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Ecology and vegetation types of oak-hornbeam and ravine forests of the Eastern Greater Caucasus, Georgia

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Abstract The Caucasus harbours unique forest vegetation so far only little studied using the Braun-Blanquet approach. This study is mostly based on a dataset (N = 110) of original phytosociological relevés of oak-hornbeam and ravine forests in the Eastern Greater Caucasus, Georgia. Their unsupervised classification produced seven communities. Five belong to oak-hornbeam forests (order *Lathyro-Carpinetalia caucasicae*). Of the zonal Caucasian alliance *Crataego-Carpinion*, the association *Corno australis-Carpinetum* inhabits valleys of the Greater Caucasus, and *Clinopodio umbrosi-Carpinetum* is confined to the warm Eastern Greater Caucasus promontories. The association *Astrantio maximae-Carpinetum* of the alliance *Astrantio-Carpinion* represents distinctive Caucasian montaneoak-hornbeam forests. The other two communities, documented by a few relevés, were described at the community level only. Within ravine forests (order *Aceretalia pseudoplatani*), we introduce a new Caucasian alliance *Pachyphragmo macrophyllae-Tilion begoniifoliae* with two associations. *Valeriano tiliifoliae-Ulmetum glabrae* comprises Caucasian montane ravine forests whereas *Hedero pastuchovii-Aceretum velutini* inhabits the foothills of the Eastern Greater Caucasian. To provide a broader context of the recognized communities, an expanded dataset (N = 231) of original relevés and previously published relevés of Georgian deciduous forests was analysed. It indicated a major turnover in species composition following biogeographical patterns presumably driven by macroclimate and vegetation history.

Keywords Biogeography · *Carpino-Fagetea* · Classification · Phytosociology · Syntaxonomy · Transcaucasia

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Introduction

The Caucasus is a rugged landscape of high mountain ridges forming the boundary between Europe and Asia. It is an approximately 1,200 km long west-east mountain chain stretching between the Black and the Caspian Sea and exceeding 5,000 m in elevation. The region is ranked among the 34 world terrestrial biodiversity hotspots due to its species-rich biota with a high level of endemism (Mittermeier et al. 2004; Barthlott et al. 2005; Zazanashvili and Mallon 2009). Its unique biota is related to high variability of environmental conditions and a distinctive history during the Pleistocene climatic oscillations, as the region harbours numerous Tertiary relicts (Denk et al. 2001; Shatilova et al. 2011), including several nowadays dominant trees (e.g. *Picea orientalis*, *Quercus macranthera*) or shrubs (e.g. *Prunus laurocerasus*, *Rhododendron ponticum*). Georgia (~ 69,700 km^2) is situated in Transcaucasia, i.e. between the main ridges of the Greater and the Lesser Caucasus. Vast areas of the country (~ 43%) are forested, of which 80% are deciduous forests representing a high proportion of the overall variability of the Caucasian forests (Gulisashvili et al. 1975; Krever et al. 2001; Akhalkatsi 2015).

The Caucasus is an area of a developing vegetation survey based on the Braun-Blanquet approach. Numerous local descriptive studies were published (e.g. Kolakovskii 1961; Ketskhoveli et al. 1975; Gulisashvili et al. 1975; Dolukhanov 2010; Nakhutsrishvili 2013), although they presented dominant-based classification systems. Only several pioneering Braun-Blanquetian studies were issued over the last decades. They were dealing with the Western Greater Caucasian subalpine birch (Onipchenko 2002), coniferous (Korotkov 1995) and xerophilous (Litvinskaya and Postarnak 2002) forests as well as mesophilous deciduous forests of Central Georgia (Passarge 1981a, b) and Colchis (Novák et al. 2019).

Our study focuses on the oak-hornbeam and ravine forests of the Eastern Greater Caucasus in Georgia, i.e. mesophilous forests dominated by *Acer campestre*, *Carpinus betulus*, *Quercus macranthera*, *Q. petraea* subsp. *iberica* and *Zelkova carpinifolia* or *Acer cappadocicum*, *A. velutinum*, *Tilia begoniifolia* and *Ulmus glabra*, respectively. Therefore, the study by Passarge (1981a) is particularly relevant because it contains the description of two alliances of oak-hornbeam forests of the southern macroslope of the Greater Caucasus in Georgia. By contrast, ravine forests have hardly been investigated so far. Besides the recently established association *Polysticho woronowii-Ulmetum glabrae* describing Colchic ravine forests in western Georgia (Zukal in Novák et al. 2019), no syntaxonomic attention has been paid to this vegetation type so far. This is likely due to their intrazonal character and polydominant tree layer that can be hardly described by a dominant-based approach (Dolukhanov 2010). Some authors (e.g. Gulisashvili et al. 1975; Nakhutsrishvili 2013) presented part of their variability under Oriental beech forest formations. Kolakovskii (1961) distinguished an individual forest type growing in ravines that likely corresponds to *Aceretalia* forests.

The environmental conditions, structure and species composition of Caucasian oak-hornbeam forests have been co-shaped by human activities (e.g. coppicing, pollarding, forest pasturing of livestock), similarly as in other parts of their broad distribution range (Bohn et al. 2000–2003; Leuschner and Ellenberg 2017). Signs of such treatments are often apparent. Locally, they are even still practised (e.g. Hübl et al. 2010; Bussmann 2017) allowing genuine opportunities to study traditional forest management, abandoned in the majority of Europe and its surroundings (e.g. Sebek et al. 2013). Nevertheless, the last decades also brought forest overexploitation to obtain firewood in places. In addition, forest grazing of domestic ungulates may be intensive at the local scale, reducing the herb layer, preventing tree rejuvenation and promoting soil erosion and invasion of alien species (Dolukhanov 2010; Akhalkatsi 2015). Compared to oak-hornbeam forests, Caucasian ravine forests are less influenced by human activities as they mostly inhabit poorly accessible sites (e.g. Kolakovskii 1961; Dolukhanov 2010; Novák et al. 2019).

Of the vegetation under study, ravine and *Zelkova carpinifolia* forests are regarded as sensitive habitats of Georgia (Akhalkatsi 2015). In the European context (Janssen et al. 2016), oak-hornbeam forests are treated as near threatened habitat (EU 28, EU 28+), similarly as ravine forests (EU 28). A better understanding of their variability should lead to classification systems that can be implemented into national or international habitat classification and thus be important for nature protection, protected areas management planning or environmental monitoring (Rodwell et al. 2018).

The aims of our study are as follows: (1) to describe the variability of oak-hornbeam and ravine forests of the study area, (2) to analyse variables driving their species composition, (3) to compare the recognized vegetation types with the previously described associations in Georgia, and (4) to present a new revised syntaxonomic system of the vegetation under study.

Material and methods

Study region

The study region (Fig. 1) stretches over the southern macroslope of the Eastern Greater Caucasus, including mountain valleys of the north-central Georgia and slopes above the Alazani River valley in the Kakheti

Fig. 1 Map of the study region with locations of relevés and their classification.

region. It spans from the piedmont (455 m a.s.l.) nearly to the timberline (1,690 m a.s.l.). The geological bedrock is rather uniform, composed mainly of Mesozoic sediments (marls, slates, turbidites), locally calcareous. They often form steep erosion-prone slopes with deeply incised river valleys separated by sharp ridges. Bodies of volcanic rocks are limited to the northwestern part of the region (Adamia 2010). Climate of the region is relatively diverse, with annual mean temperature of the sampled sites varying between 2.7 and 12.1°C (mean 8.5°C) and annual precipitation between 710 and 1,190 mm (mean 821 mm) with noticeable seasonality (Fick and Hijmans 2017).

