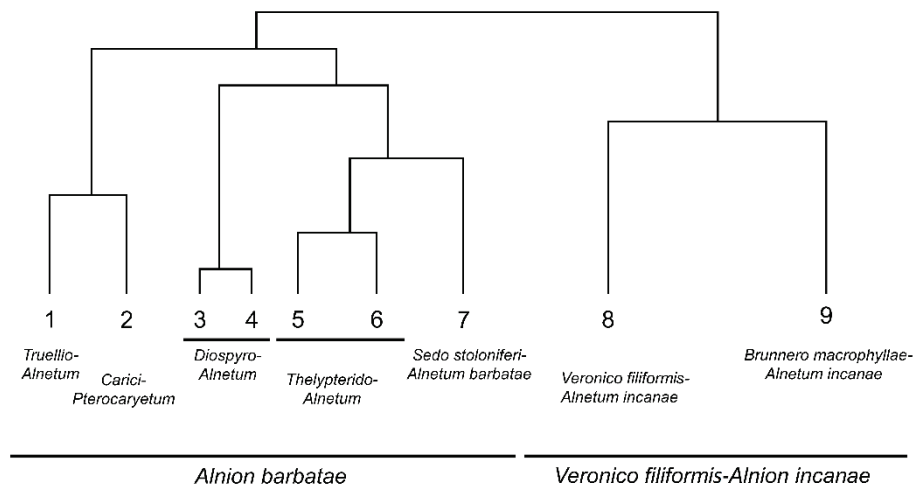


Fig. 5. Dendrogram of the classification analysis (*Beta flexible*, *Beta* = -0.5) of the Caucasian and a Colchic alluvial alder forests and syntaxonomic interpretation of the clusters. For the full names of the abbreviated association names see Methods.

Abb. 5. Dendrogramm der Klassifikationsanalyse (*Beta flexibel*, *Beta* = -0,5) der kaukasischen und kolchischen Erlen-Auenwälder und syntaxonomische Interpretation der Cluster. Die vollständigen Namen der abgekürzten Assoziationsnamen s. unter Methoden.

At the nine clusters level, the classification relatively well reproduced the associations, including some intra-association variability. At the higher level, the classification analysis produced two main clusters. The first included Colchic alder forests dominated by Euxino-Hyrcanian element *Alnus glutinosa* subsp. *barbata*. Diagnostic species of this main cluster include species characteristic of warmer and often humid regions of SW Eurasia (e.g. N Anatolia, Colchis, N Iran), for instance, *Carex pendula*, *Hedera* spp., *Hypericum Androsaemum*, *Symphytum grandiflorum*, accompanied by relict deciduous trees *Diospyros lotus* and *Pterocarya fraxinifolia* and evergreen shrubs *Daphne pontica* or *Rhododendron ponticum*. This vegetation fits well with the concept of the alliance *Alnion barbatae* originally described in the mountains of northeastern Anatolia (QUÉZEL et al. 1980, 1992). Of the original dataset, Vegetation type 3 was classified within this main group. Contrary, boreo-temperate tree *Alnus incana* exclusively dominated the Caucasian mountain main cluster. They were characterized by mountain and nemoral species (e.g. *Galium odoratum*, *Oxalis acetosella*, *Polygonatum verticillatum*, *Stachys sylvatica*) as well as numerous Caucasian endemics and subendemics. This group included tall forbs (*Jacobaea othonnae*, *Senecio propinquus*, *Symphytum asperum*), lower herbs (*Lactuca racemosa*, *Sedum stoloniferum*, *Veronica filiformis*) as well as deciduous shrubs (e.g. *Ribes biebersteinii*). The two vegetation types (associations) were reproduced by the classification analysis almost the same (one plot from *Veronico-Alnetum* was missclassified under *Brunnero-Alnetum*, presumably due to the occurrence of mountain species).

3.3 Caucasian mountain floodplain forests in the western Eurasian context

In order to present specific Caucasian *Alnus incana* alluvial forests, we performed a broad-scale comparison of the Caucasian *A. incana* forests (second main cluster as given above) with the alliance *Alnion incanae* that include also *Alnus incana*-dominated forests of the European boreal and temperate zones (DOUDA et al. 2016). The comparative analyses of the Caucasian stands against this alliance produced the following differential species with limited distribution, predominantly Caucasian endemic and subendemic herbs (e.g. *Aquilegia wittmanniana*, *Brunnera macrophylla*, *Caucasalia macrophylla*, *Cirsium uliginosum*, *Euphorbia macroceras*, *Jacobaea othonnae*, *Pachyphragma macrophylla*, *Paris incompleta*, *Sedum stoloniferum*, *Senecio propinquus*, *Silene multifida*, *Swertia iberica*, *Symphytum asperum*, *Valeriana alliariifolia* and *Veronica filiformis*) and woody species (e.g. *Acer trautveterii*, *Lonicera steveniana*). Some of them are representatives of phylogenetically relatively isolated small taxa, for instance *Brunnera macrophylla* (HILLGER et al. 2004), *Caucasalia macrophylla* (NORDENSTAM 1997) or *Pachyphragma macrophylla*, a species of the monotypic genus (MUMMENHOFF et al. 2001). These findings support the newly introduced alliance's biogeographical and even evolutionary meaning, an important viewpoint on upper-association syntaxa (WILLNER 2020). Contrary, recorded Caucasian stands were negatively delimited against *Alnion incanae* by species scarce or absent in the regions, for instance, *Anemone nemorosa*, *Chaerophyllum hirsutum*, *Ficaria verna*, *Lysimachia nemorum*, *Pulmonaria officinalis* aggr. and *Ranunculus lanuginosus*. For the complete synoptic table summarizing diagnostic (differential) species of these two vegetation units, see Supplement E8. Similar differences were revealed by the analysis of differential species between the Caucasian *A. incana* forests and the association *Alnetum incanae* (Supplement E9). It showed that these mountain *A. incana* stands of the nemoral zone of Europe significantly differ from their Caucasian counterparts. Their best differential species include trees (e.g. *Picea abies*), shrubs (e.g. *Lonicera nigra*) and herbs (e.g. *Stellaria nemorum*, *Thalictrum aquilegiifolium*) absent in the Caucasus and vice versa Caucasian endemics and subendemics (see the species list above).

In the European context, three alliances of alluvial alder forests across Europe: *Alnion incanae* (nemoral and hemiboreal zones), *Osmundo-Alnion* (oceanic regions of W Europe) and *Ligustro vulgaris-Alnion glutinosae* (Italian Peninsula) were distinguished in EuroVeg-Checklist (MUCINA et al. 2016). However, new alliances were subsequently described in specific regions, e.g. *Hyperico-Alnion* (Cantabrian watershed in Spain; BIURRUN et al. 2016), accepted in a later overview (MANDŽUKOVSKI et al. 2021). Our analyses supported a specific character of the Caucasian *Alnus incana* stands at the continental scale. Caucasian endemics and subendemics are diagnostic for this Caucasian type, analogically to the aforementioned geographically restricted alliances in the southern European peninsulas. Similar biogeographical delimitation of alliances, with specific Caucasian syntaxa, appears in the European deciduous forests, e.g. beech (PASSARGE 1981b), oak-hornbeam (NOVÁK et al. 2023) and ravine ones (ZUKAL in NOVÁK et al. 2020). It is largely caused by distribution patterns of narrow-range forest species presumably reflecting glacial forest refugia (WILLNER et al. 2009). Therefore, an idea of an individual alliance of the Caucasian alluvial alder forests is in accordance with this concept. Consequently, we formally describe a new Caucasian alliance of alluvial alder forests *Veronico filiformis-Alnion incanae*. Differential species against other alder forests of Europe are primarily Caucasian endemics and subendemics listed above. *Veronica filiformis* represents the absolute character taxa, a necessary condition of syntaxa at the alliance level (sensu WILLNER 2020), of the new alliance.

The taxonomic position of the Caucasian population of *Alnus incana* remains debatable due to its probable phylogenetic isolation. However, further sampling and genetic analyses are needed (MANDÁK et al. 2016a). If a distinct Caucasian *A. incana* taxon was formally described as a new one, it could serve as an additional absolute character taxon of the new alliance because WILLNER (2020) admits a specific role of cryptic taxa (“subspecies in statu nascedenti”) in the delineation of higher syntaxa.

The alliance *Alnion barbatae*, including vegetation type 3, can be seen as a Colchic analogy to the Hyrcanian alliance *Smilaco excelsae-Alnion barbatae* distributed in northern Iran (GHOLIZADEH et al. 2020). These alliances are differentiated by Colchic (*Rhododendron ponticum*, *Trachystemon orientalis*) and Hyrcanian species (*Acer velutinum*, *Parrotia persica*), respectively. However, they share some biogeographically distinct and presumably Tertiary relict species (e.g. *Diospyros lotus*, *Pterocarya fraxinifolia*, *Smilax excelsa*).

3.4 Patterns of species composition and forest succession

The patterns in the original dataset appear to be conditioned by both climatic and biogeographical (distribution of narrow-range species or broadly-distributed species with a limited occurrence in Georgia) differences. Vegetation type 1 (Aragvi type) is developed under comparably drier and warmer climate characterized by higher seasonality, chiefly in precipitation. The central-eastern sector of Georgia exhibits a drier and more seasonal climate (BONDYREV et al. 2015). Such conditions presumably support relatively thermophilous herb (e.g. *Clinopodium umbrosum*, *Dipsacus pilosus*, *Primula veris* subsp. *macrocalyx*, *Scutellaria altissima*) and woody species (e.g. *Acer campestre*, *A. cappadocicum*). Contrary, the second type, *Alnus incana* forests of the Enguri Region, was recorded at higher elevations, in thermally harsher conditions with higher and more balanced yearly precipitations. This type of climate favours species of mountain forests, including boreo-mountain elements (e.g. *Dryopteris carthusiana*, *Gymnocarpium dryopteris*), coniferous trees (e.g. *Abies nordmanniana*), mountain tall forbs (e.g. *Aconitum variegatum* subsp. *nasutum*, *Caucasalia macrophylla*, *Senecio propinquus*) and some mosses (e.g. *Brachythecium geheebii*, *Sanionia uncinata*). Biogeographically, Western Caucasian endemics and species whose Georgian distribution is concentrated there (e.g. *Cirsium uliginosum*, *Pojarkovia pojarkovae*, *Pulmonaria dacica*) are among its diagnostic species. The third type encompasses *Alnus glutinosa* subsp. *barbata* stands inhabiting lower parts of the Enguri Region. The climate is similarly warm as for the first type, but much less seasonal in terms of temperature and precipitation. Moreover, precipitation amounts are the highest of the analyzed clusters. This type of climate shows affinities to the Colchic area, which is generally warm and humid over the year, with mild winters (BONDYREV et al. 2015). It supports relatively thermophilous species.

