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Diversity and ecology of the river gravel-bar vegetation

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Abstrakt

Štěrkové náplavy jsou dynamickými a heterogenními biotopy vázanými na horské vodní toky. Existence štěrkových náplavů je závislá na pravidelných záplavách, které jejich vegetaci udržují v různých sukcesních stadiích, na něž jsou vázané specializované a často vzácné druhy rostlin. Štěrkové náplavy se vyskytují na tocích s přirozeným hydromorfologickým režimem a v současné Evropě patří vlivem antropogenních tlaků mezi ohrožené biotopy. Klasifikace vegetace štěrkových náplavů je v Evropě nekonzistentní a v některých zemích není tato vegetace ani rozlišována, což může komplikovat její monitoring, ochranu i management. Cílem práce proto bylo doplnit dosavadní znalosti o rozšíření a ekologii vegetace štěrkových náplavů v Evropě a navrhnout první jednotnou klasifikaci.

Na rozlišení sukcesních stadiích vegetace náplavů jsou založeny některé klasifikační přístupy. Sukcesí vegetace štěrkových náplavů, ekologickými aspekty, diverzitou, druhovou skladbou a vývojem jednotlivých stadií jsme se zabývali na čtyřech malých tocích v Západních Karpatech (Česká republika), které zasáhla padesátiletá povodeň. Studie potvrdila jako nejdůležitější faktory ovlivňující směr a rychlost sukcese vegetace nadmořskou výšku a strukturu substrátu.

Pro účel celoevropské klasifikace jsme shromáždili a digitalizovali vegetační snímky, které doposud nebyly součástí žádné dostupné vegetační databáze, a založili databázi vegetace štěrkových říčních náplavů (Gravel Bar Vegetation Database). Její součástí se staly vegetační snímky z vlastních terénních výzkumů, které probíhaly v zemích, kde byla tato vegetace méně prozkoumaná nebo údaje chyběly (především z jihovýchodní a severní Evropy a Kavkazu).

Pro Gruzii jsme na základě fyziognomie porostů a metody neřízené klasifikace nově vylišili pět vegetačních typů štěrkových náplavů: raně sukcesní vysokohorskou bylinnou vegetaci (asociace *Epilobietum colchici*), raně sukcesní podhorskou bylinnou vegetaci (společenstvo *Petrorhagia saxifraga-Crepis foetida*), porosty s *Calamagrostis pseudophragmites* (*Tussilagini farfarae-Calamagrostietum pseudophragmitae*), křoviny s *Myricaria germanica* (*Salici purpureae-Myricarietum germanicae*) a *Hippophaë rhamnoides* (*Salici incanae-Hippophaëtum rhamnoidis*). Vegetaci s *Calamagrostis pseudophragmites* a křoviny jsme přiřadili k analogickým asociacím popisovaným také ze střední Evropy. U vegetačních jednotek jsme definovali diagnostické druhy a popsali jejich ekologické nároky.

Na celoevropské úrovni jsme navrhli jednotnou klasifikaci vegetace štěrkových říčních náplavů. Raně sukcesní a křovinná vegetace byly klasifikovány v rámci dvou tříd, *Thlaspietea rotundifolii* a *Salicetea purpureae*. Celkem jsme vytvořili formální definice pro dvě subasociace, jedenáct asociací a čtyři svazy (*Calamagrostion pseudophragmitae*, *Epilobion fleischeri*, *Salicion cantabricae* a *Salicion eleagni*). Definice jsou založeny na výskytu a pokryvnostech skupin druhů s podobnou ekologií, nebo jednotlivých druhů úzce specializovaných na určitý typ vegetace náplavů.

Navržená klasifikace byla ověřena pomocí metod ordinace a neřízené klasifikace. U vegetačních jednotek jsme revidovali nomenklaturu, definovali diagnostické druhy a popsali jejich ekologické nároky a rozšíření. Ukázali jsme, že hlavní variabilita v datech je svázána s nadmořskou výškou, biogeografií, místními hydromorfologickými procesy a sukcesí vegetace.

Použitím vegetačních snímků z Balkánu a Kavkazu jsme rozšířili znalosti o druzích mechorostů, které se vyskytují na štěrkových náplavech, a nastínili jejich ekologii a vegetační vazby. Drobný ruderální mech *Bryum klinggraeffii* byl zjištěn jako nový druh pro Albánii, Černou Horu, Gruzii a Srbsko.

Abstract

The river gravel bars of mountain streams are spatiotemporally dynamic habitats. Their presence in a landscape depends on regular and relatively frequent flooding disturbances creating a variety of successional stages encompassing rare specialised species. Gravel-bar habitats became rare in Europe due to river regulations and other artificial alterations leading to the interruption of the natural hydro-morphological regime of gravel-bed rivers. The classification of gravel-bar vegetation in Europe, a keystone for the conservation planning, monitoring and management, is inconsistent or even ignored in some national schemes. Therefore, we aimed to extend the knowledge on the distribution and ecology of the vegetation types of European mountain gravel-bar habitat and propose the first unified vegetation classification.

Several classification systems emphasized the main criteria for the delimitation of vegetation types of river gravel-bar habitat to be the physiognomy related to the vegetation succession. We performed a case study focused on the ecological aspects of the vegetation succession and changes in plant diversity on river gravel bars of four streams in the Western Carpathians (Czech Republic) which experienced extreme 50-year flood event. In this study, we described the individual successional stages in terms of the species turnover, richness and other characteristics. We identified altitude and size of gravel/stone particles to be the most important factors influencing the vegetation succession.

For purpose of development of the pan-European vegetation classification of river gravel-bar habitats, we collected and digitized vegetation-plot data that had not been previously stored in electronic databases and included them in newly created Gravel Bar Vegetation Database. An important part of the database are vegetation plots from our field sampling in the countries where this vegetation had not been studied before or was less explored, especially in south-eastern and northern Europe and the Caucasus.

We studied vegetation of gravel bars of several gravel-bed rivers across Georgia. We distinguished five vegetation types based on vegetation physiognomy and unsupervised classification and described them as phytosociological vegetation units. Two of them were described as new to science, i.e. early-successional herbaceous vegetation at higher altitudes (*Epilobietum colchici*) and that at lower altitudes (*Petrorhagia saxifraga-Crepis foetida* community), and other were assigned to the associations previously described from Central Europe, i.e. the grasslands dominated by *Calamagrostis pseudophragmites* (*Tussilagini farfarae-Calamagrostietum pseudophragmitae*) and scrub vegetation (*Salici purpureae-Myricarietum germanicae* and *Salici incanae-Hippophaëtum rhamnoidis*). We established diagnostic plant species for each type and related them to environmental variables.

The main aim of the thesis is to determine the vegetation types of gravel-bar habitat in Europe and to assign them to the association and subassociation levels using formalized classification approach. We classified early-successional and scrub gravel-bar vegetation types into two classes, i.e. *Thlaspietea rotundifolii* and *Salicetea*

purpureae, respectively, and we formally defined two subassocitaions, eleven associations and four alliances (*Calamagrostion pseudophragmitae*, *Epilobion fleischeri*, *Salicion cantabricae* and *Salicion eleagni*). This distinction was supported by unsupervised classification and ordination modelling. Based on a critical revision, we merged or discarded some associations or alliances which were already defined and described in literature. We established diagnostic plant species for each type and related environmental variables to those types, as well. The main variability within the distinguished vegetation types is connected to the altitudinal gradient, biogeographical variation, local hydro-morphological processes and successional development.

As there is a general lack of knowledge on the distribution of bryophyte species growing on gravel bars and on their vegetation affinity, we used the vegetation-plot data collected in several Balkan countries and the Caucasus and described their occurrence in a geographical and ecological context. During the fieldwork, *Bryum klinggraeffii*, small ruderal moss of frequently disturbed open habitats, was found as a new species for Albania, Georgia, Montenegro and Serbia.

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Author contributions to the papers in the thesis

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VK and MC conceived the study idea; statistical analyses were performed by VK and KC; VK wrote the paper and MC and KC participated in the interpretation of the results and the manuscript improvements.

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Jeník 1955

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1. Introduction

1.1 Gravel-bar habitat

1.1.1 Basic habitat characteristics

River gravel bars are azonal habitats, similarly as mires, aquatic vegetation, or screes, hosting specialized flora and unique vegetation types. Their azonality is determined by local environmental conditions. They develop at sites with a unique combination of floodplain morphology, water discharge pattern, and sediment transport regime, usually in mountain and piedmont areas, formed of highly erodible bedrock (e.g. limestone, sandstone). Gravel bars occur especially in places where the strong current of mountain streams suddenly slows down, and thus allows the sedimentation of particles released by bank erosion in the upper reaches (Montgomery and Buffington, 1998; Richards et al., 2002; Tockner et al., 2006; Škarpich et al., 2013; Hohensinner et al., 2018). If the above-mentioned conditions are met, river gravel bars can occur anywhere from glacial floodplains and wide alpine river valleys to the piedmonts (Fyles and Bell, 1986; Tockner et al., 2006; Prach et al., 2014). Substrate and soil reaction may vary in the local habitat micromosaics as the substrate of different origin can be transported by the river from distant valleys.

1.1.2 Disturbance-dependence

Presence of gravel-bar habitats is dependent on periodically flooded channels of wandering or braided rivers (Montgomery and Buffington, 1998; Hohensinner et al., 2018; Ward et al., 2002; Tockner et al., 2006; Gostner et al., 2017). The frequency and intensity of floods varies according to the river morphology, regional topography and climatic conditions. Generally, periods of higher water level occur during early spring snow melting and later during the summer monsoons (Tockner et al., 2000). However, the rivers with glacier origin have higher summer flows and daily flood pulses, because of melting of glaciers (Millner and Petts 1994, Tockner et al., 2000; Malard et al., 2006). Although the floods are a major force structuring floodplain habitat conditions, even moderate increases in discharge, i.e. flow pulses, are important processes for sustaining high levels of gravel-bar habitat heterogeneity (Junk et al., 1989; Tockner et al., 2000).

1.1.3 Threats and protection

Gravel-bar habitat is strongly affected by human activities and is rapidly disappearing in Europe (e.g. Müller, 1995; Tockner et al., 2006; Gurnell et al., 2009; Skoulikidis et al., 2009; Rădoane et al., 2013; Janssen et al., 2016; Muhar et al., 2019). In the European Red List of Habitats (Janssen et al., 2016), it is classified as vulnerable, and considerable proportion of specialized gravel-bar species is listed on the national Red Lists in many European countries (e.g. Sochor et al., 2013; Werth et al., 2014; Skokanová et al., 2015; Sitzia et al., 2016; Werner, 2016; Fink et al., 2017).

Furthermore, several gravel-bar habitat types are listed in Annex I of the European Habitats Directive, which is the legal basis of the Natura 2000 network (European Commission, 2013) or in the Emerald Network in case of the European countries that are not members of the European Union.