Oak-hornbeam and Oriental beech forests are supposed to be the prevailing natural forest vegetation of the region, with open woodlands of *Acer trautvetteri*, *Betula litwinowii* and *Quercus macranthera* mostly forming the timberline (Bohn et al. 2000–2003). The forest flora in Kakheti is enriched by species of the Hyrcanian floral element coming from southeast (e.g. *Acer velutinum*, *Hedera pastuchovii*), including relict species shared by the Colchic and Hyrcanian refugia, for instance *Diospyros lotus* and *Prunus laurocerasus* (Denk et al. 2001; Nakhutsrishvili 2013; Nakhutsrishvili et al. 2015).

Data collection

We conducted field surveys in 2015–2018. The majority of the dataset was yielded in August 2018. The aim of the sampling was to cover a broad variability of the oak-hornbeam and ravine forests. We sampled vegetation-plot records (hereafter 'relevés'). For each relevé (100 m^2), we estimated percentage covers of tree, shrub, herb and moss layers. Species cover values in each layer were assessed in the extended nine-degree Braun-Blanquet cover-abundance scale (Dengler et al. 2008), except for bryophytes, as the latter were not identified. Inclination, slope aspect and percentage cover of rocks were assessed as well. Geographical coordinates (WGS84) and elevation were measured by the GPSMAP 60CSx receiver. Climatic data were extracted from WorldClim 2 (Fick and Hijmans 2017). In each relevé, we took a soil sample of the uppermost 15 cm of soil and measured its pH in a distilled water suspension (2:5) by a portable instrument GMH Greisinger.

Dataset and data processing

The taxonomy and nomenclature of vascular plants follow the Euro+Med PlantBase (Euro+Med 2006–).

We defined several *ad hoc* aggregates because of identification or taxonomical difficulties: *Arum maculatum* agg. (*Arum maculatum*, *A. megobrebi*, *A. orientale*), *Carex muricata* agg. (*Carex divulsa*, *C. muricata*, *C. spicata*), *Crataegus monogyna* agg. (*Crataegus microphylla*, *C. monogyna*, *C. pentagyna*, *C. pseudoheterophylla*, *C. rhipidophylla*) and *Rosa canina* agg. (*Rosa canina*, *R. corymbifera*, *R. iberica*, *R. irysthonica*, *R. marschalliana*, *R. oxyodon*). An expanded dataset (*N* = 231 relevés) was compiled to compare our dataset with relevés of the class *Carpino-Fagetea* previously recorded in Georgia (Passarge 1981a, *N* = 18; Passarge 1981b, *N* = 50; Novák et al. 2019, *N* = 53). Relevés from Passarge's studies were georeferenced based on published data on sample sites, with a maximal bias of five minutes. Relevés were stored in Turboveg 2.1 (Hennekens and Schaminée 2001) and processed mostly in Juice 7.0 (Tichý 2002). Ordination analyses were done in R 3.6.0 (R Core Team 2018), using the package 'vegan' version 2.5-6 (Oksanen et al. 2019). Occurrences of the same taxon in different layers were merged prior to the analyses applying the procedure by Fischer (2015). Vernal ephemeroids were deleted before the analyses because they were recorded only in few spring relevés.

Classification analyses were performed in PC-ORD 5 (McCune and Mefford 1999). We applied various classification strategies (Flexible Beta, modified TWINSPAN, Ward's method) and numbers of clusters. Optimal partition was indicated by the OptimClass 1 method (Tichý et al. 2010). The diagnostic value of species was determined by the *phi* coefficient (Sokal and Rohlf 1995). Prior to its calculation, the number of plots in the clusters were virtually standardized to be equal (Tichý and Chytrý 2006). We used Fisher's exact test ($P \leq 0.05$) to omit species with non-significant fidelity from the diagnostic species lists. Species with $phi \geq 0.35$ were regarded as diagnostic and those with $phi \geq 0.5$ as highly diagnostic (in bold). In addition, we applied a constancy ratio criterion (Dengler 2003); i.e. the constancy of a diagnostic species must be at least 1.3× greater than in the cluster where it reaches the second highest constancy. In the syntaxonomic part of the study, we applied the rules of phytosociological nomenclature published in the 4th edition of the Code (Theurillat et al. 2020). The nomenclature of higher syntaxa follows the EuroVegChecklist (Mucina et al. 2016).

Results

Classification

During the field surveys, we recorded 110 phytosociological relevés (stored in Tables S2 and S3 in the Electronic supplementary material) which contained 304 species in total. Based on the results of the Flexible Beta clustering ($\beta = -0.4$, square-root transformed species cover data), we recognized seven communities, all of the class *Carpino-Fagetea*, orders *Lathyro-Carpinetalia* (communities 1–5) and *Aceretalia* (communities 6 and 7). The majority of the recognized communities we interpreted as associations. Their shortened synoptic table is provided in Table 1 (see Table S4 in the Electronic supplementary material for its full version). Their overview is also provided by DCA results (Fig. 2) and boxplots (Fig. 3, see also Fig. S5 in the Electronic supplementary material). Photographs of the communities are in Fig. S6 in the Electronic supplementary material. The major division of the dataset at the level of two clusters reflected well differences between oak-hornbeam and ravine forests.

Cornus mas–Carpinus betulus community

Corno australis-Carpinetum caucasicae Passarge 1981 (Tables S2 and S3 in the Electronic supplementary material, relevés 1–16)

This community includes zonal oak-hornbeam forests of the Greater Caucasus southern forehills (750–1,210 m) in the western half of the study region, mainly in the lower parts of the Aragvi River valley. They occur on slopes of various inclination and orientation, generally without rock outcrops or scree. They preferentially grow on neutral soils (mean soil pH 6.8) usually covering calcareous turbidites. The climate is moderate (mean annual temperature 8.9°C, mean annual precipitation 780 mm).

Carpinus betulus dominates the tree layer, often accompanied by *Acer cappadocicum*, *Carpinus orientalis* and *Fagus orientalis*. Both hornbeam species used to be locally pollarded. The shrub layer is mostly well-developed (mean cover 28%) and dominated by the thermophilous shrub *Cornus mas* and species of the tree layer. Evergreen lianas are almost

Table 1 Shortened synoptic table of the recognized communities in the dataset ($N = 110$).