From the forest succession perspective, alder seedlings are highly light-demanding and require enough light to grow up (CLAESSENS et al 2010, HOUSTON DURRANT et al. 2016a, b, LEUSCHNER & ELLENBERG 2017). Consequently, we observed almost no current alder seedlings since alder trees in the forest canopy cast deep shade (LEUSCHNER & ELLENBERG 2017). The generative regeneration of alders presumably takes place exclusively after severe disturbances (e.g. floods, outbreaks of tree pathogens) which open the canopy and allow light into the understory (HOUSTON DURRANT et al. 2016a, b), as we observed on gravel river deposits, for instance (Supplement E6). Although alders, especially *Alnus incana*, are reported as relatively short-living species (HOUSTON DURRANT et al. 2016a, b), coppicing

might prolong the life span of alder individuals (AOSAAR et al. 2012). Hence, these forests probably remain relatively stable in the canopy species composition, although generative regeneration of alders is generally poor.

3.5 Nature protection and threats

Caucasian mountain floodplain forests show relatively high alpha diversity and harbours numerous endemics. The river network of the Georgian Greater Caucasus is relatively undisturbed and mostly only little altered by human activities. Therefore, it provides an opportunity to study relatively natural riverine communities (e.g. KALNÍKOVÁ et al. 2020), particularly in less inhabited valley sections. In the study regions, only upstream segments of Khevsureti Aragvi were considerably altered by human activities (river regulations, channel shifting, dam constructions) associated with building the Transcaucasian Railway connecting Tbilisi and Vladikavkaz, the abandoned unfinished project of 1980s (KORTIEV & KORTIEV 2017). The major threat nowadays is the construction of new water reservoirs planned in the Nenskra and Enguri valleys (Nenskra and Khudoni dams) that would directly destroy tens of kilometres of riverine landscape and associated habitats (BAKHIA et al. 2019) and dramatically alter the natural hydrological regime hundreds of kilometres downstream (cf. DAI & LIU 2013). Contrary to that, dam removals are currently a theme in Europe and North America (DING et al. 2019). Concerning cattle grazing, the best-preserved alder forests are developed in remote places, far away from settlements, while stands close to villages are heavily impacted, although the number of cattle has decreased by about one third in the last decades in Georgia (BONDYREV et al. 2015). Grazing supports spiny, toxic, or unpalatable species, including *Alnus incana*, and pasture herbs (e.g. *Agrostis capillaris*, *Prunella vulgaris*), whereas characteristic forest species demise by both direct consumption (broad-leaved herbs, grasses) and disturbances caused by moving of animals in wet soils (e.g. ferns) (HOUSTON DURRANT et al. 2016b, LEUSCHNER & ELLENBERG 2017).

Across Europe, alluvial forests belong among the forest habitats most invaded by vascular plant aliens (WAGNER et al. 2017). However, we recorded only a meager number of aliens (sensu KIKODZE et al. 2010) and they were generally confined to the lowest elevations of the studied area. In the Enguri Region, alien species occurred exclusively in the *Alnus glutinosa* subsp. *barbata* forests in Nakra and Nenskra valleys and they were reaching only low constancy (e.g. *Erigeron canadensis*, *Hydrocotyle ramiflora*, *Juncus tenuis*). Their occurrence is probably connected with its more favourable mild climate, as visible from the high concentration of alien species in the neighbouring Colchic Lowland (KIKODZE 2010). Within the Aragvi Region, aliens were recorded only scarcely. However, in the Georgian vascular plant alien checklist (KIKODZE et al. 2010), also *Geranium robertianum*, a widespread nitrophilous annual of local forests, figures among neophytes. This classification seems contradictory with its common occurrence across forest vegetation belts and even in relatively intact forest ecosystems (NAKHUTSRISHVILI 2013, NOVÁK et al. 2020).

From a forest management perspective, studied stands show no commercial value except firewood production (HOUSTON DURRANT et al. 2016a, b). Frequent grazing and coppicing significantly reduced the trunks' quality, resulting in polycormon and crooked trunk forming. Rot and wood decay fungi infected many trees for the same reasons. Alluvial forests ranging up to 100 m from the river bank are protected by the Forest Code of Georgia under the category of protection forest (PARLIAMENT OF GEORGIA 2020). The objective of the management of a protection forest is to preserve and enhance the protective function of

the forest and commercial timber harvesting is prohibited. In the Aragvi Region they are additionally protected within the Aragvi Protected Landscape Area while similar landscape protection in the whole Svaneti is missing yet.

4. Syntaxonomic outline

Cl.: *Alno glutinosae-Populetea albae* P. Fukarek et Fabijanic 1968

Ord.: *Alno-Fraxinetalia excelsioris* Passarge 1968

All.: *Veronico filiformis-Alnion incanae* all. nova hoc loco

Ass.: *Veronico filiformis-Alnetum incanae* ass. nova hoc loco

Ass.: *Brunnero macrophyllae-Alnetum incanae* ass. nova hoc loco

All.: *Alnion barbatae* Quézel et al. 1992

Ass.: *Sedo stoloniferi-Alnetum barbatae* ass. nova hoc loco

***Veronico filiformis-Alnion incanae* all. nova hoc loco**

Diagnostic species: *Alnus incana*, *Aquilegia wittmanniana*, *Brachythecium rivulare*, *Brunnera macrophylla*, *Caucasalia macrophylla*, *Dactylorhiza urvilleana*, *Dipsacus pilosus*, *Euphorbia macroceras*, *Jacobaea othonnae*, *Lactuca racemosa*, *Onoclea struthiopteris*, *Paris incompleta*, *Ribes biebersteinii*, *Salvia glutinosa*, *Sciuro-hypnum populeum*, *Sedum stoloniferum*, *Senecio propinquus*, *Silene multifida*, *Swertia iberica*, *Symphytum asperum*, *Valeriana alliariifolia*, *Veronica filiformis*

Holotypus: *Veronico filiformis-Alnetum incanae* ass. nova hoc loco

***Veronico filiformis-Alnetum incanae* ass. nova hoc loco**

Vegetation type 1 in the original dataset.

Diagnostic species: *Alnus incana*, *Clinopodium umbrosum*, *Dipsacus pilosus*, *Polygonatum glaberrimum*, *Primula veris* subsp. *macrocalyx*, *Salvia glutinosa*, *Scutellaria altissima*, *Sedum stoloniferum*, *Symphytum asperum*, *Telekia speciosa*, *Veronica filiformis*

Holotypus (hoc loco) of the association: Georgia, Gometari (Dusheti District): alluvial alder forest, 42.2951111° N, 44.8281667° E, 200 m², 22 May 2022, elevation: 1200 m, aspect: 360°, inclination: 10°, soil pH (H₂O): 7.52, author: V. Kalníková. Relevé 21 in Supplements E1 and E2.

E₃ (cover 75%, average height 15 m): *Alnus incana* 4, *Prunus avium* +, *Salix caprea* +; E₂ (3%, 1.5 m): *Corylus avellana* +, *Sambucus nigra* +, *Viburnum lantana* +, *Euonymus europaeus* r; E₁ (65%, 0.8 m): *Viola odorata* 2b, *Oxalis acetosella* 2a, *Salvia glutinosa* 2a, *Sedum stoloniferum* 2m, *Asperula taurina* subsp. *caucasica* 1, *Brachypodium sylvaticum* 1, *Pimpinella tripartita* 1, *Polystichum braunii* 1, *Viola sieheana* aggr. 1, *Alliaria petiolata* +, *Aquilegia wittmanniana* +, *Arum orientale* +, *Asplenium septentrionale* +, *A. trichomanes* +, *Astragalus glycyphyllos* +, *Athyrium filix-femina* +, *Calamagrostis arundinacea* +, *Cardamine bulbifera* +, *C. impatiens* aggr. +, *C. quinquefolia* +, *Carex sylvatica* +, *Chelidonium majus* +, *Chrysosplenium alternifolium* +, *Cicerbita muralis* +, *Circaea ×intermedia* +, *Cruciata glabra* +, *Dipsacus pilosus* +, *Fragaria vesca* +, *Galium aparine* +, *G. odoratum* +, *Geranium robertianum* +, *Impatiens noli-tangere* +, *Laserpitium hispidum* +, *Lactuca racemosa* +, *Moehringia trinervia* +, *Myosotis sparsiflora* +, *Onoclea struthiopteris* +, *Origanum vulgare* +, *Physospermum cornubiense* +, *Poa nemoralis* +, *Primula veris* subsp. *macrocalyx* +, *Ranunculus repens* +, *Sanicula europaea* +, *Solidago virgaurea* +, *Stachys sylvatica* +, *Telekia speciosa* +, *Urtica dioica* +, *Veronica chamaedrys* +, *Veronica fili-*

formis +, *V. magna* +, *Aruncus dioicus* r, *Euphorbia glaberrima* r, *Geum urbanum* r, *Polygonatum glaberrimum* r; *Acer cappadocicum* +, *A. platanoides* +, *Carpinus betulus* +, *Corylus avellana* +, *Fraxinus excelsior* +, *Rubus idaeus* r, *Ulmus glabra* r; E₀ (5%): *Eurhynchium angustirete* l, *Plagiomnium rostratum* l, *Homalothecium philippeanum* +, *Tortella tortuosa* +, *Brachythecium* sp. r.

***Brunnera macrophyllae-Alnetum incanae* ass. nova hoc loco**

Vegetation type 2 in the original dataset.

Diagnostic species: *Alnus incana*, *Brunnera macrophylla*, *Caucasalia macrophylla*, *Caucasoseris abietina*, *Cirsium uliginosum*, *Dactylorhiza urvilleana*, *Lonicera steveniana*, *Ribes biebersteinii*, *Sedum stoloniferum*, *Senecio propinquus*, *Symphytum asperum*, *Veronica filiformis*

Holotypus (hoc loco) of the association: Georgia, Mazeri (Mestia District): alluvial alder forest in a brook valley (right tributary of the Dolra River) NW from the village, 43.0836667° N, 42.5935000° E, 100 m², 20 August 2022, elevation: 1690 m, aspect: 90°, inclination: 7°, soil pH (H₂O): 5.07, author: P. Novák. Relevé 35 in Supplements E1 and E2.