The main reasons of the disappearance of the habitat of river gravel bars are the direct habitat destruction and changes in environmental conditions leading to eutrophication. Subsequently, the vegetation which has once been formed especially by typical specialist species homogenizes and its species composition shifts towards nutrient-supplied types, generally typical for lowland river sections. Functioning water regime is crucial for the maintenance of this habitat as it directly influences its disturbance dependence. Its disruption allows succession to progress and competitively strong species outcompete the disturbance-related or stress tolerant species which are the key component of the biodiversity of this habitat. River gravel bars are often colonized by ruderal and alien species (Müller, 1995; Planty-Tabacchi et al., 1996; Ward and Tockner, 2001; Richardson et al., 2007; Smale, 1990; Werth et al., 2014; Kalníková and Palpurina, 2015; Wilczek et al., 2015; Brummer et al., 2016). The main disruption reasons include increasing regulation of gravel-bar channels, sediment extraction and construction of dams, weirs and hydropower plants (Müller, 1995; Kondolf, 1997; Dai and Liu, 2013). The damage to the natural hydrological regime causes alteration from the multi-thread to the single-thread channels, homogenization of gravel-bar microtopography, transformation of the gravelly beds to bedrock beds and channel incision (Kondolf, 1997; Škarpich et al., 2013; Hajdukiewicz and Wyżga, 2019). Furthermore, these changes have economic impacts, such as the increase in financial requirements for water treatment and repair of hydraulic structures (e.g. Škarpich et al., 2018).

1.2 Species composition and variability of gravel-bar vegetation

1.2.1 Gravel bars as centres of diversity

Gravel-bar habitat mosaic comprises a high number of species and vegetation types (Tockner and Malard, 2003; Tockner et al., 2006; Egger et al., 2019). Diverse vegetation types are developing especially in early-successional stages, which serve as refugia for light-demanding and drought-adapted species. They even might represent the primary habitat of weed and ruderal communities (Slavík, 1978). In late-successional stages, the vegetation of river gravel bars is less diverse due to shading by scrub and tall herbs and high competition from established dominant species (Walker and del Moral, 2003; Corenblit et al., 2009; Prach et al., 2014).

Moreover, the high diversity of this habitat is also supported by the spatial mass effect. River gravel bars often hosts numerous species characteristic for adjacent and upstream non-floodplain habitats. This species enrichment is however random to a large degree especially in the early-successional stages (Jeník, 1955; Malanson and Butler, 1991; Chytrý et al., 2015; Egger et al., 2019). The decrease of diversity with altitude is a general and well-studied trend, which is in case of river gravel bars recognized also within a single habitat. Besides the pure effect of the altitude, the species richness of river gravel bars is also influenced by the land-use of the surrounding landscape, intensity of settlements and other factors that influence the regional species pools (Müller, 1995; Muhar et al., 2019).

1.2.2 Specialized gravel-bar species and their adaptations

The biodiversity of gravel bars is supported significantly by the regional species pools. These matrix-derived species are usually not adapted to environmental conditions of river gravel bars, thus their life span and abundances are limited (Müller and Sharms, 2001; Tockner et al., 2006; Corneblit et al., 2009; Prach et al., 2014). However, several plant species (further called gravel-bar specialists) developed adaptation to cope with harsh environment. These species must sustain contrasting environmental conditions, such as submersion and rapid changes of the water current during the wetter seasons, and withstand overheating and lower water availability during the drier seasons. Furthermore, species growing on rock debris must cope with coarse unstable substrate and low content of fine organic and inorganic components. The sediments poor in organic matter provide only minor amounts of nutrients compared to low altitude loodplain systems (Müller and Sharms, 2001). The survival of plants on river gravel bars depends primarily on rapid colonization, growth and development. Thus, common strategies of gravel-bar specialists are high diaspore dispersibility, fast and/or clonal growth on poor soils and disturbance tolerance.

Myricaria germanica and some species of the genus *Salix* are a good example. They have a late dissemination, which helps avoid typical spring and early summer floods. Moreover, their flexible branches, deep root system and narrow, damage-resistant leaves withstand strong water flow and related damage by the material drifted by the current (Jeník, 1955; Karrenberg et al., 2003; Francis et al., 2005; Fink et al., 2017; Leuschner and Ellenberg, 2017). Similar adaptations to cope with the periods of droughts are, e.g., very narrow, densely haired and reversibly curled leaves of *Salix eleagnos*. *Hippopäe rhamnoides* has a similar habitus as *Salix eleagnos*, and in addition, it has the ability of nitrogen-fixation and intensive vegetative reproduction from roots (Moor, 1958; Skogen, 1972; Müller, 1995; Karrenberg et al., 2003). Other gravel-bar specialists evolved similar adaptations, such as herbaceous plants of the genus *Epilobium* (Stöcklin, 1999), bryophytes, e.g. *Barbula unguiculata*, *Dichodontium pellucidum*, *Hygroamblystegium tenax*, *Racomitrium canescens* or *Syntrichia ruralis* (Vitt et al., 1986; Muotka & Virtanen, 1995), and also lichens, e.g. *Stereocaulon* spp. (Vančurová et al., submitted).

Gravel bars contain such specialist species of this habitat as a whole, and of its particular successional stages or microhabitats. The number of gravel-bar specialists in Europe is small, depending on the biogeography and altitude. The most typical gravel-bar specialized vascular plants are *Calamagrostis pseudophragmites, Chondrilla chondrilloides*, *Epilobium colchicum*, *E. dodonaei*, *E. fleischeri*, *Hippophaë* *rhamnoides*, *Myricaria germanica*, *Salix cantabrica*, *S. daphnoides*, *S. eleagnos* and *S. purpurea.*

1.2.3 Vegetation succession and factors influencing successional direction

Frequent disturbances support the development of pioneer early-successional vegetation. These early-successional stages subsequently shift into denser vegetation usually dominated by shade-tolerant species (Tockner et al., 2006). In general, on natural unregulated rivers the forest vegetation stage is often lacking (alluvial forests dominated by *Alnus* spp., *Fraxinus* spp. and on dry sites *Pinus sylvestris* forest) or it is limited in more stable floodplain parts. Scrub vegetation is usually the final stage there, however, it can develop into more mature communities once the main river channel relocates and they are no longer regularly inundated (Pettit and Froend, 2001). Successional gradient is reflected in vegetation classification. In EuroVegCheclist (Mucina et al., 2016), the early-successional plant communities are assigned to the class *Thlaspietea rotundifolii*, while scrub vegetation of more developed successional stages is assigned to the class *Salicetea purpureae*.

The succession on river gravel bars belongs to the fastest vegetation changes world-wide (Jeník, 1955; Prach et al., 2016; Caponi et al., 2019). However, the rate of succession can be influenced by several factors such as dispersal limitation, disturbance regime, environmental heterogeneity and altitude (Grime, 1979; Prach et al., 1994). The rate of succession is generally higher at lower altitudes and also in moderately wet and nutrient-rich conditions than at drier, nutrient-poor sites; it also decreases with successional age (Grime, 1979; Prach et al., 1994; Wellstein et al., 2003). The light-demanding fast-growing and short-living early-successional species are replaced by slow-growing and shade-tolerant late-successional species, which occupy the habitat for a longer period (Gurnell et al., 2005; Corenblit et al., 2009; Prach et al., 2014).

1.3 History of gravel-bar vegetation surveys

Knowledge on gravel-bar vegetation types is dependent on studies focused on vegetation succession (Jeník, 1955), and many multidisciplinary studies were published. First such comprehensive study was made by Siegrist (1913) in the Swiss Alps. The Alps were the first area where river gravel bar vegetation was studied (e.g. Rübel, 1912; Aichinger, 1933; Volk, 1939; Braun-Blanquet, 1948; Moor, 1958) followed by the Carpathians (e.g. Sillinger, 1933; Pawłowski and Walas, 1949; Jurko, 1964; Pázmány, 1969) and other European countries such as: France (Tchou, 1948), Croatia (Trinajstić, 1964), Spain (Rivas-Martínez et al., 1984), Norway (Klokk, 1978) and others. In Italy the river Tagliamento became the main model site for recent ecological gravel-bar studies in Europe (e.g. Edwards et al., 1999; Karrenberg et al., 2003; Tockner et al., 2003). Despite the long history of the gravel-bar research, there are still many unexplored areas in Europe, especially the Balkans, some parts of the Carpathians, Eastern European countries, Scandinavia and the Caucasus. Most vegetation plots sampled during the studies on river gravel bars lacks information on bryophytes (and also lichens). Thus, patterns of species composition and ecology of bryophyte communities on river gravel bars are poorly known, although they play an important role these habitats.

1.4 Classification of gravel-bar vegetation in Europe

Classification schemes of the gravel-bar vegetation in different European countries vary due to diverse classification approaches. Most of the studies are focused on restricted mountain regions, and researchers sometimes described the same vegetation type in different regions under different association names. The concepts of higher vegetation units also vary considerably. Based on the physiognomy, scrub vegetation is mostly assigned to *Salicetea purpureae* class and herbaceous vegetation to the classes *Thlaspietea rotundifolii*, *Artemisietea vulgaris* and *Phragmito-Magno-Caricetea*. The border between scrub and herbaceous vegetation is however often transitional; therefore some same vegetation units were assigned either to scrub or herbaceous vegetation. Differences are apparent when comparing national vegetation overviews (e.g. Kojić, 1998; Schubert et al., 2001; Valachovič, 2001; Matuszkiewicz, 2007; Sanda et al., 2008; Trinajstić, 2008; Chytrý, 2011, 2013).

On the European scale, Valachovič et al. (1997) reviewed the herbaceous scree vegetation (including river gravel-bar vegetation) on the association level, and the recent syntaxonomical overview of European vegetation (Mucina et al., 2016) classified it at the alliance level. However, both overviews are based on a review of the existing literature and expert knowledge rather than on data analysis and critical international revision of the classification of gravel-bar vegetation.

1.5 Aims of the thesis

The main aims of the thesis are:

i) to describe patterns of species richness, species composition and succession rate during early vegetation succession on river gravel bars, and to identify which are the most important factors influencing the succession of gravel-bar vegetation (**paper 1**),

ii) to create the Gravel Bar Vegetation Database in order to fill the gap in data availability for pan-European gravel-bar vegetation studies (**paper 2**),

iii) to propose a classification of the vegetation of river gravel-bar habitats in the Caucasus Mountains (Georgia), relate it to the habitat types used in European habitat classifications and assess the main threats to these habitats (**paper 3**),

iv) to revise and unify previous classification systems of river gravel-bar vegetation in European mountain systems, define vegetation types to the association level using the formal language for vegetation classification expert systems, describe species composition, ecology and distribution of these types, and revise their phytosociological nomenclature (**paper 4**),

v) to extend knowledge on the distribution, ecological preferences and vegetation affinity of bryophyte species growing on gravel bars, particularly in the Balkan Peninsula and the Caucasus (**papers 5** and **6**).

2. Methods

Detailed description of data sets and analyses can be found in Methods chapters of each enclosed paper. Therefore, here we summarize characterization of the data sets used and applied statistical methods.

2.1 Main methods of the gravel-bar vegetation succession case study

The research was performed on four flood-affected streams in the Western Carpathians (Czech Republic; **paper 1**), taking the advantage of big flood events that occurred in 2010. Two months after the floods, we sampled vegetation in established permanent vegetation plots and repeated the sampling each year in the following three years. Approximately the same number of plots was established on each stream and positioned along the entire stream length, from the spring to the mouth. Many permanent plots were destroyed, by gravel extraction during channel regulation. In total, we used 43 repeated plots that contained records from all four years, i.e. 172 records in total, including 16 records with no species in the first year.

For each plot, we measured or estimated values of environmental variables (elevation of each plot above the present stream water, substrate structure, gravel bar age, and shading) and described position of gravel bar in the channel. For analysis of species composition, we used the characteristics of reproduction type (Frank and Klotz, 2012), Ellenberg indicator values (Ellenberg et al., 1991) and habitat affinity (Chytrý, 2007, 2009, 2011, 2013) calculated for each vascular plant species.