Community	1	2	3	4	5	6	7
Number of relevés	16	4	16	25	8	25	16
Lathyro-Carpinetalia betuli							
Viola alba	75	100	50	92	75	20	38
Quercus petraea subsp. *iberica*	81	**100**	38	40	.	.	13
Crataegus germanica	56	.	6	48	50	.	.
Prunus avium	63	50	69	56	38	16	13
Acer campestre	69	25	38	40	38	8	6
Carex sylvatica	13	75	.	72	13	.	6
Oplismenus hirtellus subsp. *undulatifolius*	.	.	.	**76**	13	.	.
Carpinus betulus	100	100	94	92	100	52	88
Sanicula europaea	44	.	38	56	.	8	6
Geum urbanum	6	25	25	40	13	.	.
Clinopodium umbrosum	31	.	13	72	50	.	25
Pyrus communis	38	.	31	20	.	.	.
Campanula rapunculoides	75	75	75	48	25	40	.
Aceretalia pseudoplatani							
Asplenium scolopendrium	6	.	.	44	13	68	**100**
Polystichum braunii	.	.	.	12	.	48	63
Polystichum aculeatum	.	.	.	32	25	48	**88**
Asplenium trichomanes	19	.	25	36	25	84	56
Aruncus dioicus	.	.	6	.	13	**64**	6
Polygonatum multiflorum	6	.	56	4	25	**96**	13
Cystopteris fragilis	6	.	25	.	.	**72**	6
Corylus avellana	50	.	56	64	100	100	81
Sambucus nigra	.	.	.	32	13	56	38
Onoclea struthiopteris	.	.	.	.	.	24	25
Pachyphragma macrophylla	.	.	.	12	50	24	69
1. *Cornus mas-Carpinus betulus* community							
Cornus mas	**81**	.	6	32	.	4	13
Euonymus verrucosus	**44**	.	6	.	.	.	.
Physospermum cornubiense	**31**	.	.	.	.	.	.
Vincetoxicum hirundinaria	**50**	.	13	12	.	.	.
Sorbus torminalis	50	25	.	8	.	.	.
Helleborus orientalis	31	.	.	8	.	.	.
Polygonatum glaberrimum	44	.	19	4	.	.	6
Securigera varia	38	.	19	4	.	.	.
Euonymus latifolius	63	.	44	12	13	20	6
Carex digitata	69	.	38	12	25	44	.
Lonicera caucasica	44	.	31	8	.	8	.
2. *Zelkova carpinifolia-Carpinus betulus* community							
Piptatherum virescens	.	**75**	.	.	.	.	.
Zelkova carpinifolia	.	**75**	.	.	.	.	.
Ligustrum vulgare	50	**100**	.	8	.	.	.
Klasea quinquefolia	19	**75**	.	8	.	.	.

Table 1 (continued)

Community	1	2	3	4	5	6	7
Lathyrus laxiflorus	19	**75**	13	8	.	.	.
Lonicera caprifolium	44	**100**	25	24	13	28	.
Brachypodium sylvaticum	19	100	56	64	25	28	.
Carex michelii	31	50	.	8	.	.	.
Drymochloa drymeja	31	100	44	44	63	24	13
Melica uniflora	6	50	13	8	13	8	6
3. *Quercus macranthera-Carpinus betulus* community							
Quercus macranthera	.	.	**44**	.	.	.	.
Fragaria vesca	19	.	**75**	24	.	8	.
Poa nemoralis	6	.	**75**	20	.	44	.
Carex humilis	6	.	31	.	.	.	.
Rosa canina agg.	13	.	56	32	.	4	6
Sorbus aucuparia	6	.	38	.	.	12	.
Solidago virgaurea	6	.	56	16	.	36	.
Campanula alliariifolia	38	.	50	.	.	8	.
Clinopodium vulgare	19	.	38	.	.	4	.
4. *Clinopodium umbrosum-Carpinus betulus* community							
Diospyros lotus	6	.	.	**64**	.	4	6
Calystegia silvatica	6	.	.	**56**	13	12	.
Prunella vulgaris	.	.	13	**40**	.	.	.
Luzula forsteri	.	.	.	32	.	.	6
Torilis japonica	.	.	13	36	.	4	.
Castanea sativa	.	.	.	40	25	4	13
6. *Valeriana tiliifolia-Ulmus glabra* community							
Geranium robertianum	13	.	38	56	13	84	19
Impatiens noli-tangere	.	.	6	8	.	40	6
Paris incompleta	.	.	25	8	.	44	.
Salvia glutinosa	25	.	69	52	38	96	38
Urtica dioica	.	.	13	16	.	48	19
Acer platanoides	.	.	13	4	.	32	.
Scutellaria altissima	6	.	13	.	.	32	.
Arum maculatum agg.	.	.	6	24	.	40	6
Pimpinella tripartita	13	.	19	.	.	36	.
7. *Hedera pastuchovii-Acer velutinum* community							
Philadelphus coronarius	.	.	.	.	.	.	**50**
Acer velutinum	.	.	.	4	38	.	50
Dryopteris borreri	.	.	.	8	.	4	31
Species diagnostic for two communities							
Rubus subgen. *Rubus*	.	.	6	36	**100**	24	81
Hedera pastuchovii	25	25	.	48	88	12	100
Other frequent species (*f* ≥ 30% in any community, recorded in ≥ 4 communites)							
Acer cappadocicum	94	25	50	44	75	56	31
Galium odoratum	50	.	69	40	50	88	25
Fagus orientalis	81	.	75	56	75	44	13

Table 1 (continued)

Community	1	2	3	4	5	6	7
Tilia begoniifolia	50	25	.	52	75	36	81
Fraxinus excelsior	75	75	38	20	63	64	19
Ulmus glabra	13	.	13	36	63	76	13
Polypodium vulgare	19	.	25	24	38	52	56
Dryopteris filix-mas	.	.	25	56	50	56	13
Dioscorea communis	38	.	38	56	13	36	.
Cornus sanguinea	75	50	19	36	38	12	13
Lapsana communis	31	.	50	52	13	20	6
Circaea lutetiana	6	.	.	40	13	44	44
Moehringia trinervia	.	.	38	56	38	16	19
Viola reichenbachiana	13	75	13	44	50	16	19
Sedum stoloniferum	13	.	50	40	.	32	.
Carex muricata agg.	6	50	.	64	38	4	6
Veronica peduncularis	44	.	50	8	.	24	.
Lactuca muralis	13	.	31	20	.	40	6
Potentilla micrantha	6	.	19	44	25	20	6
Primula veris subsp. *macrocalyx*	19	.	38	12	.	32	6
Euonymus europaeus	13	.	.	16	13	36	25
Crataegus monogyna agg.	44	25	13	32	.	4	.
Smilax excelsa	6	50	.	48	.	8	13
Primula acaulis	31	.	19	28	.	8	6
Asplenium adiantum-nigrum	19	25	.	32	25	.	19
Carpinus orientalis	50	50	.	8	.	4	.

Values are percentage frequencies. Diagnostic species of the orders are in the upper part of the table and sorted by decreasing fidelity. Diagnostic species of communities are shaded and also sorted by decreasing fidelity. Only species reaching a frequency ≥ 30% in at least one community are shown. Diagnostic (*phi* ≥ 0.35) and highly diagnostic (*phi* ≥ 0.5, in bold) species are provided. Other frequent species (*f* ≥ 30% at least in one community and recorded at least in four communities) are at the bottom of the table and sorted by decreasing frequency. A full version of the table is provided in Table S2 in the Electronic supplementary material. Communities: 1 – *Cornus mas-Carpinus betulus*, 2 – *Zelkova carpinifolia-Carpinus betulus*, 3 – *Quercus macranthera-Carpinus betulus*, 4 – *Clinopodium umbrosum-Carpinus betulus*, 5 – *Hedera pastuchovii-Carpinus betulus*, 6 – *Valeriana tiliifolia-Ulmus glabra*, 7 – *Hedera pastuchovii-Acer velutinum*

absent, likely due to cold winters. The herb layer reaches the lowest cover among the recognized communities (mean cover 18%), usually lacking a distinctive dominant. Along forest mesophytes (e.g. *Galium odoratum*, *Veronica peduncularis*), these forests harbour thermophilous species including both species with broad distribution ranges in the submediterranean zone of western Eurasia (e.g. *Lonicera caprifolium*, *Physospermum cornubiense*) and Caucasian endemics (e.g. *Peucedanum caucasicum*, *Polygonatum glaberrimum*). The poisonous rhizomatous herb *Helleborus orientalis* may expand in patches frequently grazed by cattle. The moss layer is low in cover or missing.