E₃ (cover 80%, average height 8 m): *Alnus incana* 5; E₂ (20%, 6 m): *Corylus avellana* 2a, *Ribes biebersteinii* 1, *Sorbus aucuparia* 1; E₁ (60%, 0.65 m): *Onoclea struthiopteris* 3, *Sedum stoloniferum* 1, *Urtica dioica* 1, *Aconitum variegatum* subsp. *nasutum* +, *Agrostis capillaris* +, *Alchemilla vulgaris* aggr. +, *Anthriscus sylvestris* +, *Aruncus dioicus* +, *Athyrium filix-femina* +, *Brunnera macrophylla* +, *Calamagrostis arundinacea* +, *Cardamine impatiens* aggr. +, *Caucasalia macrophylla* +, *Clinopodium grandiflorum* +, *Dactylis glomerata* +, *Dryopteris carthusiana* +, *D. caucasica* aggr. +, *Elymus caninus* +, *Galium odoratum* +, *Gentiana asclepiadea* +, *Geranium robertianum* +, *Geum urbanum* +, *Impatiens noli-tangere* +, *Lactuca racemosa* +, *Lamium galeobdolon* subsp. *montanum* +, *Lapsana communis* +, *Myosotis sylvatica* +, *Oxalis acetosella* +, *Pimpinella rhodantha* +, *Poa nemoralis* +, *P. pratensis* +, *P. trivialis* +, *Prunella vulgaris* +, *Rubus* subgen. *Rubus* +, *Rumex arifolius* +, *R. obtusifolius* subsp. *sylvestris* +, *Selinum alatum* +, *Senecio propinquus* +, *Stachys* sp. +, *Symphytum asperum* +, *Veronica filiformis* +, *Viola odorata* +, *Aquilegia wittmanniana* r, *Heracleum sphondylium* subsp. *cyclocarpum* r, *Luzula pilosa* r, *Prenanthes petiolata* r, *Valeriana colchica* r, *Vicia sepium* r; *Abies nordmanniana* +, *Prunus avium* +, *Rubus idaeus* +, *Acer campestre* r, *A. cappadocicum* r, *Ribes biebersteinii* r, *Sorbus aucuparia* r; E₀ (2%): *Brachythecium geheebii* +, *B. rivulare* +, *Plagiomnium elatum* +, *Plagiothecium cavifolium* +, *Sciuro-hypnum populeum* +, *Eurhynchium angustirete* r.

***Sedo stoloniferi-Alnetum barbatae* ass. nova hoc loco**

Vegetation type 3 in the original dataset.

Diagnostic species: *Alnus glutinosa* subsp. *barbata*, *Clinopodium grandiflorum*, *Picea orientalis*, *Sedum stoloniferum*, *Symphytum grandiflorum*

Holotypus (hoc loco) of the association: Georgia, Nakra (Mestia District): alluvial alder forest, 43.1016111° N, 42.3886667° E, 200 m², 24 August 2022, elevation: 1300 m, aspect: 180°, inclination: 5°, soil pH (H₂O): 5.51, authors: V. Sedláček & G. Štětková. Relevé 48 in Supplements E1 and E2.

E₃ (cover 95%, average height 15 m): *Alnus glutinosa* subsp. *barbata* 5; E₂ (1%, 1.2 m): *Alnus glutinosa* subsp. *barbata* 1, *Sambucus nigra* r; E₁ (30%, 0.4 m): *Onoclea struthiopteris* 2a, *Cardamine impatiens* aggr. 1, *Circaea lutetiana* 1, *Galium odoratum* 1, *Geranium robertianum* 1, *Sedum stoloniferum* 1, *Ajuga reptans* +, *Athyrium filix-femina* +, *Carex remota* +,

C. sylvatica +, *Chaerophyllum angelicifolium* +, *Circaea ×intermedia* +, *Dryopteris carthusiana* +, *D. dilatata* +, *Epilobium montanum* +, *Geum urbanum* +, *Impatiens noli-tangere* +, *Galeopsis tetrahit* +, *Lapsana communis* +, *Lysimachia verticillaris* +, *Myosotis sylvatica* +, *Prunella vulgaris* +, *Ranunculus repens* +, *Saxifraga cymbalaria* +, *Urtica dioica* +, *Veronica beccabunga* +, *V. filiformis* +, *Brachypodium sylvaticum* r, *Fragaria vesca* r, *Lactuca marschallii* r, *Nasturtium officinale* r, *Paris incompleta* r, *Poa trivialis* r, *Pojarkovia pojarkovae* r, *Potentilla micrantha* r, *Ranunculus cappadocicus* r, *Rumex obtusifolius* subsp. *silvestris* r, *Schedonorus giganteus* r, *Viola reichenbachiana* r; *Rubus idaeus* r, *Sorbus aucuparia* r; E₀ (15%): *Brachythecium rivulare* 2a, *Rhizomnium punctatum* +, *Pellia* sp. +.

5. Conclusions

The study brings the first overview of mountain alluvial alder forests of the Greater Caucasus in Georgia based on the original phytosociological dataset recorded following the Braun-Blanquet approach. We gathered the data in two distinct regions representing two key biogeographical areas of the Georgian Greater Caucasus. The first located in western Georgia (Enguri River Basin) and the second in eastern Georgia (Aragvi River Basin). We recognized three vegetation types described as new associations, based on the variability in species composition, reflecting mainly climatic and biogeographical differences. The subsequent analyses of the broader datasets (regional, European) highlighted the uniqueness of the Caucasian *Alnus incana* forests, which were subsequently described as a new alliance *Veronico filiformis-Alnion incanae*. Recorded forest communities exhibited relatively high alpha diversity, at least in the regional context. They harbor numerous Caucasian endemics and subendemics across the vegetation strata. Their most serious threats include construction of new water reservoirs, dams, and cattle overgrazing. Therefore, further complex research on alluvial forests across the Caucasus is required.

Erweiterte deutsche Zusammenfassung

Einleitung – Der Kaukasus ist einer der globalen Biodiversitäts-Hotspots, der eine außergewöhnlich reiche Flora und eine große Vegetationsvielfalt beherbergt. Das Wissen über die lokale Vegetation beschränkt sich hauptsächlich auf dominante Vegetationsformationen von Wäldern, insbesondere von zonalen Typen. Auenwälder der Gebirge gehören zu den weniger erforschten Vegetationstypen und sind für ihre vielfältigen Ökosystemfunktionen und -leistungen wichtig, darunter Erosions- und Hochwasserschutz, Verbesserung der Wasserqualität, Kohlenstoffbindung, Schutz von Wasserläufen vor Verschmutzung sowie Erholungs- und ästhetische Funktionen. Eine pflanzensoziologische Zusammenschau lokaler Auenwaldtypen fehlt bislang (DOUDA et al. 2016). In dieser Studie führen wir die erste Untersuchung lokaler alluvialer Erlenwälder durch und beschreiben deren Ökologie, Vegetationsstruktur, Artenzusammensetzung und Variabilität in zwei entfernten Regionen im Großen Kaukasus.

Methoden – Alluviale Erlenwälder wurden in zwei Regionen des südlichen Makrohangs des Großen Kaukasus, den Flusseinzugsgebieten Enguri und Aragvi, Georgien, pflanzensoziologisch untersucht (Abb. 1). Diese Regionen weisen unterschiedliche klimatische und biogeografische Bedingungen auf, während ihre geologischen Bedingungen ähnlich sind, da mesozoische Sedimente vorherrschen (BONDYREV et al. 2015). In den Vegetationsperioden 2021 und 2022 haben wir pflanzensoziologische Aufnahmen (100–200 m²) auf einem breiten Höhengradienten (980–1830 m) erfasst. Aufgenommen wurden die prozentuale Bedeckung der Vegetationsschichten und die Bedeckung einzel-

ner Arten auf der 9-stufigen Braun-Blanquet-Skala. Darüber hinaus haben wir ihre genaue geografische Position (WGS 84), Höhe, Hangneigung und -ausrichtung, den an Oberbodenproben gemessenen Boden-pH-Wert und den Grad anthropogener Eingriffe (Beweidung, Niederholz) erfasst. Klimadaten wurden aus thematischen GIS-Layern extrahiert. Die Datenverwaltung erfolgte in Juice 7.1 (TICHÝ 2002). Wir haben drei Datensätze mithilfe unbeaufsichtigter Klassifizierungstechniken (Beta-flexibler Algorithmus) analysiert. Der Originaldatensatz enthielt Vegetationsaufnahmen, die während der eigenen Feldbeprobung der Autoren gesammelt wurden. Der regionale Datensatz umfasste den Originaldatensatz sowie Aufnahmen von Erlenwäldern aus Westgeorgien und angrenzenden Teilen der Türkei, die aus verschiedener Literatur digitalisiert wurden. Der europäische Datensatz umfasste Vegetationsaufnahmen aus dem Originaldatensatz, die von *Alnus incana* dominiert wurden, und Daten zum Verband *Alnion incanae* (DOUDA et al. 2016). Die Ähnlichkeiten zwischen Clustern wurden mithilfe der nichtmetrischen mehrdimensionalen Skalierung (NMDS) dargestellt.