We used two ordination techniques to explore compositional changes and vegetation-environment relationships during succession – Detrended Correspondence Analysis (DCA) and Canonical Correspondence Analysis (CCA). The species turnover was used as a measure of the succession rate. It was computed as the mean Bray-Curtis index of dissimilarity in species composition within the same plots between two consecutive years. Subsequently, we used the succession rate as a dependent variable and modelled it using selected environmental predictors.

2.2 Main methods of European gravel-bar vegetation studies

2.2.1 Data collection

The need for a unified critical overview of the gravel-bar vegetation in the Europe led us to the establishment of the European Gravel Bar Vegetation Survey project in 2012 as one of the pilot projects of the European Vegetation Archive (EVA; Chytrý et al., 2016). When we were starting to collect the gravel-bar vegetation data, the EVA database was not yet fully established. Thus, the process of data collection for the synthesis of European gravel-bar vegetation proceeded by following steps: (i) to request data custodians and regional vegetation ecologists for vegetation plots stored in various European national, regional or private vegetation databases, (ii) to request additional data stored in the initial version of the EVA database, (iii) to digitize vegetation plots from data-deficient countries from several literature sources, and (iv) to perform targeted field sampling in the countries or regions where the gravel-bar vegetation had not been sufficiently explored or from which were not enough data (mainly Bulgaria, France, Georgia, Montenegro, North Macedonia, Norway, Poland, Serbia, Sweden and Switzerland; **Fig. 1**; **papers 2–6**).

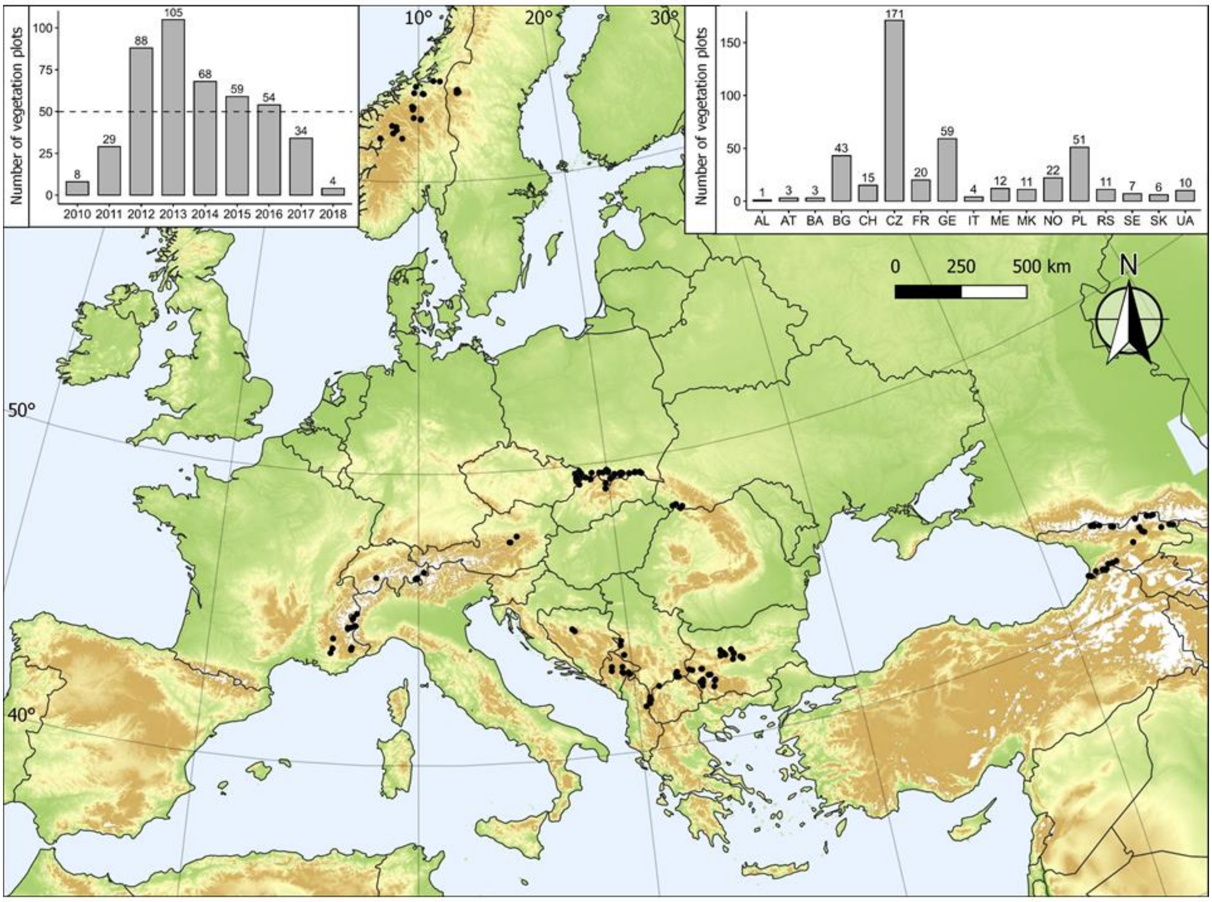

Fig. 1 Distribution map of vegetation plots (black dots) collected during own field sampling. Years of sampling and the distribution of vegetation plots within the countries are shown.

We focused on the cool-temperate and boreal gravel-bar vegetation of the phytosociological order *Epilobietalia fleischeri* (class *Thlaspietea rotundifolii*) and the alliances *Salicion eleagno-daphnoidis* and *Salicion cantabricae* of the order *Salicetalia purpureae* (class *Salicetea purpureae*). Our data selection criteria were wider as they also included non-target riparian vegetation types (e.g. *Petasites* stands or some types of ruderal and scree vegetation), which were, however, sampled on the gravel bars as well. We gathered them together with the target vegetation types as we wanted to avoid exclusion of appropriate data by a too narrowly defined request. We requested vegetation plots which (i) belonged to the habitat types 3220, 3230 and 3240 of Natura 2000 (Annex I of the EU Habitats Directive) or (ii) contained information on the origin on a river gravel bar or (iii) were assigned to the predefined vegetation types or (iv) contained at least one of the diagnostic species of gravel-bar vegetation listed in the literature. In doubtful cases, data were verified in the original literature, or the location of vegetation plots was checked with the help of aerial photographs.

2.2.2 Nomenclature

Taxa of problematic, unstable or ambiguous status unequally differentiated in all the data sources were merged into species groups or aggregates (usually sensu Ehrendorfer, 1973). This step minimized the taxonomic bias in vegetation analyses (Jansen and Dengler, 2010). Such corrections had to be done even for the prize of losing important indicator species or subspecies.

2.2.3 Main aspects of expert system creation

Our main classification output is based on a supervised method of formal definitions allowing unequivocal assignment of vegetation plots to defined vegetation unit (e.g. also Chytrý, 2007, 2009, 2011, 2013; Peterka et al., 2017; Marcenò et al., 2018; Landucci et al., 2020). We created an expert system comprising formal definitions, which combine criteria based on a threshold cover or presence of functional species groups (Landucci et al., 2015; Tichý et al., 2019). It comprises species narrowly specialized to a particular gravel-bar habitat, minimum cover or presence of a single specialist species, and the presence of sociological groups of species with a statistical tendency of co-occurrence in vegetation plots. The sociological species groups were developed using the Cocktail method (Bruelheide, 1997, 2000; Kočí et al., 2003).

To distinguish the gravel-bar vegetation from other vegetation types, we created a group of specialized gravel-bar species. As we classified vegetation of early-successional and scrub successional stages, the development of classification criteria reflected various physiognomy and structure of gravel-bar vegetation. To separate these types, functional groups of species typical for different successional stages were created and these groups were set against each other using their covers. This method was chosen because most of the collected vegetation plots were missing the information on vegetation layers, or it was recorded inconsistently. If vegetation consists mainly of the gravel-bar specialists of early-successional stages, scrub species are usually rare. In later successional stages the increasing cover of shrubs and competitive herbaceous species results in a retreat of light-demanding and competitively weak herbaceous gravel-bar specialists. Moreover, vegetation researchers usually sample well-defined, not transitional vegetation types. Such definitions should guarantee applicability to various datasets. Formal definitions based on cover thresholds of dominant species or life forms (i.e. cover of the shrub layer) were partially involved also in the classification of vegetation plots from the gravel-bar habitats in the Caucasus Mountains (**paper 3**).

Since our dataset was rather heterogeneous, we used two different approaches to logically define vegetation types for the pan-European classification. Early-successional vegetation, lacking distinct dominant species, was classified based on sociological species groups. In contrast, scrub and tall grassland with *Calamagrostis* *pseudophragmites* were defined based on their physiognomy characterized through the dominance or codominance of single species.

2.2.4 Verification of formalized classification

Supervised classification with help of expert system definitions is a subjective method (De Cáceres et al., 2015). To evaluate the results of supervised classification, we compared the resulting syntaxa with unsupervised classification and digitized both in an ordination analysis (e.g. Peterka et al., 2017; Marcenò et al., 2018). We used TWINSPAN as the method for unsupervised classification and DCA as ordination technique.

3. Results

3.1 Outline of the thesis

The river gravel bars are dynamic spatiotemporally variable habitat. The classification of gravel-bar vegetation in Europe is complicated, as classification schemes vary due to diverse classification approaches, and they are not considered in some national overviews. River gravel bars belong to endangered habitats in Europe, and their inconsistent classification could be an issue for conservation planning, monitoring and management. Therefore, we extended knowledge on the distribution and ecology of the European mountain gravel-bar vegetation types and proposed the first unified vegetation classification based on a large set of vegetation plots.

The river gravel-bar plant communities are locally determined especially by vegetation succession processes, and the proposed classification scheme followed this gradient as a basis for the division into major vegetation types. Considering that, in the first study we focused on vegetation succession and changes in plant diversity on river gravel bars of four streams in the Western Carpathians (Czech Republic). This case study identified the most important factors affecting vegetation succession and its rate. Furthermore, this study revealed the successional paths and species richness of individual successional stages.

For formalized classification of European mountain river gravel-bar vegetation, we collected and digitized vegetation-plot data that had not been previously stored in electronic databases and included them in newly created Gravel Bar Vegetation Database.

An important part of the Gravel Bar Vegetation Database were vegetation plots from our field sampling in the countries where this vegetation had not been studied before or was less explored, especially in south-eastern and northern Europe and the Caucasus. A representative dataset of gravel-bar vegetation plots from the Caucasus Mountains (Georgia) allowed us to prepare a study focused on vegetation types occurring on rivers across almost the whole country. We recognized new vegetation types for this region, related them to those known from the rest of Europe, and provided baseline data for developing conservation strategies for the Caucasian gravel-bar habitats.

In the next step we focused on the main aim of the thesis, i.e. the determination of gravel-bar vegetation types to the association and subassociation levels in Europe using formalized classification approach.

Additional studies focused on a less explored component of gravel-bar plant communities – bryophytes. Given the general lack of knowledge about the distribution and vegetation affinity of bryophyte species growing on gravel bars, we used the vegetation-plot data collected in several Balkan countries and the Caucasus and described their occurrence in geographical and ecological context.