Zelkova carpinifolia–Carpinus betulus community

Assigned directly under *Crataego-Carpinion* (Tables S2 and S3 in the Electronic supplementary material, relevés 17–20)

This community comprises xeromesophilous forests with *Zelkova carpinifolia*, a relict species of the Tertiary flora. It was recorded exclusively in the Babaneuri Reserve in Kakheti, established to protect *Zelkova* forests. They grow on neutral soils (mean pH 6.7) with various content of gravel developed on sedimentary carbonate parent rock. They occupy sunny slopes and their site represents one of the warmest and driest parts of the study area (mean annual temperature 11.5°C, annual

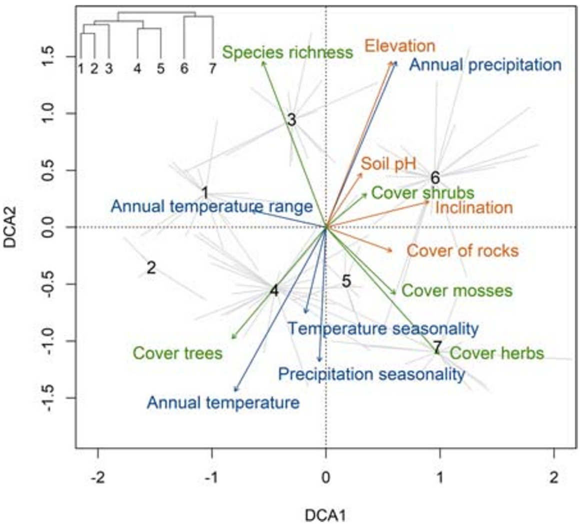

Fig. 2 DCA ordination of the dataset of original relevés (N = 110). The first two ordination axes are shown. The first axis explains 5.98%, the second one 4.90% of the variance in species composition of the dataset. Basic environmental and vegetation structure variable vectors were passively plotted. Communities: 1 – *Cornus mas–Carpinus betulus*, 2 – *Zelkova carpinifolia–Carpinus betulus*, 3 – *Quercus macranthera–Carpinus betulus*, 4 – *Clinopodium umbrosum–Carpinus betulus*, 5 – *Hedera pastuchovii–Carpinus betulus*, 6 – *Valeriana tiliifolia–Ulmus glabra*, 7 – *Hedera pastuchovii–Acer velutinum.*

precipitation 735 mm). In the driest places, such as tops of south-facing slopes, they are substituted by scrubs of *Carpinus orientalis* and *Paliurus spina-christi*. Our relevés represent the only known forests with *Zelkova carpinifolia* in eastern Georgia and likely in the whole Eastern Greater Caucasus. The rest of its Georgian sites are in Colchis in the western part of the country (Maharramova et al. 2015).

Carpinus betulus, *C. orientalis*, *Quercus petraea* subsp. *iberica* and *Zelkova carpinifolia* prevail in the tree layer. The shrub layer is usually sparse, having the lowest mean cover among the distinguished communities (6%) and being composed mainly of tree rejuvenation and the thermophilous semi-deciduous species *Ligustrum vulgare*. In the field layer, xeromesophilous graminoids (e.g. *Drymochloa drymeja*, *Piptatherum virescens*) and dicots (e.g. *Klasea quinquefolia*, *Lonicera caprifolium*) play a prominent role. The moss layer is mostly poorly developed.

Here, we classify this community under the alliance *Crataego-Carpinion*. However, further phytosociological research on the Transcaucasian *Zelkova carpinifolia* forests is needed.

Quercus macranthera–Carpinus betulus community

Astrantio maximae-Carpinetum caucasicae Passarge 1981 (Tables S2 and S3 in the Electronic supplementary material, relevés 21–36)

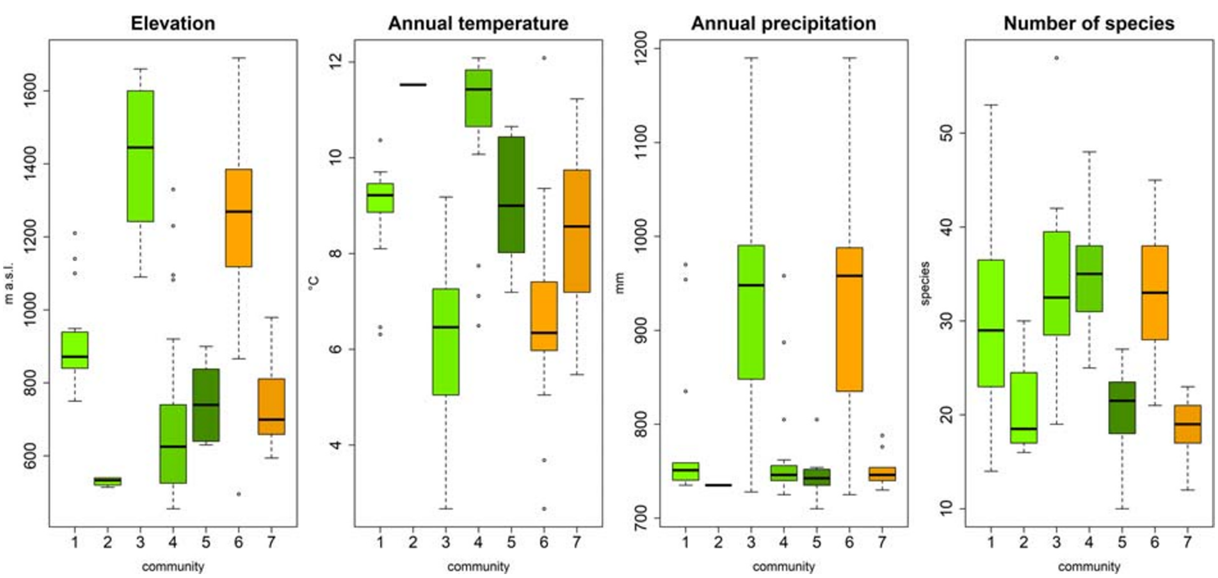

Fig. 3 Comparison of selected environmental variables and the number of species among the communities in the original dataset. Boxes indicate 25–75% interquartile range with their median (bold line) and whiskers show the range of values; outliers are also provided; communities: see Fig. 2.

This community includes the Greater Caucasian montane oak-hornbeam forests. They were recorded at the highest elevations in the study region (mean elevation 1,416 m), which is also expressed by the lowest annual temperature (mean 6.3°C) and high annual precipitations (mean 928 mm). In some mountain valleys, they even reach the timberline. They grow on slopes of various orientation, usually slightly rocky (mean cover of rocks 5%). The bedrock is formed by diverse turbidites and rarely also by basaltic lavas (Gudauri environs).

Carpinus betulus dominates the tree layer. *Quercus macranthera* and *Fagus orientalis* are its frequent canopy companions. However, the latter is likely suppressed by harsh climate (e.g. spring frost events; Dolukhanov 2010) and therefore it does not reach high covers. The shrub layer is rather well-developed (mean cover 13%). Besides mesophilous species typical of the Caucasian forests (e.g. *Euonymus latifolius*, *Lonicera caucasica*) also species forming the local treeline (*Betula litwinowii*, *Rhododendron luteum*) may be admixed. Besides forest mesophytes, tall forbs (e.g. *Valeriana tiliifolia*) and other species of the upper montane and subalpine belt (e.g. *Lactuca racemosa*, *Pimpinella rhodantha*) are characteristic for the herb layer. A boreal floral element is represented by species characteristic of the Caucasian coniferous forests (e.g. *Orthilia secunda*, *Rubus saxatilis*). On shallow soils of convex relief shapes, drought-tolerant *Carex humilis* occurs. The moss layer is usually well-developed, preferentially covering rocks. A striking difference against other recorded oak-hornbeam forests is the rare occurrence or absence of thermophilous species (e.g. *Cornus mas*, *Hedera* spp., *Sorbus torminalis*).