Ergebnisse und Diskussion – Mithilfe von Klassifizierungsanalysen haben wir im Originaldatensatz fünf Cluster unterschieden, die als drei Vegetationstypen interpretiert wurden. Der erste umfasst *Alnus incana*-Wälder in der Region Aragvi. Sie zeichnen sich durch relativ thermophile Waldarten (z. B. *Dipsacus pilosus*, *Scutellaria altissima*) und zahlreiche kaukasische Arten, insbesondere solche aus wärmeren Regionen (z. B. *Clinopodium umbrosum*, *Polygonatum glaberrimum*) aus. Sie weisen eine beträchtliche interne Heterogenität auf, die sich in der unbeaufsichtigten Klassifizierung nach drei Clustern entsprechend dem Gradienten der anthropogenen Beeinflussung ausdrückte. Der zweite Vegetationstyp umfasst *Alnus incana*-Wälder aus der Enguri-Region. Sie enthielten eine größere Anzahl von montanen Arten (z. B. *Campanula latifolia*, *Polygonatum verticillatum*, *Sanionia uncinata*), gepaart mit westkaukasischen (z. B. *Cirsium uliginosum*) und kaukasischen Endemiten (*Dactylorhiza urvilleana*, *Swertia iberica*). Sie wurden in vergleichsweise kälterem und feuchterem Klima aufgenommen. Der dritte Vegetationstyp waren *Alnus glutinosa* subsp. *barbata*-Wälder; sie besiedeln die tiefsten Lagen der Enguri-Region, näher an der Kolchischen Tiefebene. Sie enthalten eine größere Anzahl thermophiler und gebietsfremder Arten (z. B. *Erigeron annuus*) und sind in relativ warmem und feuchtem Klima entwickelt. Unterschiede in den biogeografischen und klimatischen Bedingungen erwiesen sich als die Haupttreiber für die Gradienten ihrer Artenzusammensetzung. Die Analyse des regionalen Datensatzes bestätigte die Zugehörigkeit des dritten Vegetationstyps zum kolchischen Verband *Alnion barbatae*, der den ersten Hauptcluster bildete, während die kaukasischen *Alnus incana*-Wälder den zweiten Hauptcluster bildeten. Der Vergleich der kaukasischen *Alnus incana*-Wälder mit der Vegetation des boreo-nemoralen Verbandes *Alnion incanae* hebt die Individualität des kaukasischen Typs durch das Vorkommen vieler kaukasischer Endemiten und Subendemiten hervor. Daher haben wir ihn als einen neuen Verband beschrieben.

Syntaxonomisches Schema des Originaldatensatzes:

Kl.: *Alno glutinosae-Populetea albae* P. Fukarek et Fabijanic 1968

O.: *Alno-Fraxineta excelsioris* Passarge 1968

V.: *Veronico filiformis-Alnion incanae* all. nova hoc loco

Ass.: *Veronico filiformis-Alnetum incanae* ass. nova hoc loco

Ass.: *Brunnero macrophyllae-Alnetum incanae* ass. nova hoc loco

V.: *Alnion barbatae* Quézel et al. 1992

Ass.: *Sedo stoloniferi-Alnetum barbatae* ass. nova hoc loco

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Author contribution statement

V.K. and P.N. conceived the idea of the research. P.N. led the writing and the performed numerical analyses. V.K. and P.N. prepared the syntaxonomic scheme. M.V. processed spatial data. Š.P. compiled the electronic supplements. All the authors participated in the field sampling, 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 original dataset.

Anhang E1. Vegetationsaufnahmen des originalen Datensatzes

Supplement E2. Header data of the relevés of the original dataset (Supplement E1).

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

Supplement E3 Aggregated species in the original dataset.

Anhang E3. Arten-Aggregate im originalen Datensatz.

Supplement E4. Synoptic table of the diagnostic species of the vegetation types (associations) distinguished in the original dataset.

Anhang E4. Übersichtstabelle der im originalen Datensatz unterschieden diagnostischen Arten der Vegetationstypen (Assoziationen).

Supplement E5. Data on soil characteristics of selected relevés.

Anhang E5. Daten zu den Bodenmerkmalen ausgewählter Vegetationsaufnahmen.

Supplement E6. Further photographs of the studied vegetation.

Anhang E6. Weitere Fotos der untersuchten Vegetation.

Supplement E7. Synoptic table of the diagnostic species of the clusters distinguished in the regional dataset.

Anhang E7. Übersichtstabelle Tabelle der diagnostischen Arten der Cluster, die im regionalen Datensatz unterschieden werden.

Supplement E8. Synoptic table of the diagnostic species of the alliance *Alnion incanae* and Caucasian *Alnus incana* forests (alliance *Veronico filiformis-Alnion incanae*) in the European dataset.

Anhang E8. Übersichtstabelle der diagnostischen Arten des Verbandes *Alnion incanae* und Kaukasische *Alnus incana* Wälder (Verband *Veronico filiformis-Alnion incanae*) im europäischen Datensatz.

Supplement E9. Synoptic table of the diagnostic species of the association *Alnetum incanae* and Caucasian *Alnus incana* forests (alliance *Veronico filiformis-Alnion incanae*) in the European dataset.

Anhang E9. Übersichtstabelle der diagnostischen Arten des *Alnetum incanae* und Kaukasischer *Alnus incana* Wälder (Verband *Veronico filiformis-Alnion incanae*) im europäischen Datensatz.

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Supplement E2. Header data of the relevés of the original dataset (Supplement E1).

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

#	Municipality	Region	N (°)	E (°)	Area (m²)	Altitude (m a. s. l.)	Slope (°)	Aspect (°)	Cover (%)				Average height			Cluster	Pasture intensity	Coppicing	Soil pH (H ₂ O)	Date (YYYY-MM-DD)
									Tree layer	Shrub layer	Herb layer	Moss layer	Tree layer (m)	Shrub layer (m)	Herb layer (cm)					
1	Sharakhevi	Aragvi	42.318056	44.887333	200	980	0	-	80	1	85	10	14	1.5	40	1	3	1	N/A	2021-08-10
2	Barisakho	Aragvi	42.453000	44.928222	200	1200	0	-	70	5	75	20	17	1.5	20	1	3	1	6.23	2021-08-05
3	Korsha	Aragvi	42.487111	44.929444	200	1307	0	-	55	5	80	5	8	1.5	30	1	3	1	5.48	2021-08-03
4	Gudarakhi	Aragvi	42.349722	44.906389	200	1000	0	-	75	1	80	2	17	2	45	1	2	1	5.27	2021-08-10
5	Tkhiliana	Aragvi	42.427000	44.947444	200	1129	0	-	95	20	70	5	13	2	40	1	3	1	4.47	2021-08-21
6	Korsha	Aragvi	42.497222	44.905556	200	1400	0	-	85	5	90	2	15	2.5	70	2	1	1	5.23	2021-08-04
7	Kobulo	Aragvi	42.478722	44.945889	200	1222	0	-	75	5	70	10	12	2	130	2	1	1	5.24	2022-09-17
8	Gudani	Aragvi	42.533278	44.950056	100	1560	5	270	85	5	80	1	9	1.5	90	2	1	1	4.32	2021-08-19
9	Korsha	Aragvi	42.495778	44.910222	200	1380	0	-	75	15	85	2	12	3	60	2	2	1	5.20	2021-08-04
10	Chokhi	Aragvi	42.463944	44.697389	200	1530	10	23	80	15	75	1	14	2	100	3	2	1	7.37	2022-09-20
11	Katsalkhevi	Aragvi	42.363222	44.851333	200	1330	3	360	70	40	70	5	17	5	80	3	2	1	7.29	2022-09-19
12	Betischrdili	Aragvi	42.411722	44.930444	200	1100	0	-	90	25	70	2	22	4	100	3	3	1	4.94	2022-09-29
13	Apsho	Aragvi	42.387389	44.919833	200	1090	0	-	80	50	75	3	17	4	85	3	2	1	7.46	2022-09-28
14	Apsho	Aragvi	42.385056	44.927722	200	1120	3	293	75	35	80	2	22	3.5	110	3	2	1	7.63	2022-09-28
15	Pakhviji	Aragvi	42.444778	44.789889	200	1390	0	-	90	5	65	3	10	2.5	100	3	3	1	7.51	2022-09-23
16	Lutxubi	Aragvi	42.374778	44.790222	200	1281	5	23	70	5	40	25	12	1.2	70	3	2	1	N/A	2022-09-22
17	Sharakhevi	Aragvi	42.339944	44.889444	200	1100	7	135	80	60	80	3	18	3.5	40	3	2	1	6.79	2021-08-17
18	Datvisi	Aragvi	42.442722	44.922278	200	1340	3	90	75	30	65	60	20	3	70	3	2	1	5.02	2021-08-16
19	Chargali	Aragvi	42.317556	44.942778	200	1270	7	325	80	15	60	2	14	1.8	50	3	2	1	5.22	2021-08-08
20	Apsho	Aragvi	42.395500	44.913167	200	1120	0	-	80	30	80	2	20	6	140	3	1	1	7.84	2022-05-24
21	Gometsari	Aragvi	42.295111	44.828167	200	1200	10	360	75	3	65	5	15	1.5	80	3	2	1	7.52	2022-05-22
22	Bakhani	Aragvi	42.364889	44.739444	200	1260	2	285	70	20	85	3	19	5	120	3	1	1	6.02	2022-06-01
23	Mazeri	Enguri	43.082778	42.597389	100	1620	0	-	85	3	75	1	15	1	65	4	1	1	4.78	2022-08-19
24	Adishi	Enguri	43.019833	42.847556	200	1610	2	200	80	5	80	1	12	1.8	20	4	2	1	7.57	2022-08-21
25	Lalkhori	Enguri	42.933722	42.919500	100	1760	45	315	80	3	70	1	11	1.6	100	4	2	1	4.6	2022-08-23
26	Davberi	Enguri	42.926833	42.930278	100	1830	10	360	80	1	20	3	12	0.7	15	4	3	1	5.23	2022-08-23
27	Lalkhori	Enguri	42.929944	42.924000	100	1780	55	45	80	30	60	7	10	3.5	90	4	1	1	4.21	2022-08-23
28	Vichnashi	Enguri	42.970278	42.871000	200	1620	2	210	90	2	80	1	22	1.5	80	4	1	0	7.29	2022-08-22
29	Vichnashi	Enguri	42.966611	42.876056	200	1630	1	308	90	2	85	5	15	1.8	120	4	1	0	5.33	2022-08-23
30	Zegani	Enguri	42.989722	42.809389	100	1650	2	350	95	2	50	1	8	1.5	15	4	2	1	6.07	2022-08-21
31	Adishi	Enguri	43.015944	42.859333	200	1660	3	210	90	10	85	1	12	1.8	25	4	1	0	6.65	2022-08-21
32	Zegani	Enguri	42.994667	42.814389	100	1600	1	45	85	5	65	1	8	1.5	20	4	3	1	6.08	2022-08-21
33	Mazeri	Enguri	43.082722	42.597444	200	1620	2	140	85	1	80	2	16	1.5	90	4	1	1	4.62	2022-08-19
34	Kashveti	Enguri	43.029278	42.692222	100	1320	20	345	80	4	65	10	13	1.7	30	4	3	1	5.28	2022-08-20
35	Mazeri	Enguri	43.083667	42.593500	100	1690	7	90	80	20	60	2	8	6	65	4	3	1	5.07	2022-08-20
36	Mestia	Enguri	43.098222	42.740111	200	1590	0	-	85	5	80	5	9	2.5	60	4	2	1	6.02	2022-08-19
37	Lakhushdi	Enguri	43.016333	42.650556	200	1240	20	10	85	1	60	5	16	2	25	4	3	1	6.96	2022-08-19
38	Zhabeshi	Enguri	43.050500	42.862444	200	1600	3	180	80	4	85	4	16	1.5	80	4	1	0	4.54	2022-08-21
39	Zegani	Enguri	42.990500	42.809389	100	1650	35	70	85	2	70	20	12	1	40	4	2	1	6.21	2022-08-21
40	Vichnashi	Enguri	42.969944	42.871389	200	1620	0	-	90	8	85	1	21	1.8	70	4	1	1	5.6	2022-08-22
41	Adishi	Enguri	43.015889	42.859056	200	1660	7	270	85	5	75	1	13	1.4	40	4	1	0	6.93	2022-08-21
42	Adishi	Enguri	43.019889	42.846111	200	1600	2	250	85	5	65	3	14	1.6	40	4	2	1	7.55	2022-08-21
43	Tita	Enguri	43.099389	42.185444	200	1140	8	270	90	10	40	1	12	2	25	5	2	1	5.22	2022-08-25
44	Nakra	Enguri	43.107778	42.397444	200	1400	5	180	80	40	70	0	9	5	70	5	2	0	6.39	2022-08-24
45	Nakra	Enguri	43.101778	42.387833	200	1310	5	158	90	0	40	30	16	-	25	5	2	1	5.96	2022-08-24
46	Tita	Enguri	43.089000	42.191722	100	1090	15	150	90	45	30	10	18	3	20	5	2	0	5.12	2022-08-25
47	Nakra	Enguri	43.108778	42.397944	200	1410	5	150	90	4	15	1	7	1.8	12	5	3	0	5.8	2022-08-24
48	Nakra	Enguri	43.101611	42.388667	200	1300	5	180	95	1	30	15	15	1.2	40	5	2	1	5.51	2022-08-24
49	Nakra	Enguri	43.107111	42.395722	200	1380	5	160	90	1	40	5	8	1.5	40	5	2	0	5.23	2022-08-24