In conclusion, the thesis highlights the importance of gravel-bar habitat protection. This habitat is strongly affected by human activities. Remnants gravel bars experience a considerable decline in biological quality of their natural vegetation. Despite the long history of the gravel-bar vegetation research, there are still many less explored or unexplored areas and gravel-bar vegetation types in Europe.

3.2 Main results of the thesis

3.2.1 Succession on gravel bars

We took the opportunity to perform a case study on vegetation succession immediately after a significant flood event that happened in the Western Carpathians (Czech Republic), where no similar study has been done before (**paper 1**). During the first years of the succession, species richness increased very quickly until the scrub and competitive shade-tolerant herbaceous species spread out. We observed very high species richness for some plots in early-successional stage, with a maximum of 72 vascular plant species in a plot of 15 m^2 in the second year, which is close to the highest values of species richness recorded in Central European vegetation, disregarding the world-record semi-dry basiphilous grasslands of the White Carpathians and Slovak Paradise (Chytrý et al., 2015). However, species richness in this plot quickly decreased in the next year. In the fourth year, nutrient-demanding tall herbs and alien species dominated the communities and typical scrub gravel-bar vegetation started to develop only in a few places. Species capable of vegetative dispersal prevailed over species dispersed exclusively by seeds. As the studied streams were influenced by human interventions, they host only few gravel-bar specialists which typically occur on more natural gravel-bar habitats (e.g. Moor, 1958; Müller, 1995; Karrenberg et al., 2003; Leuschner and Ellenberg, 2017).

Our results reflected that the main gradient in species composition of the gravel-bar vegetation is connected with the riverine altitudinal continuum (Vannote et al., 1980): altitude and size of gravel/stone particles were identified as the most important factors affecting vegetation succession. We showed that succession ran faster on gravelly substrates at lower altitudes than on stony substrates at higher altitudes. The gravelly and stony plots differed also in species richness and cover of bryophytes, both being higher in stony plots. Stony bars have more structured microtopography, providing different microsites important for colonization and survival (Muotka and Virtanen, 1995, Tockner et al., 2006).

3.2.2 European Gravel Bar Vegetation Database

For a unified revision and overview of the gravel-bar vegetation in Europe, it was necessary to perform a broad-scale vegetation synthesis based on vegetation plot data. The need for representative data set led us to the establishment of the European Gravel Bar Vegetation Database (**paper 2**). The database consists of vegetation plots digitized from the literature and from own targeted field research in the countries where this vegetation has not been previously studied or is less explored. The database was included in the European Vegetation Archive (Chytrý et al., 2016).

3.2.3 Exploring less known gravel-bar habitats

As an important part of the European data gathering was my own field research, I have focused also on the gravel-bar rivers of Georgia (Caucasus Mountains). Their vegetation has not been classified or systematically described yet (**paper 3**). We studied vegetation on gravel bars of rivers restricted to the Greater and Lesser Caucasus and Central Georgia. Five vegetation types based on vegetation physiognomy and unsupervised classification, were distinguished. Early-successional herbaceous vegetation at higher altitudes was described as the new association *Epilobietum colchici* and that at lower altitudes as the *Petrorhagia saxifraga-Crepis foetida* community. The grassland dominated by *Calamagrostis pseudophragmites* and scrub vegetation were assigned to the associations previously described from Central Europe (*Tussilagini farfarae-Calamagrostietum pseudophragmitae*, *Salici purpureae-Myricarietum germanicae* and *Salici incanae-Hippophaëtum rhamnoidis*). We established diagnostic plant species for each type and related these types to environmental variables.

We further compared them with the previously published data on gravel-bar vegetation from the Russian part of the Caucasus (Onipchenko, 2002) and with European systems of vegetation classification (e.g. Valachovič, 2001; Schubert et al., 2001; Chytrý 2011, 2013). This study demonstrates that vegetation and habitat types occurring in Georgia largely correspond to those recognized earlier in Europe, and can be linked to the European systems of habitat classification (European Commission, 2013; Janssen et al., 2016). Unlike in other parts of Europe, these habitats are still well-preserved on rivers with natural hydrological dynamics in Georgia, but they are threatened by plans of dam building and other river regulations (e.g. Bakhia et al., 2019).

3.2.4 Classification of gravel-bar vegetation in Europe

We proposed the first formalized classification of pan-European mountain gravel-bar herbaceous and scrub communities based on hierarchical classification expert system with formal definitions of vegetation types to the association and subassociation levels (**paper 4**). We mapped the distribution of individual vegetation types and identified their diagnostic species. The large-scale distribution of herbaceous and scrub gravel-bar pioneer communities was defined mainly by biogeography of diagnostic species and altitudinal zonation. Gravel-bar communities were locally determined especially by hydro-morphological processes and vegetation succession.

We defined eleven vegetation associations and four alliances: *Calamagrostion pseudophragmitae* (gravel-bar grasslands with *Calamagrostis pseudophragmites*), *Epilobion fleischeri* (herbaceous early-successional vegetation of alpine to submontane river gravel bars of the temperate and boreal European mountains and the Caucasus), *Salicion cantabricae* (Cantabrian subalpine to montane willow-scrub vegetation of river gravel bars) and *Salicion eleagno-daphnoidis* (scrub vegetation of subalpine to submontane river gravel bars of the temperate and boreal European mountains and the Caucasus). Early-successional and scrub gravel-bar vegetation types were respectively classified to the classes *Thlaspietea rotundifolii* and *Salicetea purpureae*. As we revised the syntaxonomical nomenclature of distinguished units, some associations or alliances defined in the previous literature were merged or discarded.

Results were supported by unsupervised classification, which we applied to early-successional vegetation types. Besides, the functionality of the expert system was tested on the whole European dataset using the EUNIS habitat classification (Chytrý et al., submitted), to guarantee that the formal definitions of gravel-bar vegetation would not misidentify plots of other vegetation types as gravel-bar vegetation. However, as in case of any classification, the proposed classification suffers from the lack of data from some vegetation types and areas. This specifically applies to more thermophilous early-successional vegetation types and to northern Europe where the development of gravel-bar vegetation classification should continue.

The knowledge on the distribution of the gravel-bar vegetation types in Europe was significantly improved. Nevertheless, in a detailed overview of the distribution of accepted gravel-bar vegetation associations which was based on our data and the most important literature sources, we showed in how many European countries this vegetation could occur but no data or reports exist.

3.2.5 Bryophytes as a part of gravel-bar plant communities

In our study on bryophytes occurring within gravel-bar communities sampled on Balkan rivers, we showed that the spatiotemporal variability in environmental conditions on gravel bars enables the coexistence of bryophyte species of different ecological groups (**paper 5**). We outlined a complex gradient of moisture and light conditions, stretching from early-successional stages with sparse and open vegetation on drier sites (e.g. initial or sparse *Myricaria germanica* scrub vegetation) to denser, shadier condition on wetter sites (e.g. grasslands of *Calamagrostis pseudophragmites*). The fact that natural disturbance caused by water flow is important for maintaining high bryophyte diversity on gravel bars by opening space for less-competitive species has been already shown by Vitt et al. (1986) and Muotka and Virtanen (1995). In contrast, stable conditions allow strong bryophyte competitors to monopolize suitable habitats (Muotka and Virtanen, 1995). We also found many bryophytes typical of streams that have special adaptations to survive the pressure of flowing water on gravel bars. Interestingly, most of these adaptations are also mentioned as common xerophytic adaptations (Watson, 1919; Vitt and Glime, 1984) and could, therefore, be an advantage when species grow on a rocky shoreline or higher parts of gravel bars that may dry out in summer.

Bryoflora of river gravel-bar habitat has rarely been explored, especially in some countries, in which the level of bryological research is generally low. Therefore we compiled a list of bryophytes found during the field research in several countries of the Balkan Peninsula (Albania, Bulgaria, Montenegro, North Macedonia and Serbia). Several species we recorded were data-deficient or vulnerable. *Bryum klinggraeffii* was found as a new species for Albania, Montenegro, Serbia (**paper 5**) and Georgia (**paper 6**). This species is a widespread small ruderal moss that inhabits a wide altitudinal gradient and typically grows on the bare ground of frequently disturbed open habitats (e.g. Dierßen, 2001).

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Paper 1

Kalníková, V., Chytrý, K. and Chytrý, M. (2018) Early vegetation succession on gravel bars of Czech Carpathian streams. *Folia Geobotanica*, 53, 317–332.

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Early vegetation succession on gravel bars of Czech Carpathian streams

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Abstract Rivers with a natural flooding regime and gravel accumulations are an important natural habitat endangered by regulations and other types of human impact. Succession after disturbances by floods creates a mosaic of different vegetation types, some of them containing rare specialist species. We studied vegetation succession and changes in plant diversity on river gravel bars of four streams in the Western Carpathians and their foothills in the eastern Czech Republic. This area experienced extreme 50-year flood event in May 2010. Gravel bar vegetation was destroyed, some of the former bars were covered by sediments, and some new bars arose. We sampled gravel bar vegetation two months after the floods and repeated the sampling on each site during the next three years. Initial vegetation has developed through a sparse and species-rich stage into denser stands with more shade-tolerant species. In the fourth year, tall herbs, such as *Urtica dioica*, *Phalaris arundinacea* and the alien *Impatiens glandulifera*, dominated the communities, but shrub vegetation started to develop only in a few places. Species capable of vegetative dispersal prevailed over species dispersed by seeds only. Altitude and size of gravel/stone particles were identified as important factors affecting vegetation succession. The succession ran faster on gravelly substrates at lower altitudes than on stony substrates at higher altitudes. Although the studied streams are partly influenced by human interventions and host only few gravel bar specialists, they are of considerable conservation importance.

Keywords Disturbance · Floods · Gravel bar vegetation · Moravskoslezské Beskydy Mts · Plant communities · Riverine habitats · Succession rate · Western Carpathians

Introduction

Gravel bars are very dynamic habitats of gravel-bed rivers (Tockner et al. 2006). They develop at sites with a specific combination of floodplain morphology, water discharge pattern, and sediment transport regime in mountain and piedmont areas with easily eroded bedrock. Gravel bars occur especially in places where the strong current of mountain streams slows down, allowing the deposition of particles released by bank erosion in the upper reaches. Such places are characterized by irregular gravel accumulations and a combination of straight, braided, wandering, or meandering river channels (Montgomery and Buffington 1998; Richards et al. 2002; Škarpich et al. 2013).

River gravel bar habitats are known from various streams worldwide (Tockner et al. 2006; Prach et al. 2014), but human interventions made this habitat extremely endangered in many areas (Tockner et al. 2006; Gurnell et al. 2009). For example, the cumulative length of the braided reaches of Austrian rivers decreased by 95%

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during the twentieth century (Muhar et al. 2007). The high conservation value of gravel bar habitats in Europe has been reflected by their inclusion on the list of natural habitat types in Annex I of the European Habitats Directive, which is the legal basis of the Natura 2000 network (European Commission 2013). In the European Red List of Habitats (Janssen et al. 2016), the habitat type 'Unvegetated or sparsely vegetated shore with mobile sediments in montane and alpine regions' was evaluated as vulnerable because of a large reduction in its area over the last 50 years.