Concerning syntaxonomy, this community probably corresponds to montane types of the Caucasian oak-hornbeam forests described by Passarge (1981a) under the names *Astrantio-Carpinetum*, *Clinopodio-Carpinetum* and *Rhododendro-Carpinetum*.

Clinopodium umbrosum–Carpinus betulus community

Clinopodio umbrosi-Carpinetum betuli Novák *ass. nova hoc loco* (Tables S2 and S3 in the Electronic supplementary material, relevés 37–61). Nomenclature type: relevé 41 (*holotypus*; see below)

This community represents zonal vegetation of the Greater Caucasian promontories in Kakheti (455–1,330 m). It occurs on slopes of various inclination and orientation. It was mostly recorded on slightly acidic soils (mean soil pH 6.2) developed on black slates and turbidites. With 35 species per relevé on average, it is the species richest community. The climate is relatively warm (mean temperature 10.8°C).

The tree layer is dominated by *Carpinus betulus*, with some other rather mesophilous species (e.g. *Acer cappadocicum*, *Fagus orientalis*, *Ulmus glabra*) in admixture. The shrub layer is mostly well developed (mean cover 18%) with prevailing thermophilous (e.g. *Cornus mas*, *Crataegus germanica*) and mesophilous (e.g. *Cornus sanguinea*, *Corylus avellana*) species. The common relict shrub *Diospyros lotus* prefers canopy gaps which it can rapidly colonize via endozoochory. Evergreen lianas (*Hedera helix*, *H. pastuchovii*, *Smilax excelsa*) climb the shrubs and trees as they favour rather mild winters characteristic for the region (mean temperature of the coldest quarter the year 0.8°C). The herb layer is often dominated by stoloniferous grasses, *Drymochloa drymeja* on drier soils, whereas the alien *Oplismenus hirtellus* subsp. *undulatifolius* on mesic soils. Forest mesophytes (e.g. *Dryopteris filix-mas*, *Salvia glutinosa*) and shade-tolerant nitrophytes (e.g. *Geum urbanum*, *Lapsana communis*) are frequent. Thermophilous drought-tolerant species (e.g. *Asplenium adiantum-nigrum*, *Luzula forsteri*) are admixed mostly on shallow soils. Near settlements, these woodlands occasionally serve as intermittent cow pastures, which has resulted in spreading of pasture weeds (e.g. *Euphorbia stricta*, *Pteridium aquilinum*). The moss layer varies in cover (mean 7%).

Hedera pastuchovii–Carpinus betulus community

Assigned directly under *Crataego-Carpinion* (Tables S2 and S3 in the Electronic supplementary material, relevés 62–69)

These forests are typical for fertile soils in the valleys of the Greater Caucasus in Kakheti. They preferentially grow on slightly wet and nutrient rich soils (mean pH 6.1) covering higher river terraces and slope bases. Nevertheless, the cover of rocks is very limited. Black slates and other turbidites prevail in the bedrock.

The tree layer is dominated by *Carpinus betulus*, with *Acer cappadocicum* and *Fagus orientalis* as common co-dominants. The shrub layer is often constituted by *Acer cappadocicum*, *Corylus avellana* and *Crataegus germanica*. The herb layer is frequently predominated by species forming dense grows such as

Drymochloa drymeja, *Hedera pastuchovii* and *Rubus* subgen. *Rubus*. Stony soils and vicinity of ravine forests support the local occurrence of ravine forest specialists, mainly *Pachyphragma macrophylla*.

This community represents a transition between *Lathyro-Carpinetalia* and *Aceretalia* forests. As it was grouped together with the other oak-hornbeam forests in the unsupervised classification, we keep this assignment.

Valeriana tiliifolia–Ulmus glabra community

Valeriano tiliifoliae-Ulmetum glabrae Zukal *ass. nova hoc loco* (Tables S2 and S3 in the Electronic supplementary material, relevés 70–94). Nomenclature type: relevé 86 (*holotypus*; see below)

This community comprises mountain ravine forests of Caucasian valleys in the western part of the study area. Although relevés of this community were documented over a broad elevation range (495–1,690 m a.s.l.), all but two relevés were recorded higher than 1,000 m a.s.l. Stands from the highest elevations can be transitional to subalpine scrub and elfin forests. They inhabit steep (mean inclination 45°) and usually north- or west-facing slopes that can be either loamy or with scree accumulations (mean cover of rocks 13%) formed mostly of turbidites, locally also carbonates, with basic soils (mean pH 7.2). With respect to the broad elevation range of study localities, the climatic data are diverse, with the mean annual temperature between 2.7–12.1°C (mean 6.6°C) and annual precipitations between 725 and 1,190 mm (mean 924 mm). Compared to the following community, it is colder during the whole year. This community is also richer in species, with 32 species per relevé on average.

The tree layer is dominated by noble hardwood tree species (*Acer platanoides*, *Fraxinus excelsior*, *Ulmus glabra*) including the Caucasian subendemics *Acer cappadocicum* and *Tilia begoniifolia*. The tree canopy can be rather open (mean cover 74%). However, the shrub layer is usually well-developed (mean cover 24%), species-rich and contains mesophilous shrubs (e.g. *Corylus avellana*, *Euonymus europaeus*, *Sambucus nigra*) as well as tree rejuvenation. The occurrence of typical ravine forest species (*Aruncus dioicus*, *Impatiens noli-tangere*, *Pachyphragma macrophylla*) and other stolon-forming species (e.g. *Lamium album*, *Scutellaria altissima*) indicating occasionally moving substrate are diagnostic for the herb layer. Specialists of rock crevices are mainly represented by mesophilous species (e.g. *Asplenium scolopendrium*, *A. trichomanes*, *Cystopteris fragilis*). Forest ferns are common (e.g. *Dryopteris filix-mas*, *Polystichum braunii*) and in comparison to the following community, also the species spectrum of forest mesophytes is much broader (e.g. *Galium odoratum*, *Polygonatum multiflorum*), including Caucasian subendemics (e.g. *Paris incompleta*, *Pimpinella tripartita*) and montane tall forbs (e.g. *Telekia speciosa*, *Valeriana tiliifolia*). Mean cover of the moss layer is the highest among all communities (9%), even though it can vary markedly from place to place.

Hedera pastuchovii–Acer velutinum community

Hedero pastuchovii-Aceretum velutini Zukal *ass. nova hoc loco* (Tables S2 and S3 in the Electronic supplementary material, relevés 95–110). Nomenclature type: relevé 108 (*holotypus*; see below)

This community represents ravine forests confined to the deeply incised valleys in the Greater Caucasian foothills in Kakheti (594–979 m). They occur on slopes of various orientations usually covered by scree, mainly on immobilized scree accumulations on slope bases. The parent rock is mostly formed of black slates with basalt or carbonate admixture (mean pH 6.7). The climate is warmer compared to the previous community (mean annual temperature 8.7°C). Annual precipitations (mean 749 mm) are lower, however, as this community is confined to deeply incised valleys, air humidity is relatively high thanks to shading of valley slopes and adjacent rivers. Cover of rocks is the highest compared to other communities (mean cover 22%). Among the recognized communities, this one has the lowest mean number of species per relevé (18 species). On moving screes, this forest community rapidly transits to open tall-herb vegetation with *Datisca cannabina*.