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Supplement E3. Aggregated species in the original dataset.

Anhang E3. Arten-Aggregate im originalen Datensatz.

Alchemilla vulgaris aggr. – all *Alchemilla* species reported from the Georgian floristic regions 2, 10 and 11 (GVINIANIDZE & LACHASHVILI 1980), except for the subsect. *Argentaria*

Cardamine impatiens aggr. – *Cardamine impatiens*, *C. pectinata*

Carex muricata aggr. – *Carex divulsa*, *C. muricata*, *C. spicata*

Dryopteris caucasica aggr. – *Dryopteris caucasica*, *D. filix-mas*

Lilium szovitsianum aggr. – *Lilium monadelphos*, *L. szovitsianum*

Polystichum braunii aggr. – *Polystichum braunii*, *P. kadyrovii*

Rubus subgen. *Rubus* sensu SOCHOR & TRÁVNÍČEK (2016)

Viola sieheana aggr. – *Viola caspia*, *V. sieheana*

Literature

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.

GVINIANIDZE, Z. I. & LACHASHVILI, I. IA. (Eds.) (1980): Sakartvelos plora (Flora of Georgia VI) [in Georgian]. – Metsniereba, Tbilisi: 158.

Supplement E4. Synoptic table of the diagnostic species of the vegetation types (associations) distinguished in the original dataset. Species frequencies are provided. Species names are followed by layer codes (1 – tree, 4 – shrub, 6 – herb, 7 – juvenile, 9 – moss). Highly diagnostic ($\phi \geq 0.5$, grey shaded, in bold) and diagnostic species ($\phi \geq 0.25$, grey shaded) of the associations are sorted by decreasing ϕ . Species with non-significant ϕ values ($P = 0.05$) were excluded based on Fisher's exact test. Additionally, we applied Constancy Ratio criterion ($CR \geq 2$). Association name abbreviations: $V-A$ – *Veronico filiformis-Alnetum incanae*, $B-A$ – *Brunnero macrophyllae-Alnetum incanae*, $S-A$ – *Sedo stoloniferi-Alnetum barbatae*.

Anhang E4. Übersichtstabelle der im originalen Datensatz unterschieden diagnostischen Arten der Vegetationstypen (Assozia-tionen). Aufgeführt sind prozentuale Stetigkeiten. Den Artnamen Codes der Schichten nachgestellt (1 – Baum, 4 – Strauch, 6 – Kraut, 7 – Jungwuchs, 9 – Moos). Höchst diagnostische ($\phi \geq 0.5$, grau schattiert, fett gedruckt) und diagnostische Arten ($\phi \geq 0,25$, grau schattiert) der Assoziationen sind nach absteigendem ϕ sortiert. Arten mit nicht signifikanten ϕ -Werten ($p = 0,05$) wurden mittels Fishers exaktem Test ausgeschlossen. Zusätzlich wandten wir das Constancy Ratio-Kriterium an ($CR \geq 2$). Abkürzungen der Assoziations-namen s. o:

Vegetation type (association)		1 (<i>V-A</i>)	2 (<i>B-A</i>)	3 (<i>S-A</i>)
Number of relevés		22	20	7
1 – <i>Veronico filiformis-Alnetum incanae</i>				
<i>Dipsacus pilosus</i>	6	91	15	.
<i>Chrysosplenium alternifolium</i>	6	45	.	.
<i>Sambucus nigra</i>	4	86	10	43
<i>Plagiomnium rostratum</i>	9	59	15	.
<i>Fraxinus excelsior</i>	7	68	.	29
<i>Scutellaria altissima</i>	6	45	5	.
<i>Primula veris</i> subsp. <i>macrocalyx</i>	6	50	10	.
<i>Polygonatum glaberrimum</i>	6	36	.	.
<i>Alliaria petiolata</i>	6	41	5	.
<i>Fraxinus excelsior</i>	4	32	.	.
<i>Glechoma hederacea</i>	6	32	.	.
<i>Asplenium scolopendrium</i>	6	32	.	.
<i>Sambucus nigra</i>	7	50	15	.
<i>Chaerophyllum aureum</i>	6	50	15	.
<i>Euonymus europaeus</i>	4	32	5	.
<i>Carpinus betulus</i>	7	32	5	.
<i>Acer campestre</i>	4	32	5	.
<i>Torilis japonica</i>	6	41	.	14
<i>Solanum dulcamara</i>	6	23	.	.
<i>Arum orientale</i>	6	23	.	.
<i>Petasites hybridus</i>	6	23	.	.
<i>Polygonatum multiflorum</i>	6	27	5	.
<i>Euonymus europaeus</i>	7	27	5	.
<i>Telekia speciosa</i>	6	27	5	.
<i>Salix euxina</i>	1	18	.	.
<i>Acer platanoides</i>	4	18	.	.
<i>Euonymus latifolius</i>	4	18	.	.
<i>Stellaria media</i>	6	18	.	.
<i>Cruciata laevipes</i>	6	18	.	.
<i>Viola sieheana</i> aggr.	6	18	.	.
<i>Sanicula europaea</i>	6	41	10	14
<i>Clinopodium umbrosum</i>	6	32	5	14
2 – <i>Brunnero macrophyllae-Alnetum incanae</i>				
<i>Ribes biebersteinii</i>	4	.	65	.
<i>Dactylorhiza urvilleana</i>	6	.	55	.
<i>Alchemilla vulgaris</i> aggr.	6	9	75	14
<i>Senecio propinquus</i>	6	18	75	14
<i>Plagiothecium cavifolium</i>	9	.	35	.
<i>Rumex obtusifolius</i> subsp. <i>silvestris</i>	6	14	70	29
<i>Sanionia uncinata</i>	9	.	30	.
<i>Sorbus aucuparia</i>	4	.	30	.
<i>Dactylis glomerata</i>	6	5	35	.
<i>Caucasalia macrophylla</i>	6	.	25	.
<i>Campanula latifolia</i>	6	.	25	.
<i>Ribes biebersteinii</i>	7	.	25	.
<i>Polygonatum verticillatum</i>	6	23	50	.
<i>Elymus caninus</i>	6	5	45	14
<i>Lonicera steveniana</i>	4	5	30	.
<i>Swertia iberica</i>	6	5	30	.
<i>Cirsium uliginosum</i>	6	.	40	14
<i>Dryopteris carthusiana</i>	6	23	65	29
<i>Brachythecium geheebii</i>	9	.	20	.
<i>Dryopteris expansa</i>	6	.	20	.
<i>Pulmonaria dacica</i>	6	.	20	.
<i>Caucasoseris abietina</i>	6	.	20	.
<i>Aconitum variegatum</i> subsp. <i>nasutum</i>	6	5	25	.
<i>Acer trautvetteri</i>	4	5	25	.
<i>Poa pratensis</i>	6	9	30	.
<i>Brunnera macrophylla</i>	6	.	30	14
3 – <i>Sedo stoloniferi-Alnetum barbatae</i>				
<i>Alnus glutinosa</i> subsp. <i>barbata</i>	1	5	.	100
<i>Alnus glutinosa</i> subsp. <i>barbata</i>	4	.	.	71
<i>Picea orientalis</i>	7	.	.	57
<i>Clinopodium grandiflorum</i>	6	.	25	71
<i>Persicaria hydropiper</i>	6	.	.	43
<i>Lycopus europaeus</i>	6	.	.	43
<i>Erigeron annuus</i>	6	.	5	43
<i>Tussilago farfara</i>	6	.	5	43
<i>Carex remota</i>	6	.	5	43
<i>Acer trautvetteri</i>	7	.	10	43
<i>Veronica beccabunga</i>	6	.	.	29
<i>Galium rotundifolium</i>	6	.	.	29
<i>Salix caprea</i>	4	.	.	29
<i>Digitalis schischkinii</i>	6	.	.	29
<i>Pteridium aquilinum</i>	6	.	.	29
<i>Betula litwinowii</i>	4	.	.	29
<i>Symphytum grandiflorum</i>	6	.	.	29
<i>Chaerophyllum angelicifolium</i>	6	.	.	29
<i>Angelica sylvestris</i>	6	.	.	29
<i>Sambucus ebulus</i>	6	14	.	43
<i>Plantago major</i>	6	5	.	29
<i>Tanacetum partheniifolium</i>	6	5	.	29
<i>Atrichum undulatum</i>	9	.	5	29

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Supplement E5. Data on soil characteristics of selected relevés.