There are several processes forming gravel bars, but the main one, both disturbing and creating these habitats, are floods. The occurrence of the typical gravel bar scrub composed of willows (*Salix* spp.) and other shrub species and of specialized herbaceous plant communities depend on river dynamics and disturbances by floods. Natural disturbances of the gravel bar surface cause vegetation in different parts of gravel bars to develop into a variety of successional stages of different ages (Lacina 2007; Gilvear et al. 2008). A disruption of the usual disturbance regime, e.g. missing or too strong floods, can threaten the characteristic biodiversity of the habitat, change abundances of many species, and support ruderal and alien species, especially on the rivers that are no longer in natural conditions (Müller 1995; Planty-Tabacchi et al. 1996; Ward and Tockner 2001; Richardson et al. 2007; Gostner et al. 2017).

The succession of gravel bar vegetation can be influenced by flood frequency and magnitude, sediment type, nutrient content in water and sediments, site elevation above the normal water level and ground water table, surface temperature and moisture, light availability, and microhabitat heterogeneity. Unvegetated gravel bars in early successional stages provide an opportunity for the establishment of many species in an environment free of competition from established plants (Tockner et al. 2000, 2006; Richards et al. 2002; Gilvear et al. 2008; Corenblit et al. 2009). Having an ecotonal position between the aquatic and terrestrial environments and providing a fine-scale habitat mosaic, river gravel bars can host species with different biological traits and ecological requirements (Tockner et al. 2006; Gilvear et al. 2008; Uziębło and Barć 2015). Moreover, local effects of environmental factors depend on the site position along the stream length, which is coupled with the altitudinal gradient (Karrenberg et al. 2003; Prach et al. 2014). Also, the species pool of potential colonizers and other biogeographical factors can be influenced by the site location along that gradient (Prach and Řehounková 2006; Prach et al. 2014).

Considerable dynamics of gravel bar habitats result in high species richness and habitat diversity (Tockner et al. 2006). Diverse habitat mosaics develop especially in the early and mid-successional stages, i.e. before the formation of a closed canopy and increase in competition from established dominant species (Walker and del Moral 2003). On gravel bars, this pattern was shown, for example, by Corenblit et al. (2009) or Prach et al. (2014). The dynamics of successional changes can be assessed by calculating the species turnover (Prach 1990; Prach et al. 1993; Anderson 2007), which is usually measured as the dissimilarity between repeated vegetation records taken in the same plots (Prach et al. 1993). The rate of succession is hypothesized to be higher in moderately wet and nutrient-rich conditions than at dry and nutrient-poor sites (Grime 1979; Prach et al. 1993). Comparisons of several successional series (Prach et al. 1993; Anderson 2007) showed that rates of community change often decrease with successional age. The fast-growing and short-lived early-successional species are replaced by those with slower growth rates and better adaptation to competition for light (higher stature and denser canopy), which occupy the sites for a longer period than early-successional species (Gurnell et al. 2005; Corenblit et al. 2009). Besides these changes in species traits, the rate of succession can be influenced by other factors such as dispersal limitation, disturbance regime and environmental heterogeneity (Grime 1979; Prach et al. 1993; Török et al. 2008). Moreover, the type and severity of the initial disturbance influences the subsequent succession. It is hypothesized that it is more difficult for species to establish after severe infrequent disturbances than at sites with less severe and frequent disturbances (Huston 1979; Turner et al. 1998). Turner et al. (1998) suggest that in a case of a severe disturbance affecting a large area, the densities of propagules of suitable species could be low, community composition in the initial stage less predictable, and the succession rate and recovery of community structure slower than after smaller disturbances. Although the patterns of changing species turnover rate during succession have been described from various habitats and after different disturbance events, to our knowledge, they have never been described for gravel bars of temperate montane and submontane streams immediately after extreme floods.

Vegetation succession on gravel bars has been already studied by Siegrist (1913) in the Swiss Alps and Jeník (1955) or Zaliberová (1982) in the Slovak Carpathians. The Italian river Tagliamento has become the main model site for recent studies in Europe (e.g. Edwards et al. 1999; Gurnell et al. 2001; Karrenberg et al. 2003; Tockner et al. 2003). Noteworthy are also studies of environmental controls of vegetation diversity and dynamics on gravel bars in Scotland (Gilvear et al. 2000, 2008). In the Czech Republic, several studies of succession on river gravel deposits have been performed in the Bohemian Massif (e.g. Kopecký 1957; Loučková 2011). However, most of these successional studies were based on the space-for-time substitution approach (Pickett 1989) rather than on sampling in permanent plots. Almost all of these studies were focused on alluvia of larger rivers which was also the case of the studies from the submontane reaches of the river Bečva in the Czech part of the Western Carpathians. The 1997 floods transformed the artificially regulated Bečva channel and enabled the redevelopment of its natural features including gravel bars. This process was studied mostly in a short river section, in the context of the surrounding riverine landscape (Lacina 2007; Klečka 2004; Babej 2012; Grohmanová 2012). Of those studies, Klečka (2004) and Grohmanová (2012) published results from three- and ten-year (though incomplete) successional series made on channel transects. There is also a six-year successional study made on gravel bars of several streams in the Polish Carpathians (Uziębło 2011), focusing on dynamics of vegetation containing *Petasites kablikianus*, one of the specialist species of young gravel bars.

A new succession on river gravel bars was triggered by extreme floods that occurred in the eastern Czech Republic in 2010. Two consecutive floods in the spring and early summer deposited a huge amount of new sediments, modified stream channels, and destroyed some plant communities on the Carpathian stream floodplains. We used this opportunity to study succession on river gravel bars of small streams using permanent plots distributed across a relatively long altitudinal gradient, as opposed to previous studies mainly based on space-for-time substitution focused on shorter stream sections.

The aims of this study are: (1) to describe patterns of species richness, species composition and succession rate during early succession on river gravel bars with no direct human interventions, and (2) to identify which factors influence this succession.

Material and methods

Study area

Geography and geology

Vegetation succession was studied on river gravel bars of four small streams in the eastern Czech Republic (Moravian-Silesian region, Frýdek-Místek district; 49°27′43″–49°48′07″ N, 18°20′41″–18°37′20″ E): Čeladenka, Mohelnice, Ropičanka and Stonávka. These streams are located in the Moravskoslezské Beskydy Mts (Moravian-Silesian Beskids) and their foothills (Fig. 1), which are a part of the flysch zone of the Outer Western Carpathians (Pánek and Lenart 2016). All the streams have their springs in these mountains.

The altitude of the study sites varied within a range of 241–669 m a.s.l. (Table 1). The lithological composition of the stream bed sediments is derived from the Cretaceous-Oligocene rhythmically alternating flysch layers. Flysch is a geologically labile and easily erodible bedrock. In the study area it is composed of sandstone, claystone and siltstone, rarely of marl, conglomerate and limestone (Bubík et al. 2004). The stream beds are predominantly formed of sandstone whereas claystone is soft and less resistant, and therefore transported only at short distances from the source in the form of stones or gravel (Galia and Hradecký 2012).

Climate and hydrology

The mean annual temperature of the studied stream sections ranges between 5.3 and 8.5°C and that in their spring areas between 4.5 and 5.7°C (Tolasz 2007). Precipitation in the study area peaks in summer, especially due to storm events (Brázdil and Kirchner 2007). The total annual precipitation is between 786 and 1,325 mm in the stream sections under study and between 1,190 and 1,313 mm in their spring areas (Tolasz 2007).

The studied streams are characterized by high discharge variation (Table 1). Most floods occur in spring after fast snow melting and at the beginning of summer after intense rainfall events (Šilhán 2012). Highly intense rainfall occurred at the end of May and the beginning of June 2010 (Table 1). The first rainfall event resulted in floods on the study streams, which reached a magnitude of 50-year flood on Mohelnice and Stonávka (Štercl et al. 2011). The studied stream

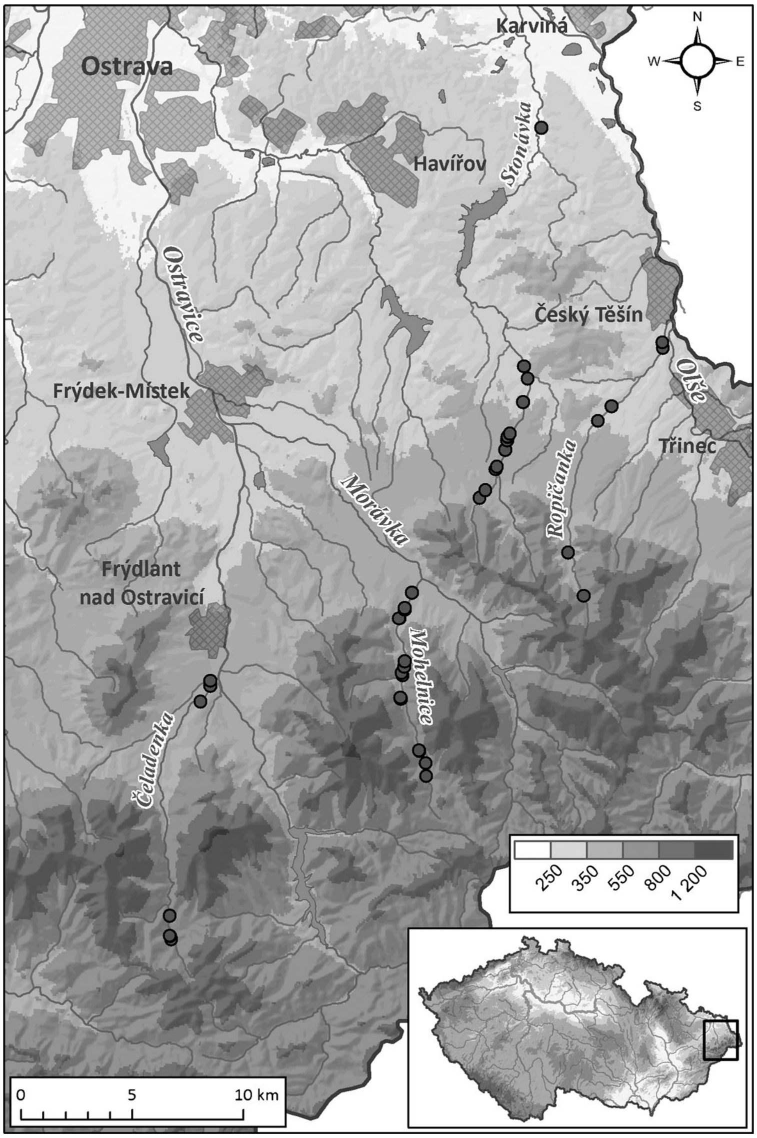

Fig. 1 Location of 43 study plots along the Čeladenka, Mohelnice, Ropičanka and Stonávka streams in the eastern Czech Republic

channels were reshaped, some gravel bars covered by new sediments and others were newly created, and gravel bar vegetation was damaged or removed.