The tree layer is mostly dominated by noble hardwood tree species, mainly by typical species of the warm parts of Eastern Transcaucasia (*Acer velutinum*, *Tilia begoniifolia*). Other noble hardwood tree species commonly occurring in the previous community are less common or even absent (*Acer platanoides*). The shrub layer is formed by mesophilous species, *Corylus avellana* and *Sambucus nigra* reach the highest cover. *Philadelphus coronarius*, frequently colonizing shaded scree slopes, is highly diagnostic for this community. Numerous fern species occur in the herb layer including species of rock crevices. Compared to the previous community, *Dryopteris filix-mas* is often substituted by *D. borreri* indicating warmer and more humid climate. The evergreen liana *Hedera pastuchovii*, often also climbing the trees, or stoloniferous *Rubus* subgen. *Rubus* form dense growths, presumably due to the mild climate. Other ravine forest species are mostly represented by *Pachyphragma macrophylla*. The diversity of forest mesophytes of phanerogams is usually low, *Salvia glutinosa* and *Viola alba* are among the most frequent. The moss layer is developed, although usually does not reach high cover.

Ordination

Similarly to the unsupervised classification, DCA revealed a clear pattern distinguishing between *Lathyro-Carpinetalia* and *Aceretalia* forests along the first ordination axis. It shows that *Aceretalia* forests favour steeper slopes with a higher cover of rocks. The second ordination axis represents a complex gradient of elevation and related increasing annual precipitation and decreasing annual temperature together with precipitation and temperature seasonality. Montane communities (1,3) are therefore situated in the upper part of the diagram and communities of lower elevations in the lower part.

Expanded dataset

In order to evaluate the position of the studied vegetation in a context of mesophilous deciduous vegetation of Transcaucasia, we analysed an expanded dataset containing both our original relevés and relevés from the literature (231 relevés in total). The classification analysis setting was the same as for the original dataset. We recognize eleven clusters. The results are summarized in an ordination diagram (Fig. 4) and in a synoptic table (Table S5 in the Electronic supplementary material).

The first ordination axis mainly represents a biogeographical gradient connected with macroclimate and vegetation history. The Caucasian forests are situated to the right side, while forests recorded in Kakheti, a Caucasian region enriched by the Colchic-Hyrcanian floral element, are situated to the centre. Colchic forests are grouped to the left side. The second axis likely corresponds to a gradient of productivity as it is strongly correlated with cover of herb layer. Forests with nutrient- and moisture-demanding forbs and shade-

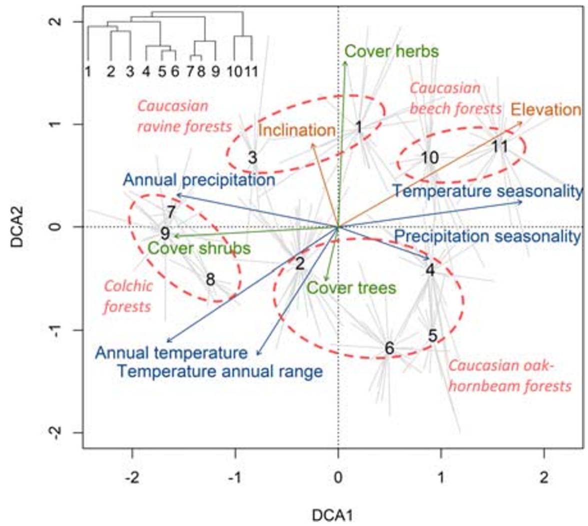

Fig. 4 DCA ordination of the expanded dataset ($N = 231$). The first two ordination axes are shown. The first axis explained 4.96% and the second axis explained 4.08% of the variance in species composition of the dataset. Basic environmental and vegetation structure variable vectors were passively plotted. Principal groups of the clusters are indicated by dashed lines.

tolerant nitrophytes are grouped to the upper part of the diagram while forests of drier soils are at the bottom.

These results revealed a clear difference between Colchic types (clusters 7, 8 and 9) and Caucasian types (other clusters) of forest vegetation, at least in the context of the analysis. Within the Caucasian vegetation, there is a clear separation of ravine (clusters 1, 3), oak-hornbeam (clusters 2, 4, 5, 6) and Oriental beech (clusters 10, 11) forests.

The majority of the communities described in our dataset were well-reproduced by the unsupervised classification of the expanded dataset. Regarding oak-hornbeam forests, the Kakhetian communities (*Clinopodium umbrosum–Carpinus betulus*, *Hedera pastuchovii–Carpinus betulus*) formed own cluster 2. The montane *Quercus macranthera–Carpinus betulus* community was grouped with Passarge's associations recorded at high elevations (*Astrantio-Carpinetum*, *Clinopodio-Carpinetum* and *Rhododendro-Carpinetum*) in cluster 4. The *Cornus mas–Carpinus betulus* community and the *Zelkova carpinifolia–Carpinus betulus* community were included in cluster 6, with one of Passarge's relevés of the association *Corno-Carpinetum*. The rest of its relevés were unified in cluster 5. The Caucasian ravine forests (clusters 1, 3) formed two sharp clusters identical to the communities distinguished in the original dataset.

Discussion

Species composition and species richness

Most of the studied communities have mean species richness exceeding 30 species per plot. The lowest species richness was recorded within the communities from Kakheti. Local ravine and nutrient-rich oak-hornbeam forests, with the mean number of species per relevé 18.3, resp. 20.4 were apparently species-poor. A climate with hot summers and mild winters resulted in the dominance of species with high ability of clonal spreading (*Hedera pastuchovii*, *Rubus* subgen. *Rubus*), especially observed in sheltered valleys with higher air humidity as reported also by Dolukhanov (2010). It is partly analogical to the situation in some Colchic forests where the thick evergreen shrub layer suppresses the development of the herb layer (Korotkov 1995; Novák et al. 2019). The *Zelkova carpinifolia*-*Carpinus betulus* community was also species-poor (20.8). It is probably due to summer drought periods which are strengthened on the sunny slopes where this community was recorded. Compared to the thermophilous oak forests, *Carpinus* spp. and *Zelkova carpinifolia* often form dense canopy reducing light in the herb layer. A combination of such stress factors may lead to the low species richness, at least in summer aspect.

Alien species (sensu Kikodze et al. 2009) are much less frequent in the studied forests compared to the Colchic ones (Novák et al. 2019). This is presumably due to the fact that the study region was much less affected by the introduction of subtropical crops with which numerous aliens were unintentionally brought to Colchis (Nakhutsrishvili 2013; Akhalkatsi 2015). The shallowly rooted perennial grass *Oplismenus hirtellus* subsp. *undulatifolius* is the only frequent alien taxon recorded. It can rapidly invade forests via stolons. Spreading over large distances is provided by epizoochory (Beauchamp and Koontz 2013). However, it was recorded only in the Kakhetian mesophilous oak-hornbeam forests (reported also by Dolukhanov 2010) where it is still apparently less frequent than in Colchis (cf. Novák et al. 2019).

A relationship between the two major zonal forest communities of the studied region, Oriental beech and oak-hornbeam forests (Bohn et al. 2000–2003), requires further research. Their distributions were most likely influenced by human interventions lasting here at least four millennia (Conor 2006). Traditional forests management, still locally practised, generally favours oak-hornbeam forests at the expense of beech forests (Bradshaw et al. 2010; Leuschner and Ellenberg 2017). Additionally, beech could be preferentially cut as an important source of timber (Bussmann 2017). Beech was presumably suppressed not only by forest management but also by climatic events as harsh winters, spring and autumn frosts and summer droughts (Bradshaw et al. 2010; Leuschner and Ellenberg 2017), which are common features in the diverse topography of the Caucasus (Dolukhanov 2010; Nakhutsrishvili 2013). Beech was often admixed in the recorded oak-hornbeam forests. However, it did not attain dominance hence these forests were classified as oak-hornbeam forests and not as beech forests.