Anhang E5. Daten zu den Bodenmerkmalen ausgewählter Vegetationsaufnahmen.

Relevé number	Soil unit	Soil depth (cm)	Soil skeleton (%)
10	Calcaric Skeletic Fluvisol	<15	>80
11	Calcaric Skeletic Fluvisol	15-40	50-80
12	Calcaric Fluvic Skeletic Regosol	15-40	>80
13	Calcaric Skeletic Fluvisol	15-40	>80
14	Calcaric Skeletic Fluvisol	15-40	>80
15	Calcaric Skeletic Fluvisol	15-40	>80
18	Calcaric Skeletic Fluvisol	15-40	>80
19	Dystric Fluvic Skeletic Regosol	<15	>80
20	Calcaric Skeletic Fluvisol	15-40	50-80
21	Calcaric Fluvic Skeletic Regosol	15-40	>80
22	Calcaric Skeletic Fluvisol	15-40	50-80

Supplement E6. Further photographs of the studied vegetation. a) Alluvial alder forests in a brook alluvium with fresh gravel deposits after a spring flood in the Khevsuretis Aragvi River valley near Barisakho Village. b) The same, ibidem. c) A short rotation coppice of *Alnus incana* in the Enguri River valley near Becho Village. d) Frequently grazed alluvial forests in the Pshavis Aragvi River valley near Sharakhevi Village. e) Expansion of *Alnus incana* on river gravel deposits in the Enguri River valley near Adishi Village. f) Cattle grazing in an alluvial forest in the Enguri River valley near Mestia City. (Photos: V. Kalníková a), b) September 2022, P. Novák c), e), f) August 2022, d) August 2021).

Anhang E6. Weitere Fotos der untersuchten Vegetation. a) Alluviale Erlenwälder in einem Bachschwemmland mit frischen Kiesablagerungen nach einer Frühjahrsflut im Khevsuretis-Aragvi-Flusstal in der Nähe des Dorfes Barisakho. b) Das Gleiche, ebenda. c) Ein Kurzumtriebswald von *Alnus incana* im Enguri-Flusstal in der Nähe des Dorfes Becho. d) Häufig beweidete Auwälder im Tal des Flusses Pshavis Aragvi in der Nähe des Dorfes Sharakhevi. e) Ausbreitung von *Alnus incana* auf Flusskiesvorkommen im Enguri-Flusstal in der Nähe des Dorfes Adishi. f) Rinder grasen in einem Schwemmwald im Enguri-Flusstal in der Nähe der Stadt Mestia. (Fotos: V. Kalníková a), b) September 2022, P. Novák c), e), f) August 2022, d) August 2021).



Supplement E7. Synoptic table of the diagnostic species of the clusters distinguished in the regional dataset. Species frequencies are provided. Highly diagnostic ($\phi \geq 0.5$, grey shaded, in bold) and diagnostic species ($\phi \geq 0.25$, grey shaded) of the associations are sorted by decreasing ϕ . Species with non-significant ϕ values ($P = 0.05$) were excluded based on Fisher's exact test. Additionally, we applied Constancy Ratio criterion ($CR \geq 2$). Clusters are separated by a dashed line according to their alliance affiliation (*Alnion barbatae* and *Veronico filiformis-Alnion incanae*, respectively). Association name abbreviations: *T-A* – *Truello thurnbergii-Alnetum barbatae*, *C-P* – *Carici remotae-Pterocaryetum pterocarpae*, *D-A* – *Diospyro loti-Alnetum barbatae*, *H-A* – *Theliptero limbospermae-Alnetum barbatae*, *S-A* – *Sedo stoloniferi-Alnetum barbatae*, *V-A* – *Veronico filiformis-Alnetum incanae*, *B-A* – *Brunnero macrophyllae-Alnetum incanae* (one plot assigned in the original dataset to the association *V-A* was classified to the association *B-A* in the regional dataset classification).

Anhang E7. Übersichtstabelle Tabelle der diagnostischen Arten der Cluster, die im regionalen Datensatz unterschieden werden. Aufgeführt sind prozentuale Stetigkeiten. Höchst diagnostische ($\phi \geq 0.5$, grau schattiert, fett gedruckt) und diagnostische Arten ($\phi \geq 0,25$, grau schattiert) der Assoziationen sind nach absteigendem ϕ sortiert. Arten mit nicht signifikanten ϕ -Werten ($p = 0,05$) wurden mittels Fishers exaktem Test ausgeschlossen. Zusätzlich wandten wir das Constancy Ratio-Kriterium an ($CR \geq 2$). Cluster sind entsprechend ihrer Verbandszugehörigkeit (*Alnion barbatae* bzw. *Veronico filiformis-Alnion incanae*) durch eine gestrichelte Linie getrennt. Abkürzungen der Assoziationsnamen s. o: Eine Aufnahme, die im Originaldatensatz der Assoziation *V-A* zugeordnet war, wurde in der regionalen Datensatzklassifizierung der Assoziation *B-A* zugeordnet.

Cluster	1	2	3	4	5	6	7	8	9
Association	<i>T-A</i>	<i>C-P</i>	<i>D-A</i>	<i>D-A</i>	<i>H-A</i>	<i>H-A</i>	<i>S-A</i>	<i>V-A</i>	<i>B-A</i>
Number of relevés	7	8	6	4	5	10	7	21	21
Cluster 1									
<i>Ajuga orientalis</i>	29	13	.	.	.	.	.	.	.
<i>Oenanthe abchasica</i>	29	13	.	.	.	.	.	.	.
Cluster 2									
<i>Cardamine tenera</i>	.	63	.	.	.	.	.	.	.
<i>Aegopodium podagraria</i>	.	50	.	.	.	.	.	.	.
<i>Euphorbia squamosa</i>	.	50	.	.	.	.	.	.	.
<i>Carex remota</i>	14	88	.	.	.	.	43	.	5
<i>Ruscus aculeatus</i>	29	63	.	.	.	.	.	.	.
<i>Stellaria media</i>	14	63	.	.	.	.	.	19	.
<i>Ranunculus grandiflorus</i>	.	38	.	.	.	.	.	.	.
<i>Vinca pubescens</i>	14	50	.	.	.	.	.	.	.
<i>Acer campestre</i>	43	88	.	.	.	.	.	38	19
<i>Lonicera caprifolium</i>	14	63	.	.	.	.	.	19	10
<i>Viola alba</i>	14	38	.	.	.	.	14	10	.
Cluster 3									
<i>Bistorta carnea</i>	.	.	100	.	.	.	.	.	.
<i>Chaerophyllum byzantinum</i>	.	.	83	.	.	.	.	.	.
<i>Geranium subcaulescens</i>	.	.	83	.	.	.	.	.	.
<i>Polypodium vulgare</i> aggr.	14	25	100	.	.	.	.	.	.
<i>Potentilla crantzii</i>	.	.	67	.	.	.	.	.	.
<i>Clinopodium vulgare</i>	.	.	50	.	.	.	.	10	.
<i>Stachys officinalis</i>	.	.	33	.	.	.	.	.	.
<i>Arctium minus</i>	.	.	33	.	.	.	.	14	.
Cluster 4									
<i>Hedera helix</i>	.	.	33	100	.	.	.	.	.
Cluster 5									
<i>Calystegia sepium</i>	.	.	.	.	80	.	.	.	.
<i>Pteris cretica</i>	.	.	.	.	60	.	.	.	.
<i>Ficus carica</i>	.	.	.	.	40	.	.	.	.
<i>Asplenium scolopendrium</i>	29	38	50	.	100	10	.	33	.
<i>Glechoma hederacea</i>	14	13	33	.	80	.	.	33	.
<i>Lactuca bourgaei</i>	.	.	.	.	40	20	.	.	.
Cluster 6									
<i>Rhododendron ponticum</i>	.	.	.	.	40	100	.	.	.
<i>Cardamine wiedemanniana</i>	.	.	.	.	.	60	.	.	.
<i>Rhynchosorys elephas</i>	.	.	33	25	.	90	.	.	.
<i>Gentiana asclepiadea</i>	.	.	.	.	.	80	14	5	24
<i>Blechnum spicant</i>	.	.	.	.	.	40	.	.	.
<i>Osmunda regalis</i>	.	.	.	.	.	40	.	.	.
<i>Heracleum crenatifolium</i>	.	.	.	.	.	40	.	.	.
<i>Castanea sativa</i>	.	.	.	.	.	40	.	.	.
<i>Rhododendron luteum</i>	.	.	.	.	.	60	14	.	14