Current vegetation cover

The highest parts of the basins of the studied streams are covered by forest (Table 1). Forest vegetation prevails along the Mohelnice and Čeladenka, while larger parts of the Stonávka and Ropičanka basins are used as arable land and hay meadows. Spruce plantations dominate the forested area, but natural beech forests are also common. Alluvial broadleaf forests of the *Alnion incanae* alliance are frequent on the wider piedmont floodplains. Small patches of *Alnus incana* vegetation growing in a mixture with *Acer pseudoplatanus* occur rarely along the upper streams, especially on the Mohelnice. Herbaceous vegetation lining the streams is often dominated by *Petasites hybridus* or *P. kablikianus*. Nowadays, well-preserved gravel bar habitats are found at a few sites only, especially along the Mohelnice and Čeladenka, where remnants of *Salix elaeagnos* and *S. purpurea* scrub (alliance *Salicion elaeagno-daphnoidis*) are preserved. Herbaceous vegetation is represented mainly by riverine reed stands with *Phalaris arundinacea*, *Mentha longifolia* and *Lythrum*

Table 1 Characteristics of the under study streams (Štercl et al. 2011, www.pod.cz/plan-oblasti-povodi-Odry/inf_listy/inf_listy_vu_pov.html)

	Čeladenka	Mohelnice	Ropičanka	Stonávka
Stream length [km]	17.3	12.9	16.4	33.7
Length of the studied stream section [km]	15	10	15	27
Stream basin area [km^2]	43	41	36	131
Forest cover within the stream basin [%]	85	83	36	25
Altitudinal range of the studied stream section [m a.s.l.]	375–669	435–632	289–552	241–448
Mean altitude of the studied stream section [m a.s.l.]	530	530	366	363
Altitude of the spring [m a.s.l.]	850	720	850	750
Average annual discharge near the mouth [$m^3 \cdot s^{-1}$]	1.08	1.09	0.62	1.7 (0.96 above the dam)
Culmination flow of the 2010 floods [$m^3 \cdot s^{-1}$]	39.1	62.0	20.3	92.3
Recurrence interval of floods of similar magnitude as the 2010 floods [years]	5–10	20–50	10–20	20–50

salicaria. On more sandy and muddy gravel bars of the piedmont, especially on the Ropičanka and Stonávka streams, shrubby vegetation of *Salix triandra* and *S. euxina* (association *Salicion triandrae*) and herbaceous vegetation with *Persicaria mitis*, *P. hydropiper*, *Bidens frondosa* and *Chenopodium polyspermum* (alliance *Bidention tripartitae*) is developed (Chytrý 2009, 2011, 2013; Šigutová 2009; Klečková 2013).

Data sampling

The first sampling was done two months after the 2010 floods in permanent plots that were repeatedly sampled in the next three years, during which no other significant flood occurred (Fig. 2). The size of each permanent plot was 5 × 3 m. Due to the instability of the gravel bars, no plot markings could be used. Therefore, the plots were located using GPS (Garmin 60CSx) and detailed notes on their position were taken. In each plot, we recorded both vascular plants and bryophytes, and visually estimated the cover of each species using the 9-degree Braun-Blanquet cover-abundance scale (Westhoff and van der Maarel 1978). Some plants, especially juvenile individuals, could be identified only to the genus level. Lichens, represented mainly by crustose species growing on stones, were not recorded. We tried to establish approximately the same number of plots on each of the four streams and to place them regularly along the entire stream length, from the spring to the mouth. Unfortunately, many plots were destroyed, especially by gravel extraction during channel regulation works. In the end, we were able to use 43 plots that contained records from all four years, i.e. 172 records in total, including 16 records with no species in the first year (Tables 2 and 3).

For each plot, we measured or estimated values of environmental variables (Table 2). The elevation of each plot above the present stream water level was roughly measured with a tape measure during the first sampling period. The area (m^2) of each gravel bar was also roughly measured in the field. Estimation of the bar age was based on aerial photographs from 2003, 2006 and 2009 (www.mapy.cz). Older bars were probably created by the extreme floods in 1997. Additional information on the gravel bar age was obtained by counting the tree rings of willow stems at 0.5–1 m above the ground surface.

For each vascular plant species, the following characteristics were used:

- Type of reproduction according to Frank and Klotz (1990), modified categories: s – only by seed/spore, sv – by seed and vegetatively (only one of the recorded species reproduced purely vegetatively, therefore this type of reproduction was disregarded in the analyses);
- Ellenberg indicator values (EIV) – for light, temperature, moisture, soil reaction and nutrients (Ellenberg et al. 1991);
- Habitat affinity – species occurrence in vegetation types (forests, scrub, grasslands, wetlands, and ruderal and weed vegetation) based mainly on their diagnostic status for the vegetation units as given in the national vegetation classification (Chytrý 2007, 2009, 2011, 2013).

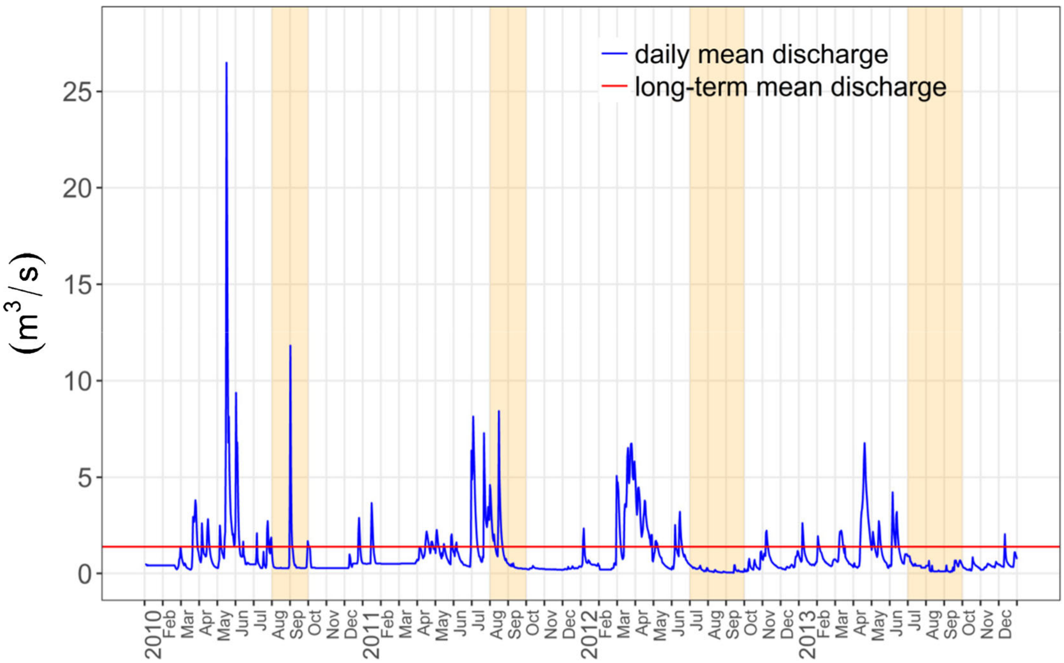

Fig. 2 Daily and long-term mean discharge on the Čeladenka stream. Flood events occurred at the end of May 2010. Sampling periods are indicated by shading. Discharge data were provided by the Odra River Basin State Enterprise

Data analysis

Taxon concepts and nomenclature of vascular plants and bryophytes were unified according to Danihelka et al. (2012) and Kučera et al. (2012), respectively. Some critical taxa were merged into groups: *Centaurea jacea* agg. (*C. jacea* + *C. oxylepis*) and *Myosotis palustris* agg. (*M. nemorosa* + *M. palustris*). For ordination analysis and dissimilarity calculations, the records of juvenile individuals determined in the first year only to the genus level were merged with the species of the same genus recorded in the same plots in the next years. Alternatively, all of these records were merged to the genus level in cases of uncertainty.

We stored our data in the database software Turboveg for Windows v. 2 (Hennekens and Schaminée 2001) and

Table 2 Variables measured in this study. Numbers of plots within categories (N) are indicated for categorical variables.

Variable	Type of variable	Minimum	Maximum	Mean	Categories
Stream identity	Categorical	–	–	–	Čeladenka (*N* = 9), Mohelnice (*N* = 15), Ropičanka (*N* = 6), Stonávka (*N* = 13)
Year of sampling	Categorical	–	–	–	2011, 2012, 2013, 2014
Altitude [m a.s.l.]	Quantitative	241	669	465	–
Shading by the nearby forest canopy or topographic features	Categorical	–	–	–	Sunny (*N* = 12), partly shady (*N* = 24), shady (*N* = 7)
Substrate structure	Categorical	–	–	–	Stone, i.e. > 20 cm in diameter (*N* = 21), gravel, i.e. < 20 cm (*N* = 22)
Elevation above water level [m]	Quantitative	0.1	3	0.5	–
Position in the channel	Categorical	–	–	–	Mid-channel bar (*N* = 4), side bar (*N* = 39)
Gravel bar area [m^2]	Quantitative	21	4,000	234	–
Age of the gravel bar	Categorical	–	–	–	Created by the 2010 floods (*N* = 24), older than 10 years (*N* = 19)

Table 3 Cumulative numbers of taxa recorded on each studied stream in individual years.

	Čeladenka	Mohelnice	Ropičanka	Stonávka	Total
No. of plots	9 (4 without vegetation in the first year, 1 in the second)	15 (2 without vegetation in the first year)	6 (3 without vegetation in the first year)	13 (6 without vegetation in the first year)	43
No. of taxa – vascular plants					
2010	57	62	42	55	116
2011	111	116	74	63	192
2012	101	139	101	109	210
2013	111	154	94	97	212
No. of taxa – bryophytes					
2010	5	10	4	4	14
2011	22	20	12	16	41
2012	13	28	10	14	41
2013	27	38	15	22	57

deposited them in the Czech National Phytosociological Database (Chytrý and Rafajová 2003). We prepared the dataset for analyses using JUICE (Tichý 2002), in which we also calculated Pielou's evenness index (Pielou 1975).

We used two ordination techniques to explore compositional changes and vegetation-environment relationships during succession – Detrended Correspondence Analysis (DCA) and Canonical Correspondence Analysis (CCA). DCA was computed using R software (R Core Team 2016) and its 'vegan' library (Oksanen et al. 2017). CCA analysis was performed using Canoco for Windows 5 (ter Braak and Šmilauer 2012). The length of the first DCA axis of 2.98 SD units suggested that both the ordination methods assuming linear and those assuming unimodal response of species to the environment would work well in our case (Šmilauer and Lepš 2014), and we opted for unimodal methods. In both DCA and CCA, rare species were downweighted and percentage species covers were log transformed. Environmental and vegetation variables were displayed passively on the DCA diagram. Hill's scaling focused on inter-specific distances was chosen in the CCA model. To answer which variables significantly influenced temporal vegetation change, we calculated marginal, pure and conditional effects of the interaction between the year of sampling and each of the environmental variables listed in Table 2. Effect sizes were then expressed as percentages of explained variation. Effect significances were tested using a Monte-Carlo permutation test (999 runs) in a hierarchical design based on so-called whole-plots containing split-plots at a lower hierarchical level. Each permanent plot was defined as a whole-plot and its four repeated samples as split-plots. The permutation was applied to the split-plot level. The Holm correction was applied to the *P*-values (ter Braak and Šmilauer 2012). First, independent marginal effect of each variable*year interaction was calculated. Next, pure effect of each variable*year interaction was calculated in a model in which all other variables and variable*year interactions were used as covariables (i.e. their effects were partialled out). Finally, conditional effects within the forward selection procedure were calculated, showing the amount of variation that is explained by a particular variable*year interaction if added to a model already containing other variables or variable*year interactions (Šmilauer and Lepš 2014).

Mean percentage cover of species with affinities to different vegetation types or with different reproduction types was calculated for each plot record in JUICE (Tichý 2002). Differences among years were then tested using the Kruskal–Wallis test in Statistica 13 (StatSoft Inc 2001).