Syntaxonomy of oak-hornbeam forests

For the Caucasian oak-hornbeam forests, Passarge (1981a) described the separate order *Lathyro-Carpinetalia*. His concept was accepted in the EuroVegChecklist (Mucina et al. 2016) where *Lathyro-Carpinetalia* stands next to the order *Carpinetalia betuli* unifying oak-hornbeam forests of the rest of Europe. However, *Lathyro-Carpinetalia* is an invalid name (Art. 3g). Çoban and Willner (2019) proposed to merge these two orders because Caucasian oak-hornbeam forests lack their own dominant tree species. Its key species *Carpinus caucasica* is mostly supposed to be conspecific with *C. betulus* (Holstein and Weigend 2017). Recent numerical analyses of the variability of oak-hornbeam forests across the whole of Europe and its surroundings (Novák and data contributors 2019) also supported the unification of these two orders.

At the level of alliance, both units described by Passarge, the zonal alliance *Crataego-Carpinion* and the high-elevation alliance *Astrantio-Carpinion*, were adopted in the EuroVegChecklist. The former contains only one validly described association *Corno-Carpinetum*, while the other two (*Clinopodio-Carpinetum*, *Rhododendro-Carpinetum*) are invalid (§ 3b). These two associations were mentioned together with the association *Astrantio-Carpinetum* (*Astrantio-Carpinion*) as oak-hornbeam forests of higher elevations, although classified within the *Crataego-Carpinion* alliance. In our paper, we provisionally keep the concept of two Caucasian alliances because these forests are still very undersampled, especially the high-elevation types which are supposed to be natural vegetation across extensive regions of the Caucasus (Bohn et al. 2000–2003; Dolukhanov 2010; Nakhutsrishvili 2013). Moreover, high-elevation oak-hornbeam forests represent a rather unique feature of the Caucasus. Probably the only analogy reported so far are mixed forests of *Carpinus betulus* and *Quercus macranthera* described from the mountains of northern Iran (Gholizadeh et al. 2020).

The correct name of the *Crataegus* species in the alliance *Crataego-Carpinion* needs further investigation. In its type association, the *Corno-Carpinetum*, Passarge (1981a) recorded a single *Crataegus* species, '*Crataegus* cf. *kyrtostyla*'. Passarge cited the compendium Flora of the Caucasus (Fedorov 1952) as the nomenclature source and in this publication, *C. kyrtostyla* is the (probably misapplied; Euro+Med 2006-) name for *C. rhipidophylla*. Therefore, if we accept Passarge's determination as correct, since *C. rhipidophylla* is a common member of Transcaucasian forests (Fedorov 1952), the full alliance name must be corrected to *Crataego rhipidophyllae-Carpinion caucasicae nom. corr.* (Art. 44).

Oak-hornbeam and ravine forests recorded in Kakheti (comm. 2, 4, 5, 7) show a significant level of Hyrcanian floristic influence. However, they lack numerous diagnostic species of the Hyrcanian forests, including both woody (e.g. *Alnus subcordata*, *Parottia persica*, *Quercus castaneifolia*) and herb (e.g. *Danae racemosa*, *Ruscus hyrcanus*) species (Gholizadeh et al. 2020). Therefore, we assign them into the Caucasian higher syntaxa rather than the Hyrcanian ones.

The analysis of the expanded dataset confirmed that the Caucasian oak-hornbeam forests (clusters 2, 4, 5, 6) differ from the Colchic ones (clusters 8, 9) growing along the southern coast of the Black Sea, unified under the alliance *Castaneo sativae-Carpinion* (or *Trachystemono orientalis-Carpinion*, see Çoban and Willner 2019). The most important feature of the Colchic forests, relict evergreen shrubs (e.g. *Ilex colchica*, *Rhododendron ponticum*, *Rh. ungernii*), are almost absent in the Caucasian types. In Eastern Transcaucasia, the evergreen Colchic liana *Hedera colchica* is substituted by closely related *Hedera pastuchovii* (Nakhutsrishvili 2013). *Castanea sativa*, a very frequent tree in the Colchic oak-hornbeam forests, is rather scarce in the Caucasian ones (Dolukhanov 2010). However, there are some common species in the herb layer (e.g. *Clinopodium umbrosum*, *Oplismenus hirtellus* subsp. *undulatifolius*). Therefore, we classify the newly recorded communities within the Caucasian alliances of oak-hornbeam forests (see below). The *Clinopodium umbrosum–Carpinus betulus* community is described as a new association due to its genuine species composition combining typical species of the Caucasian mesophilous forests with species of Colchic-Hyrcanian or Hyrcanian-Eastern Caucasian distribution. The other two communities (1, 3) are identified with previously described associations by Passarge (1981a), *Corno-Carpinetum* and *Astrantio-Carpinetum*, respectively. The name-giving species of *Corno-Carpinetum*, *Cornus australis*, is listed as *Cornus sanguinea* subsp. *australis* in Euro+Med (2006–). It is reported as the only subspecies of *Cornus sanguinea* (sensu Euro+Med 2006–) in the Caucasus (Shishkin 1951). Accordingly, all our records of *Cornus sanguinea* are assumed to belong to this subspecies. However, we did not distinguish infraspecific taxa of *Cornus sanguinea* as its variability needs further research (Liesebach and Götz 2008). The *Hedera pastuchovii–Carpinus betulus* community represents rather a transition between oak-hornbeam and ravine forests. The *Zelkova carpinifolia–Carpinus betulus* community contains xeromesophilous forests with *Zelkova carpinifolia*. It is geographically very limited and documented by only four relevés. We do not formally describe these communities as new associations and classify them directly under the alliance *Crataego-Carpinion*.

Syntaxonomy of ravine forests

Caucasian ravine forests have not yet been studied phytosociologically. In Europe and its surroundings, they are classified within the order *Aceretalia pseudoplatani*, comprising scree and ravine maple-lime forests of the nemoral zone of temperate Europe (Mucina et al. 2016). As Caucasian ravine forests are dominated by noble hardwood trees (even though frequently by different species of the same genera, including *Acer cappadocicum*, *A. velutinum* and *Tilia begoniifolia*) and many of characteristic species of ravine forests of the order *Aceretalia* occur in the undergrowth (e.g. *Aruncus dioicus*, *Asplenium scolopendrium*, *Dryopteris filix-mas*), we also classify them into this order.

Until now, only the association *Polysticho woronovii-Ulmetum glabrae* has been recognized in Georgia, describing Colchic ravine forests of the southwesternmost part of the country (Zukal in Novák et al. 2019). As *Alnus glutinosa subsp. barbata* and *Castanea sativa* are common tree dominants, it has been classified within the alliance *Alnion barbatae*, including both Colchic ravine and riverine forests. Comparing Caucasian ravine forests with *Polysticho-Ulmetum*, they share several characteristics (e.g. similar site conditions, occurrence of noble hardwood trees and some other typical ravine forest species). On the other hand, there are also numerous differences: *Alnus glutinosa* subsp. *barbata* is much rarer in the Caucasian ravine forests, most probably due to a drier climate. Conversely, dominance of the endemic and subendemic Caucasian trees *Acer cappadocicum*, *A. velutinum* and *Tilia begoniifolia* is characteristic. Another striking differential feature of *Polysticho-Ulmetum* is the occurrence of evergreen shrubs that are missing in the Eastern Greater Caucasus. Clear differences can also be found in the herb layer, as there are numerous relict or endemic species that are rare or missing in Georgia outside Colchis (e.g. *Polystichum woronowii*, *Pteris cretica*, *Ruscus colchicus*, *Trachystemon orientalis*). Vice versa, the Caucasian types are richer in species of higher elevations (e.g. *Gentiana asclepiadea*, *Primula veris* subsp. *macrocalyx*, *Valeriana tiliifolia*) and in forest mesophytes of broad distribution ranges (e.g. *Galium odoratum*, *Polygonatum multiflorum*). Considering these differences, we describe ravine forests of the Caucasus as a new alliance with two associations.