Cluster	1	2	3	4	5	6	7	8	9
Association	<i>T-A</i>	<i>C-P</i>	<i>D-A</i>	<i>D-A</i>	<i>H-A</i>	<i>H-A</i>	<i>S-A</i>	<i>V-A</i>	<i>B-A</i>
Number of relevés	7	8	6	4	5	10	7	21	21
<i>Aruncus dioicus</i>	.	.	.	.	20	80	14	29	10
<i>Viola sieheana</i> aggr.	.	.	.	.	.	50	.	19	.
<i>Asperula cimulosa</i>	.	.	.	.	.	30	.	.	.
<i>Staphylea pinnata</i>	.	.	.	.	.	30	.	.	.
<i>Rhamnus imeretina</i>	.	.	.	.	.	30	.	.	.
<i>Campanula alliariifolia</i>	.	.	.	.	20	50	.	10	.
<i>Vaccinium arctostaphylos</i>	.	.	.	.	.	40	14	.	.
<i>Milium effusum</i>	.	.	.	.	.	50	.	14	19
<i>Frangula alnus</i>	29	13	33	25	40	80	.	.	.
<i>Digitalis grandiflora</i>	.	.	.	.	.	20	.	.	.
<i>Chrysosplenium dubium</i>	.	.	.	.	.	20	.	.	.
Cluster 7									
<i>Clinopodium grandiflorum</i>	.	.	.	.	.	.	71	.	24
<i>Persicaria hydropiper</i>	.	.	.	.	.	.	43	.	.
<i>Picea orientalis</i>	.	.	.	.	.	20	71	.	24
<i>Erigeron annuus</i>	.	.	.	.	.	.	43	.	5
<i>Digitalis schischkinii</i>	.	.	.	.	.	.	29	.	.
<i>Chaerophyllum angelicifolium</i>	.	.	.	.	.	.	29	.	.
<i>Angelica sylvestris</i>	.	.	.	.	.	.	29	.	.
<i>Galium rotundifolium</i>	.	.	.	.	.	.	29	.	.
<i>Betula litwinowii</i>	.	.	.	.	.	.	29	.	.
<i>Veronica beccabunga</i>	.	.	.	.	.	.	29	.	.
<i>Plantago major</i>	.	.	.	.	.	.	29	5	.
<i>Tanacetum partheniifolium</i>	.	.	.	.	.	.	29	5	.
<i>Tussilago farfara</i>	.	.	.	.	20	10	43	.	5
<i>Salix caprea</i>	.	.	.	.	.	.	29	5	10
<i>Pojarkovia pojarkovae</i>	.	.	.	.	.	.	29	.	14
<i>Potentilla reptans</i>	.	.	.	.	.	.	29	10	5
Cluster 8									
<i>Dipsacus pilosus</i>	.	.	.	.	.	.	.	95	14
<i>Primula veris</i> subsp. <i>macrocalyx</i>	.	.	.	.	.	.	.	52	10
<i>Scutellaria altissima</i>	.	.	.	.	.	.	.	48	5
<i>Polygonatum glaberrimum</i>	.	.	.	.	.	.	.	38	.
<i>Chrysosplenium alternifolium</i>	.	.	.	.	.	.	.	43	5
<i>Chaerophyllum aureum</i>	.	.	.	.	.	.	.	48	19
<i>Torilis japonica</i>	.	.	.	.	.	.	14	43	.
<i>Alliaria petiolata</i>	.	.	17	.	.	.	.	43	5
<i>Arum orientale</i>	.	.	.	.	.	.	.	24	.
<i>Polygonatum multiflorum</i>	.	.	.	.	.	.	.	29	5
<i>Telekia speciosa</i>	.	.	.	.	.	.	.	29	5
<i>Viburnum opulus</i>	.	.	.	.	.	.	.	38	19
<i>Pachyphragma macrophylla</i>	.	.	.	.	.	.	.	29	10
<i>Acer platanoides</i>	.	.	.	.	.	.	.	24	5
<i>Salix euxina</i>	.	.	.	.	.	.	.	19	.
<i>Cruciata laevipes</i>	.	.	.	.	.	.	.	19	.
<i>Clinopodium umbrosum</i>	.	.	.	.	.	.	14	33	5
<i>Solanum dulcamara</i>	.	.	.	.	.	10	.	24	.
<i>Lonicera caucasica</i>	.	.	.	.	.	.	.	19	5
<i>Geranium sibiricum</i>	.	.	.	.	.	.	.	14	.
<i>Polystichum setiferum</i>	.	.	.	.	.	.	.	14	.
<i>Physospermum cornubiense</i>	.	.	.	.	.	.	.	14	.
<i>Cardamine quinquefolia</i>	.	.	.	.	.	.	.	14	.
<i>Cystopteris fragilis</i>	.	.	.	.	.	.	.	14	5
<i>Prenanthes petiolata</i>	.	.	.	.	.	.	.	14	5
<i>Cruciata glabra</i>	.	.	.	.	.	.	.	14	5
<i>Aethusa cynapium</i>	.	.	.	.	.	.	.	14	5
Cluster 9									
<i>Ribes biebersteinii</i>	.	.	.	.	.	.	.	.	62
<i>Senecio propinquus</i>	.	.	.	.	.	.	14	14	76
<i>Dactylorhiza urvilleana</i>	.	.	.	.	.	.	.	.	52
<i>Alchemilla vulgaris</i> aggr.	.	.	.	.	.	.	14	10	71
<i>Dactylis glomerata</i>	.	.	.	.	.	.	.	.	38
<i>Rumex obtusifolius</i> subsp. <i>silvestris</i>	.	.	.	.	.	.	29	14	67

[illegible]

Supplement E8. Synoptic table of the diagnostic species of the alliance *Alnion incanae* and Caucasian *Alnus incana* forests (alliance *Veronico filiformis-Alnion incanae*) in the European dataset. Species frequencies are provided. Highly diagnostic (*phi* ≥ 0.5, grey shaded, in bold) and diagnostic species (*phi* ≥ 0.25, grey shaded) of the associations are sorted by decreasing *phi*. Rare species were excluded from the lists of diagnostic species by Fisher’s Exact Test (*P* > 0.05). Additionally, we applied Constancy Ratio criterion (CR ≥ 2).

Anhang E8. Übersichtstabelle der diagnostischen Arten des Verbandes *Alnion incanae* und Kaukasische *Alnus incana* Wälder (Verband *Veronico filiformis-Alnion incanae*) im europäischen Datensatz. Aufgeführt sind prozentuale Stetigkeiten. Höchst diagnostische (*phi* ≥ 0.5, grau schattiert, fett gedruckt) und diagnostische Arten (*phi* ≥ 0,25, grau schattiert) der Assoziationen sind nach absteigendem *phi* sortiert. Arten mit nicht signifikanten *phi*-Werten (*p* = 0,05) wurden mittels Fishers exaktem Test ausgeschlossen. Zusätzlich wandten wir das Constancy Ratio-Kriterium an (CR ≥ 2).

Alliance	<i>Alnion incanae</i>	<i>Veronico filiformis</i>
Number of relevés	2094	42
<i>Alnion incanae</i>		
<i>Aegopodium podagraria</i>	52	.
<i>Alnus glutinosa</i>	54	2
<i>Acer pseudoplatanus</i>	43	.
<i>Lamium galeobdolon</i> agg.	43	2
<i>Ficaria verna</i>	37	.
<i>Filipendula ulmaria</i>	36	.
<i>Anemone nemorosa</i>	35	.
<i>Crataegus</i> sp.	33	.
<i>Deschampsia cespitosa</i>	42	5
<i>Pulmonaria officinalis</i> agg.	30	.
<i>Quercus robur</i>	30	.
<i>Stellaria nemorum</i>	28	.
<i>Rubus caesius</i>	27	.
<i>Chaerophyllum hirsutum</i>	25	.
<i>Carex remota</i>	30	2
<i>Caltha palustris</i>	23	.
<i>Primula elatior</i>	22	.
<i>Senecio ovatus</i>	22	.
<i>Picea abies</i>	22	.
<i>Angelica sylvestris</i>	21	.
<i>Cirsium oleraceum</i>	21	.
<i>Lysimachia nummularia</i>	20	.
<i>Prunus padus</i>	34	7
<i>Hedera helix</i>	19	.
<i>Fagus sylvatica</i>	19	.
<i>Cardamine amara</i>	19	.
<i>Asarum europaeum</i>	24	2
<i>Mercurialis perennis</i>	24	2
<i>Lamium maculatum</i>	22	2
<i>Myosotis palustris</i> agg.	16	.
<i>Ranunculus lanuginosus</i>	16	.
<i>Crepis paludosa</i>	26	5
<i>Impatiens parviflora</i>	15	.
<i>Humulus lupulus</i>	15	.
<i>Heracleum sphondylium</i>	14	.
<i>Ulmus minor</i>	13	.
<i>Geum rivale</i>	13	.
<i>Tilia cordata</i>	13	.
<i>Adoxa moschatellina</i>	13	.
<i>Lonicera xylosteum</i>	13	.
<i>Paris quadrifolia</i>	23	5
<i>Lysimachia nemorum</i>	12	.
<i>Silene dioica</i>	12	.
<i>Veronico filiformis-Alnion incanae</i>		
<i>Alnus incana</i>	22	100
<i>Sedum stoloniferum</i>	.	60
<i>Viola odorata</i>	2	60
<i>Veronica filiformis</i>	.	55
<i>Fragaria vesca</i>	16	76
<i>Dipsacus pilosus</i>	1	55
<i>Galium odoratum</i>	18	74
<i>Dryopteris caucasica</i> aggr.	21	76
<i>Geranium robertianum</i> agg.	38	90
<i>Senecio propinquus</i>	.	45
<i>Symphytum asperum</i>	.	43
<i>Lapsana communis</i>	7	55
<i>Salvia glutinosa</i>	8	52
<i>Circaea ×intermedia</i>	3	43
<i>Prunella vulgaris</i>	3	43
<i>Alchemilla vulgaris</i> aggr.	2	40
<i>Polystichum braunii</i> aggr.	1	36
<i>Myosotis sylvatica</i>	3	40
<i>Lactuca racemosa</i>	.	33
<i>Potentilla micrantha</i>	1	33
<i>Chaerophyllum aureum</i>	1	33
<i>Cardamine impatiens</i> aggr.	6	43
<i>Epilobium montanum</i>	9	48
<i>Aquilegia wittmanniana</i>	.	31
<i>Acer cappadocicum</i>	.	31
<i>Valeriana alliariifolia</i>	.	31
<i>Ribes biebersteinii</i>	.	31
<i>Onoclea struthiopteris</i>	3	36
<i>Rumex obtusifolius</i>	5	40
<i>Lamium album</i>	1	31
<i>Primula veris</i>	1	31
<i>Pyrus communis</i> aggr.	1	29
<i>Paris incompleta</i>	.	26
<i>Dactylorhiza urvilleana</i>	.	26
<i>Scutellaria altissima</i>	1	26
<i>Polygonatum verticillatum</i>	6	36
<i>Rubus idaeus</i>	29	64
<i>Acer trautvetteri</i>	.	21
<i>Lysimachia verticillaris</i>	.	21
<i>Jacobaea othonnae</i>	.	21
<i>Galeopsis tetrahit</i> aggr.	10	40
<i>Polygonatum glaberrimum</i>	.	19
<i>Cirsium uliginosum</i>	.	19
<i>Clinopodium umbrosum</i>	.	19
<i>Pachyphragma macrophylla</i>	.	19
<i>Prunus avium</i>	9	36
<i>Schedonorus giganteus</i>	32	64
<i>Agrostis capillaris</i>	2	24
<i>Cicerbita muralis</i>	10	36
<i>Plagiomnium elatum</i>	1	19
<i>Saxifraga cymbalaria</i>	.	17
<i>Swertia iberica</i>	.	17
<i>Lonicera steveniana</i>	.	17
<i>Euphorbia stricta</i>	1	17
<i>Poa pratensis</i>	1	19
<i>Dryopteris carthusiana</i>	16	43
<i>Euonymus latifolius</i>	1	17
<i>Torilis japonica</i>	3	21
<i>Euphorbia macroceras</i>	.	14
<i>Brunnera macrophylla</i>	.	14
<i>Sanionia uncinata</i>	1	14
<i>Tilia begoniifolia</i>	1	14
<i>Telekia speciosa</i>	1	17
<i>Nasturtium officinale</i>	1	14
<i>Solidago virgaurea</i>	5	24
<i>Trifolium pratense</i>	1	14
<i>Lonicera caprifolium</i>	1	14
<i>Hesperis matronalis</i>	1	14
<i>Silene multifida</i>	.	12
<i>Abies nordmanniana</i>	.	12
<i>Caucasalia macrophylla</i>	.	12
<i>Heracleum sphondylium</i> subsp. <i>cyclocarpum</i>	.	12
<i>Picea orientalis</i>	.	12
<i>Arum orientale</i>	.	12
<i>Lonicera caucasica</i>	.	12