The species turnover was used as a measure of the succession rate. It was computed as the mean Bray-Curtis index of dissimilarity in species composition within the same plots between two consecutive years using JUICE (Tichý 2002). To allow inclusion of 16 plots that were empty in the first (or second, in one case) year of the study, one species, occurring in the respective previously empty plot in the following year, was added to that plot for the first year. The Bray-Curtis index ranges from 0 to 1, where 0 indicates that two plot records have the same species composition and 1 indicates that they do not share any species. We used the succession rate as a dependent variable and modelled it using selected predictors (substrate structure, position in the channel, gravel bar age, shading and stream identity). The significance of differences between groups was tested using the non-parametric Mann-Whitney or Kruskal-Wallis test in Statistica 13 (StatSoft Inc 2001). The former test was also used to compare the number of species belonging to different categories, vegetation cover, maximum height of the herb layer and evenness index between the substrate categories.

Results

In all 172 plot records, a total of 384 taxa were found (330 without those determined only at the genus level), including 302 (259) vascular plants and 82 (71) bryophytes (Table 3). The most frequent species for each of the four years are shown in the Electronic supplementary material, Table S1. In the first year (or in the first two years in some plots), vegetation was in an initial successional stage with low number of species and low cover; the poorest plots were empty ($N = 16$) and the richest one contained 34 species. The highest number of species (72) was observed in a plot on the Čeladenka stream during the second year (2011); this plot had 33 species in 2010, but only 16 species in 2012 and 22 in 2013. The poorest plots of the last years were those in which some species attained strong dominance, with a minimum of nine species. Otherwise the number of species varied greatly among plots and years.

Vegetation composition and development

DCA of the four-year successional series identified two major gradients along the first and second ordination axes (Fig. 3). The first axis correlates best with altitude and related substrate structure and the second with successional age. The number of species and community evenness increased, while total cover and the number of nutrient-demanding and thermophilous species decreased with altitude. The sites located at higher altitudes were characterized by mesophilous species such as *Stellaria alsine* and *Impatiens noli-tangere*. A common bryophyte was *Dichodontium pellucidum*, a cushion moss typical of frequently submerged or moist gravel and stones. Broad-leaved nitrophytes such as *Urtica dioica* and *Rumex obtusifolius* appeared on the opposite end of the altitudinal gradient. At lower altitudes and on more gravelly substrate, clonal perennial species represented by competitive tall grass *Phalaris arundinacea* and alien species such as *Impatiens glandulifera* were both more frequent. The second most important gradient reflected successional age, but the response of species composition to this gradient was weaker than its response to altitude. With increasing successional age, the proportion of light-demanding (e.g. *Myosoton aquaticum*, *Stellaria media*) and moisture-demanding species (e.g. *Ranunculus repens*, *Veronica beccabunga*) decreased, while juveniles of *Fraxinus excelsior*, more typical of older successional stages, increased.

Ruderal and weed species occurred more frequently in the second, third and fourth year (Fig. 4a, Table S2 in the Electronic supplementary material) than in the first year, in which all the types of gravel bars had very similar species composition. The increase in ruderal and weed species was faster than in the other species groups. The second most frequent group, through all the years, were species of scrub and forest vegetation, while wetland and grassland species were less frequent, although their numbers were also increasing with time. Species reproducing both vegetatively and generatively were more successful than those reproducing only generatively (Fig. 4b). However, this pattern was less obvious during the first two years when we found only weak ($P < 0.05$) or non-significant difference between these two groups. The species with both vegetative and generative reproduction outcompeted most other species in later years. Despite the general trend of increasing species numbers over time (Table 3), sites with increasing dominance of these species were most species-poor in the third and fourth years.

Environmental factors affecting the gravel bar succession

All explanatory variables considered in CCA explained 6.2% of the total inertia. Tests of the interactions between environmental variables and successional time indicated that succession ran differently at different altitudes, on different streams, and on different types of gravel bar substrate (Table 4). If the first two interactions were included in the model, the third interaction did not explain any additional variation in species composition (see conditional effects in Table 4).

Species turnover expressed by the Bray-Curtis dissimilarity between the pairs of consecutive years (Fig. 5) was fastest between the first two years of succession and

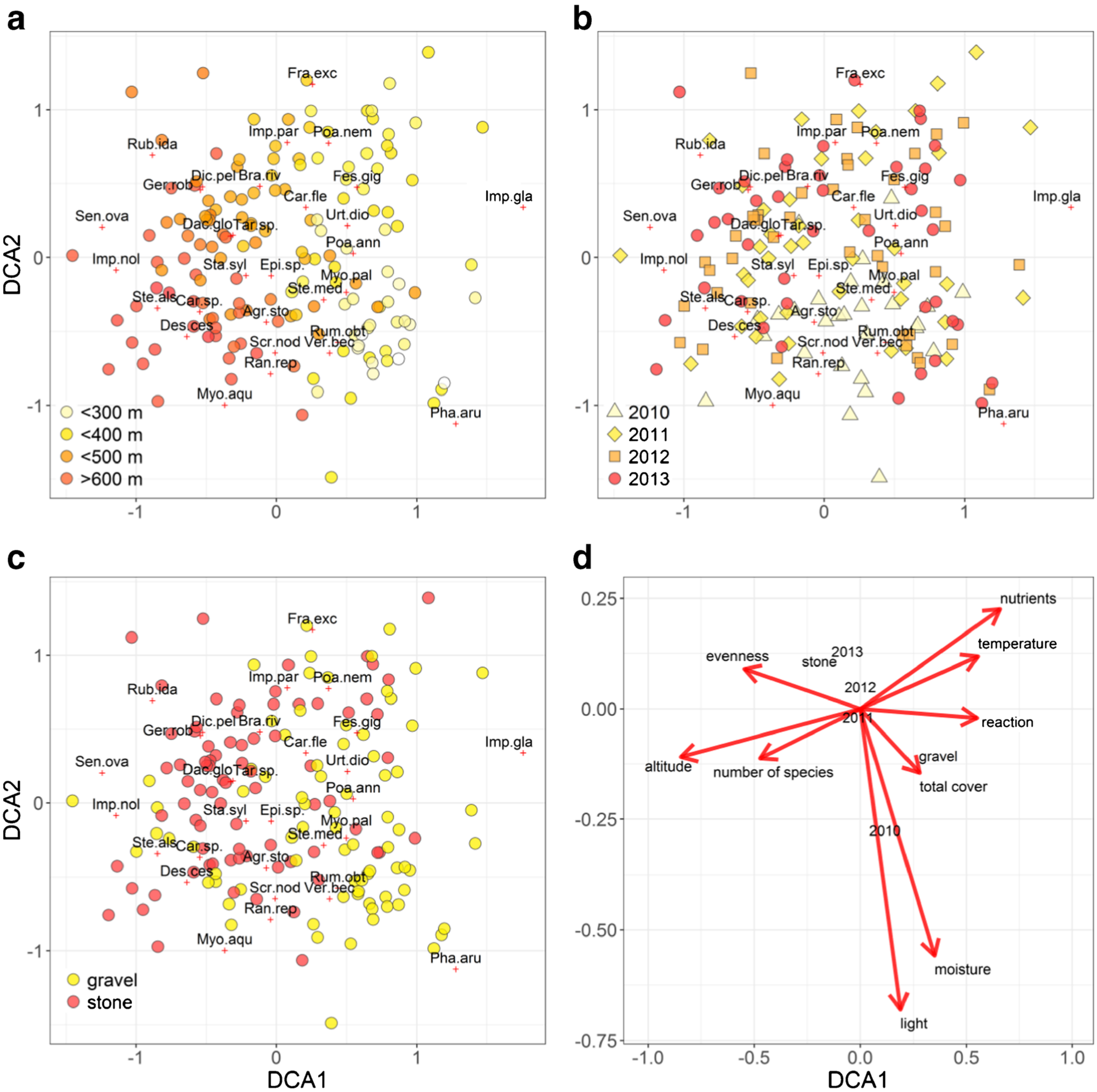

Fig. 3 DCA ordination. **a** – Species and plot records in the space of the first two ordination axes with plots classified by altitude. **b** – The same ordination with plots classified by year of sampling, **c** – substrate structure and **d** – with all passively projected variables (year of sampling, Pielou's evenness index, altitude, number of species, total cover and Ellenberg indicator values for light, temperature, moisture, soil reaction and nutrients). The first axis explained 6.1% and the second 4.4% of the total variation in species composition (the first four cumulatively explained 15.7%). Only species with the highest weight in the ordination are shown: Agr.sto – *Agrostis stolonifera*, Bra.riv – *Brachythecium rivulare*, Car.fle – *Cardamine flexuosa,* Car.sp. – *Carex* sp., Des.ces – *Deschampsia cespitosa*, Dich.pel – *Dichodontium pellucidum,* Epi.sp. – *Epilobium* sp., Fra.exc – *Fraxinus excelsior* juv., Ger.rob – *Geranium robertianum*, Imp.gla – *Impatiens glandulifera*, Imp.nol – *I. noli-tangere*, Imp.par – *I. parviflora*, Myo.aqu – *Myosoton aquaticum*, Myo.pal – *Myosotis palustris* agg., Pha.aru – *Phalaris arundinacea*, Poa.ann – *Poa annua*, Poa.nem – *P. nemoralis,* Ran.rep – *Ranunculus repens*, Rub.ida – *Rubus idaeus*, Rum.obt – *Rumex obtusifolius*, Sco.nod – *Scrophularia nodosa*, Sen.ova – *Senecio ovatus*, Ste.als – *Stellaria alsine*, Ste.med – *S. media*, Tar.sp. – *Taraxacum* sp., Urt.dio – *Urtica dioica* and Ver.bec – *Veronica beccabunga*

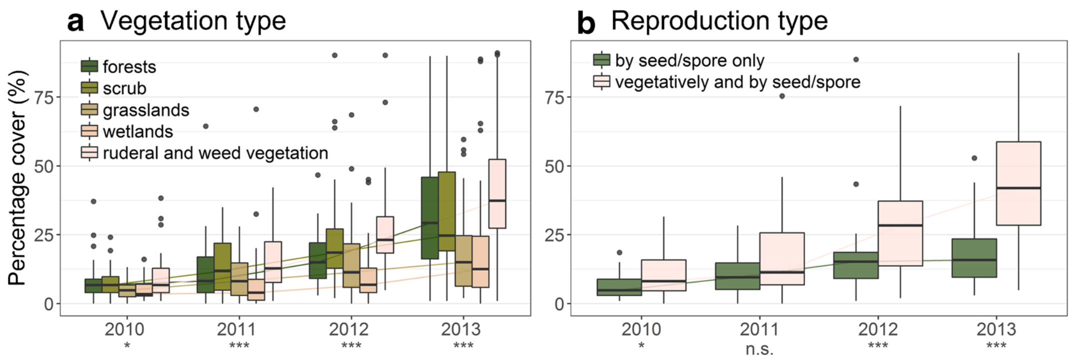

Fig. 4 Changes in species composition of gravel bars expressed by percentage covers of the groups of species assigned to different **a** – vegetation types and **b** – reproduction types. The black horizontal lines within the boxes represent medians (connected with lines) and the black points represent outliers. Significant differences between groups within particular years based on Kruskal-Wallis test (Table S2 in the Electronic supplementary material) are indicated below the x-axis (n.s. – non-significant; * – $P < 0.05$; ** – $P < 0.01$; *** – $P < 0.001$)

gradually slowed down. Species turnover was compared between plots with different substrate structure, position in the channel, gravel bar age, shading and located on different streams (Table S3 in the Electronic supplementary material). It was shown that between the 2nd and 4th year, the succession rate was significantly faster on gravelly bars than on stony bars (the latter were prevailing at higher altitudes). Succession was also faster in partly shady places between the 2nd and 3rd year.