Syntaxonomic outline

Syntaxonomic scheme

Carpino-Fagetea Jakucs ex Passarge 1968
- *Lathyro-Carpinetalia caucasicae* Passarge 1981
- *Crataego rhipidophyllae-Carpinion caucasicae* Passarge 1981 *nom. corr. hoc loco*
  - *Corno australis-Carpinetum caucasicae* Passarge 1981 (comm. 1)
  - *Clinopodio umbrosi-Carpinetum betuli* Novák *ass. nova hoc loco* (comm. 4)
- *Astrantio maximae-Carpinion caucasicae* Passarge 1981
  - *Astrantio maximae-Carpinetum caucasicae* Passarge 1981 (comm. 3)

Aceretalia pseudoplatani Moor 1976
- *Pachyphragmo macrophyllae-Tilion begoniifoliae* Zukal *all. nova hoc loco*.
  - *Valeriano tiliifoliae-Ulmetum glabrae* Zukal *ass. nova hoc loco* (comm. 6)
  - *Hedero pastuchovii-Aceretum velutini* Zukal *ass. nova hoc loco* (comm. 7)

Typification of the new syntaxa

Crataego rhipidophyllae-Carpinion caucasicae Passarge 1981 *nom. corr. hoc loco*

Clinopodio umbrosi-Carpinetum betuli Novák *ass. nova hoc loco*. *Holotypus (hoc loco)* of the association: Georgia, Lagodekhi district, Khizabavra: a slope above the N edge of the village, 630 m a.s.l. 41.8738889° N, 46.2391667° E. Relevé area: 10 m × 10 m; Aspect: 150°; Slope: 7°; Soil pH: 5.84; Cover of rocks: 0%. Covers: tree layer 85%, shrub layer 15%, herb layer 30%, moss layer 2%. Recorded on 3 August 2018. Author: Pavel Novák.

Tree layer: *Carpinus betulus* 5, *Tilia begoniifolia* 2a;

Shrub layer: *Cornus sanguinea* 2a, *Pyrus communis* 1, *Prunus domestica* 1, *Castanea sativa* +, *Carpinus betulus* +, *Crataegus germanica* +, *Diospyros lotus* +, *Hedera pastuchovii* +, *Ulmus minor* +;

Herb layer: *Oplismenus hirtellus* subsp. *undulatifolius* 2a, *Hedera pastuchovii* 2m, *Carex muricata* agg. 1, *C. sylvatica* 1, *Rubus* subgen. *Rubus* 1, *Viola alba* 1, *Brachypodium sylvaticum* +, *Clinopodium umbrosum* +, *Dryopteris filix-mas* +, *Glechoma hederacea* +, *Poa angustifolia* +, *Polystichum aculeatum* +, *Potentilla micrantha* +, *Schedonorus giganteus* +, *Smilax excelsa* +, *Cephalanthera longifolia* r, *Sanicula europaea* r; *Carpinus betulus* +, *Cornus sanguinea* +, *Crataegus germanica* +, *Diospyros lotus* +, *Prunus avium* +, *P. domestica* +, *Tilia begoniifolia* +.

Pachyphragmo macrophyllae-Tilion begoniifoliae Zukal *all. nova hoc loco*.

Nomenclature type: *Hedero pastuchovii-Aceretum velutini* Zukal *ass. nova* (see below) (*holotypus*). Noble hardwood forests on steep slopes, in ravines and narrow valleys of the Greater Caucasus.

Valeriano tiliifoliae-Ulmetum glabrae Zukal *ass. nova hoc loco*. *Holotypus (hoc loco)* of the association: Georgia, Dusheti district, Vashlobi: forest on a slope above the left bank of the stream, 0.65 km NNW from the centre of the village, 1,268 m a.s.l. 42.2966667° N, 44.7286111° E. Relevé area: 12.5 m × 8 m; Aspect: 345°; Slope: 35°; Soil pH: 7.46; Cover of rocks: 20%. Covers: tree layer 85%, shrub layer 6%, herb layer 27%, moss layer 3%. Recorded on 10 August 2018. Author: Dominik Zukal.

Tree layer: *Carpinus betulus* 3, *Tilia begoniifolia* 2b, *Acer campestre* 2a, *Fagus orientalis* 2a, *Ulmus glabra* 2a;

Shrub layer: *Carpinus betulus* 1, *Corylus avellana* 1, *Sambucus nigra* 1, *Acer cappadocicum* +, *Euonymus latifolius* +, *Fraxinus excelsior* r;

Herb layer: *Pimpinella tripartita* 1, *Polystichum aculeatum* 1, *Primula veris* subsp. *macrocalyx* 1, *Salvia glutinosa* 1, *Viola odorata* 1, *Actaea spicata* +, *Aruncus dioicus* +, *Asplenium scolopendrium* +, *A. trichomanes* +, *Brunnera macrophylla* +, *Campanula rapunculoides* +, *Carex digitata* +, *Circaea lutetiana* +, *Dioscorea communis* +, *Galium odoratum* +, *Geranium robertianum* +, *Heracleum* sp. +, *Hordelymus europaeus* +, *Lactuca muralis* +, *Melica nutans* +, *Poa nemoralis* +, *Polygonatum multiflorum* +, *Sanicula europaea* +, *Scutellaria altissima* +, *Solidago virgaurea* +, *Valeriana tiliifolia* +, *Arum maculatum* agg. r, *Dipsacus pilosus* r, *Paris incompleta* r, *Polypodium vulgare* r; *Corylus avellana* +, *Fraxinus excelsior* r, *Sambucus nigra* r.

Hedero pastuchovii-Aceretum velutini Zukal *ass. nova hoc loco*. *Holotypus (hoc loco)* of the association: Georgia, Lagodekhi district, Khizabavra: a forest above the left bank of a brook, 2.7 km SW from Ninoskhevi waterfall, 646 m a.s.l. 41.8805556° N, 46.2447222° E. Relevé area: 10 m × 10 m); Aspect: 300°; Slope 40°; Soil pH: 6.08; Cover of rocks: 30%. Covers: tree layer 85%, shrub layer 6%, herb layer 75%, moss layer 10%. Recorded on 3 August 2018. Author: Dominik Zukal.

Tree layer: *Acer velutinum* 5, *Tilia begoniifolia* 1, *Carpinus betulus* +, *Hedera pastuchovii* +;

Shrub layer: *Euonymus latifolius* 1, *Philadelphus coronarius* 1, *Sambucus nigra* +;

Herb layer: *Hedera pastuchovii* 3, *Rubus* subgen. *Rubus* 2b, *Pachyphragma macrophylla* 2a, *Polystichum aculeatum* 2m, *Asplenium scolopendrium* 1, *Galium odoratum* 1, *Polystichum kadyrovii* 1, *Dryopteris borreri* +, *Geranium robertianum* +, *Onoclea struthiopteris* +, *Polystichum braunii* +, *Viola alba* +, *V. odorata* +; *Carpinus betulus* r.

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Author contributions P.N. and D.Z. designed the study. P.N., D.Z., M.H. and P.V. participated in the field sampling. P.N. led the writing and did the numerical analyses. D.Z. wrote the parts dealing with the ravine forests. M.H. prepared the map. O.A. provided data on the ecology of some species and assisted in the selection of sampling sites. W.W. significantly helped with the parts dealing with phytosociological nomenclature. All the authors critically revised the manuscript.

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