Supplement E9. Synoptic table of the diagnostic species of the association *Alnetum incanae* and Caucasian *Alnus incana* forests (alliance *Veronico filiformis-Alnion incanae*) in the European dataset. Species frequencies are provided. Highly diagnostic ($\phi \geq 0.5$, grey shaded, in bold) and diagnostic species ($\phi \geq 0.25$, grey shaded) of the associations are sorted by decreasing ϕ . Species with non-significant ϕ values ($P = 0.05$) were excluded based on Fisher's exact test. Additionally, we applied Constancy Ratio criterion ($CR \geq 2$).

Anhang E9. Übersichtstabelle der diagnostischen Arten des *Alnetum incanae* und Kaukasischer *Alnus incana* Wälder (Verband *Veronico filiformis-Alnion incanae*) im europäischen Datensatz. Aufgeführt sind prozentuale Stetigkeiten. Höchst diagnostische ($\phi \geq 0.5$, grau schattiert, fett gedruckt) und diagnostische Arten ($\phi \geq 0.25$, grau schattiert) der Assoziationen sind nach absteigendem ϕ sortiert. Arten mit nicht signifikanten ϕ -Werten ($p = 0,05$) wurden mittels Fishers exaktem Test ausgeschlossen. Zusätzlich wandten wir das Constancy Ratio-Kriterium an ($CR \geq 2$).

Syntaxon	<i>Alnetum incanae</i>	<i>Veronico filiformis</i> - <i>Alnion incanae</i>
Number of relevés	232	42
<i>Alnetum incanae</i>		
<i>Chaerophyllum hirsutum</i>	73	.
<i>Picea abies</i>	71	.
<i>Aegopodium podagraria</i>	63	.
<i>Stellaria nemorum</i>	56	.
<i>Deschampsia cespitosa</i>	62	5
<i>Senecio ovatus</i>	51	.
<i>Acer pseudoplatanus</i>	50	.
<i>Lamium galeobdolon</i> agg.	51	2
<i>Filipendula ulmaria</i>	46	.
<i>Thalictrum aquilegifolium</i>	45	.
<i>Geum rivale</i>	41	.
<i>Angelica sylvestris</i>	39	.
<i>Petasites albus</i>	58	12
<i>Cirsium oleraceum</i>	38	.
<i>Caltha palustris</i>	37	.
<i>Primula elatior</i>	37	.
<i>Petasites hybridus</i>	55	12
<i>Ranunculus lanuginosus</i>	33	.
<i>Carduus personata</i>	33	.
<i>Myosotis palustris</i> agg.	31	.
<i>Silene dioica</i>	31	.
<i>Aconitum napellus</i> agg.	30	.
<i>Crepis paludosa</i>	40	5
<i>Viola biflora</i>	29	.
<i>Valeriana officinalis</i>	27	.
<i>Lonicera xylosteum</i>	27	.
<i>Pulmonaria officinalis</i> agg.	26	.
<i>Asarum europaeum</i>	29	2
<i>Lamium maculatum</i>	27	2
<i>Heracleum sphondylium</i>	20	.
<i>Phyteuma spicatum</i>	20	.
<i>Rubus caesius</i>	19	.
<i>Cardamine amara</i>	19	.
<i>Maianthemum bifolium</i>	18	.
<i>Campanula trachelium</i>	18	.
<i>Mercurialis perennis</i>	23	2
<i>Geranium phaeum</i>	17	.
<i>Senecio nemorensis</i> agg.	17	.
<i>Salix purpurea</i>	17	.
<i>Paris quadrifolia</i>	27	5
<i>Galium album</i> agg.	22	2
<i>Daphne mezereum</i>	30	7
<i>Equisetum sylvaticum</i>	15	.
<i>Rumex alpestris</i>	15	.
<i>Lysimachia nummularia</i>	14	.
<i>Astrantia major</i>	14	.
<i>Equisetum palustre</i>	14	.

Syntaxon	<i>Alnetum incanae</i>	<i>Veronica filiformis</i> - <i>Alnion incanae</i>
Number of relevés	232	42
<i>Anemone nemorosa</i>	14	.
<i>Symphytum tuberosum</i> agg.	13	.
<i>Chaerophyllum aromaticum</i>	13	.
<i>Prunus padus</i>	27	7
<i>Knautia dipsacifolia</i>	13	.
<i>Eurhynchium hians</i>	13	.
<i>Salix eleagnos</i>	13	.
<i>Melica nutans</i>	18	2
<i>Lonicera nigra</i>	12	.
<i>Veronica filiformis-Alnion incanae</i>		
<i>Sedum stoloniferum</i>	.	60
<i>Viola odorata</i>	.	60
<i>Galium odoratum</i>	11	74
<i>Veronica filiformis</i>	.	55
<i>Dipsacus pilosus</i>	.	55
<i>Brachythecium rivulare</i>	9	64
<i>Geum urbanum</i>	32	88
<i>Lapsana communis</i>	5	55
<i>Senecio propinquus</i>	.	45
<i>Symphytum asperum</i>	.	43
<i>Circaea ×intermedia</i>	1	43
<i>Brachypodium sylvaticum</i>	32	81
<i>Plagiomnium rostratum</i>	.	38
<i>Dryopteris caucasica</i> aggr.	28	76
<i>Polystichum braunii</i> aggr.	.	36
<i>Lactuca racemosa</i>	.	33
<i>Sciuro-hypnum populeum</i>	.	33
<i>Potentilla micrantha</i>	.	33
<i>Chaerophyllum aureum</i>	1	33
<i>Ribes biebersteinii</i>	.	31
<i>Primula veris</i>	.	31
<i>Aquilegia wittmanniana</i>	.	31
<i>Acer cappadocicum</i>	.	31
<i>Lamium album</i>	.	31
<i>Valeriana alliariifolia</i>	.	31
<i>Sambucus nigra</i>	18	60
<i>Prunus avium</i>	3	36
<i>Prunella vulgaris</i>	7	43
<i>Pyrus communis</i> aggr.	.	29
<i>Paris incompleta</i>	.	26
<i>Scutellaria altissima</i>	.	26
<i>Dactylorhiza urvilleana</i>	.	26
<i>Dryopteris carthusiana</i>	9	43
<i>Carex sylvatica</i>	28	67
<i>Myosotis sylvatica</i>	8	40
<i>Rumex obtusifolius</i>	8	40
<i>Cardamine impatiens</i> aggr.	10	43
<i>Schedonorus giganteus</i>	28	64
<i>Onoclea struthiopteris</i>	6	36
<i>Acer campestre</i>	3	29
<i>Acer trautvetteri</i>	.	21
<i>Jacobaea othonnae</i>	.	21
<i>Lysimachia verticillaris</i>	.	21
<i>Corylus avellana</i>	22	55
<i>Torilis japonica</i>	1	21
<i>Moehringia trinervia</i>	9	36
<i>Cirsium uliginosum</i>	.	19
<i>Polygonatum glaberrimum</i>	.	19
<i>Pachyphragma macrophylla</i>	.	19
<i>Clinopodium umbrosum</i>	.	19
<i>Alchemilla vulgaris</i> aggr.	12	40
<i>Salvia glutinosa</i>	22	52
<i>Carpinus betulus</i>	2	21

Syntaxon	<i>Veronico filiformis</i>	
	<i>Alnetum incanae</i>	<i>-Alnion incanae</i>
Number of relevés	232	42
<i>Epilobium montanum</i>	19	48
<i>Lonicera steveniana</i>	.	17
<i>Saxifraga cymbalaria</i>	.	17
<i>Euphorbia stricta</i>	.	17
<i>Swertia iberica</i>	.	17
<i>Agrostis capillaris</i>	3	24
<i>Stellaria holostea</i>	1	17
<i>Asplenium scolopendrium</i>	1	17
<i>Alliaria petiolata</i>	4	24
<i>Poa trivialis</i>	8	31
<i>Galeopsis tetrahit</i> agg.	15	40
<i>Sanicula europaea</i>	6	26
<i>Euonymus europaeus</i>	4	24
<i>Euonymus latifolius</i>	1	17
<i>Plagiomnium medium</i>	1	17
<i>Sanionia uncinata</i>	.	14
<i>Lonicera caprifolium</i>	.	14
<i>Nasturtium officinale</i>	.	14
<i>Tilia begoniifolia</i>	.	14
<i>Euphorbia macroceras</i>	.	14
<i>Brunnera macrophylla</i>	.	14
<i>Trifolium pratense</i>	1	14
<i>Hesperis matronalis</i>	1	14
<i>Plagiomnium elatum</i>	3	19
<i>Plagiothecium cavifolium</i>	2	17
<i>Silene multifida</i>	.	12
<i>Lonicera caucasica</i> subsp. <i>orientalis</i>	.	12
<i>Heracleum sphondylium</i> subsp. <i>cyclocarpum</i>	.	12
<i>Abies nordmanniana</i>	.	12
<i>Asperula taurina</i>	.	12
<i>Picea orientalis</i>	.	12
<i>Caucasalia macrophylla</i>	.	12
<i>Arum orientale</i>	.	12
<i>Homalothecium philippeanum</i>	.	12