Effect of substrate type on changes in vegetation structure

Species richness and cover of both vascular plants and bryophytes were increasing more or less constantly over the four years of succession whereas evenness was decreasing (Fig. 6). These trends were associated with increasing biomass, which was caused by an increase in both the herb layer height and species covers. There were significant differences in the number and cover of bryophytes, and in evenness, between the stony and gravelly plots (Table S4 in the Electronic supplementary material).

No significant relations of the number, cover and maximum height of vascular plants to substrate types were found. Bryophyte richness and cover differed on both substrates strikingly in 2011–2013, with more species and greater covers on stony substrates. Vegetation of gravelly plots had lower evenness in the last year of the study. Over the whole study period except the first year, stony plots had more species of bryophytes and a greater cover of bryophytes than gravelly plots.

Discussion

General trends and direction of the early succession on river gravel bars

The flood in the Czech part of the Western Carpathians in May 2010 was a large infrequent disturbance which led to the rejuvenation of riparian vegetation, channel transformation, creation of new gravel bars and reshaping of old ones. Succession on river gravel bars belongs to fast vegetation changes (Jeník 1955; Prach 1994). The average time needed to reach the final successional stage, alluvial forest, is estimated at about 150 years in Central Europe (Prach et al. 2016). However, the succession trajectory on gravel bars may not be straightforward and it is questionable which direction of succession can be projected based on the data from the first four years of succession. High discharge variation of mountain rivers (Montgomery and Buffington 1998; Tockner et al. 2000; Šilhán 2012; Škarpich et al. 2013) often causes disruption of vegetation development. Flow pulses may have contrasting effects on different parts of gravel bars (Tockner et al. 2000), resulting in a mosaic of different successional stages even on a single gravel bar (Walker and del Moral 2003). Apart from the May 2010 flood, there was no other big flood during the study period, but smaller discharge variation obviously did appear.

During the first years of the post-flood succession, species richness increased quickly until the spread of scrub and competitive herbaceous species. We observed very high species richness for some plots in this stage, with a maximum of 72 vascular plant species in a plot of

Table 4 Variation explained by interactions of particular environmental variables and the year of sampling in CCA. Interactions are sorted by their decreasing marginal effects. The interactions that were significant ($P < 0.05$) after the Holm correction (H) are in bold. Conditional effects refer to the forward selection model whereas marginal and pure effects refer to models for a single interaction (and for the pure effect with all the other interactions and variables used as covariables).

	Marginal effects			Pure effects				Conditional effects			
	F	*P* (H)	%	*F*	*P*	*P* (H)	%	*F*	*P*	*P* (H)	%
Altitude*year	**1.9**	**0.001**	**1.3**	**1.9**	**0.001**	**0.008**	**1.3**	**1.9**	**0.001**	**0.008**	**1.3**
Stream*year	**1.4**	**0.002**	**1**	**1.4**	**0.003**	**0.021**	**1**	**1.4**	**0.004**	**0.028**	**1**
Substrate structure*year	**1.5**	**0.003**	**1**	**1.5**	**0.004**	**0.024**	**1**	1	0.582	1	0.6
Shading*year	1.1	0.307	0.8	1.1	0.276	1	0.8	1.1	0.297	1	0.7
Elevation above water level*year	1.1	0.414	0.7	1.1	0.42	1	0.7	1.1	0.35	1	0.7
Position in channel*year	1	0.447	0.7	1	0.493	1	0.7	0.9	0.8	1	0.6
Gravel bar size*year	0.9	0.685	0.6	0.9	0.699	1	0.6	0.9	0.823	1	0.6
Age of gravel bar*year	0.9	0.797	0.6	0.9	0.803	1	0.6	0.9	0.85	1	0.6

15 m^2 in the second year, which is close to the highest values of species richness recorded in Central European vegetation, disregarding the world-record semi-dry basiphilous grasslands of the White Carpathians and the Slovak Paradise (Chytrý et al. 2015). However, species richness in this plot quickly decreased in the next year. These initial stages are quite unstable and can change dramatically within a few years. The succession rate decreases and vegetation becomes more stable with the increase in herb-layer cover. In ideal conditions of well-preserved natural gravel-bed rivers, the final vegetation stage of dense alluvial forest (alliance *Alnion incanae*) is rarely reached on gravel bars, because they are influenced by recurrent disturbances (e.g. Pettit and Froend 2001; Loučková 2011). Woody vegetation therefore develops as scrub, mostly of narrow-leaved willows that are resistant to strong and frequent floods (Karrenberg et al. 2003; Ellenberg and Leuschner 2010; Loučková 2011) and start developing even during early successional stages.

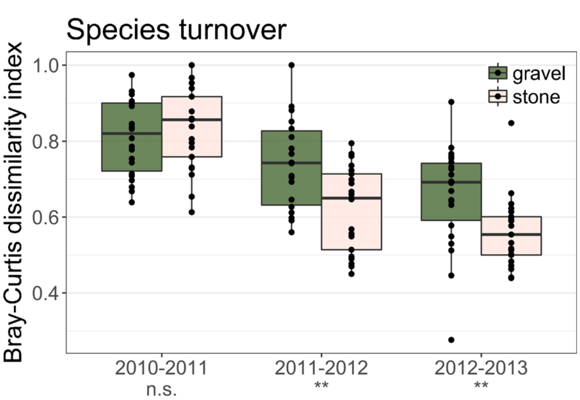

Fig. 5 Species turnover on different substrate types. Horizontal lines within the boxes indicate medians and black points indicate individual plots. Significances indicated below the x-axis refer to differences between the two substrate types within individual years (Mann-Whitney test; see Table S3 in the Electronic supplementary material for detailed results of statistical tests; n.s. – non-significant; ** – $P < 0.01$)

A succession leading to willow scrub was observed on the river Bečva, another Carpathian stream in the Czech Republic, within less than ten years since a large disturbance (Klečka 2004; Lacina 2007; Grohmanová 2012). However, it was also observed in these studies that the dense herbaceous vegetation dominated by the tall grass *Phalaris arundinacea* inhibited the succession of woody vegetation. A similar trend was observed in most of our permanent plots where in the later successional stage vegetation became denser and dominated by *Phalaris arundinacea* or, less frequently, by *Petasites hybridus* and *P. kablikianus*, and usually contained a high proportion of ruderal species, especially *Urtica dioica* (alliances *Phalaridion arundinaceae*, *Petasition hybridi*). *Phalaris arundinacea* prefers sandy or clayey substrate with high nutrient content, which usually occurs on gravel bars that contain finer soil fraction, especially along middle river courses at lower altitudes (Kopecký 1961; 1957). On nutrient-poorer alluvial deposits at higher altitudes of the Western Carpathians, *Phalaris* tends to be replaced by a competitively weaker gravel-bar specialist tall grass, *Calamagrostis pseudophragmites* (Jeník 1955; Kopecký 1961, 1969; Kalníková and Eremiášová 2013). This species, included in the national Red List in the Czech Republic (Grulich 2012), is known from a

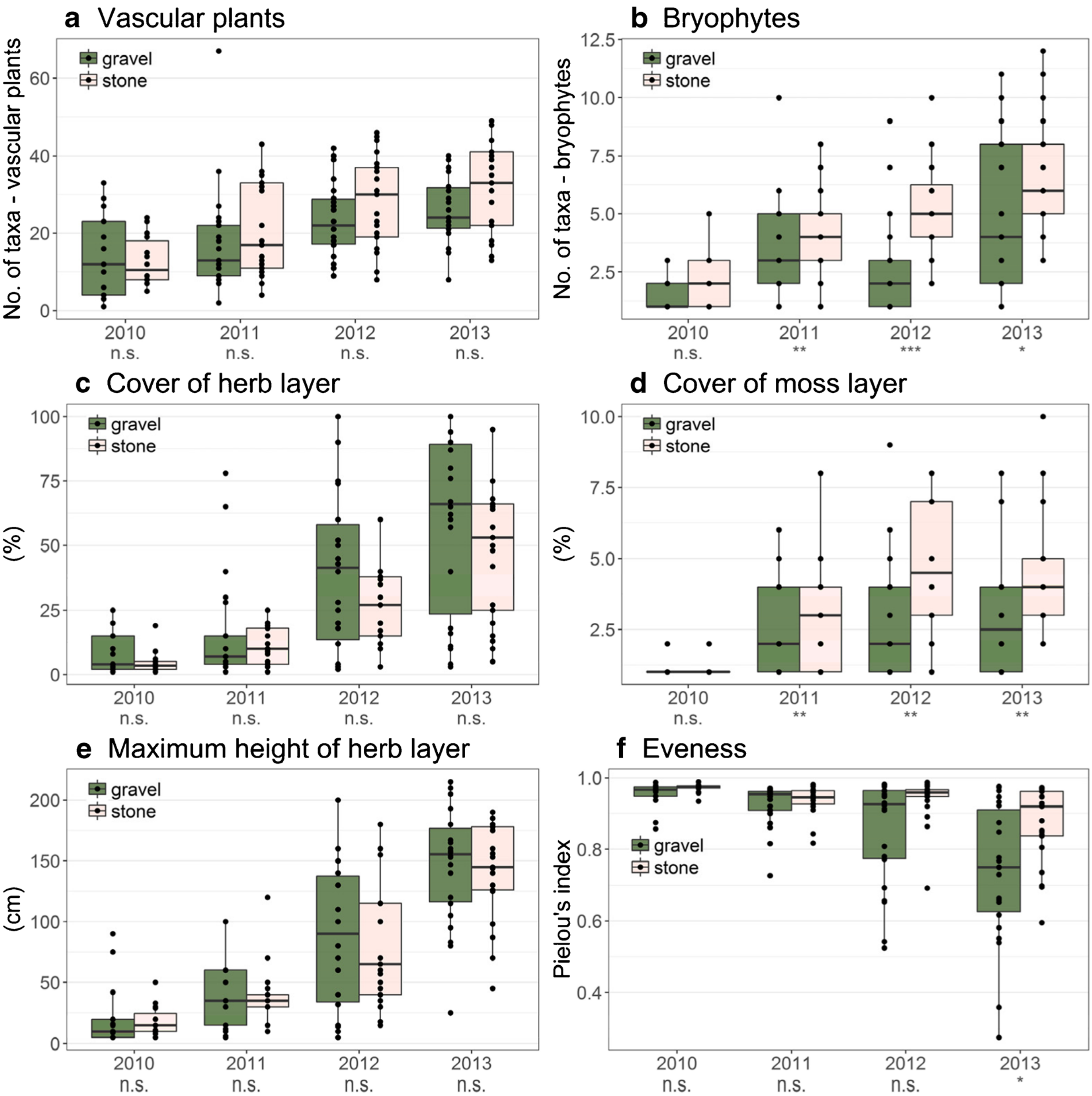

Fig. 6 Comparisons of vegetation changes during succession on gravelly and stony accumulations. Horizontal lines within the boxes indicate medians and black points indicate individual plots. Significances of the difference between the two substrate types within individual years are indicated below the x-axis (Mann-Whitney test; see Table Sx4 in the Electronic supplementary material for details of statistical tests; n.s. – non-significant; * – $P < 0.05$; ** – $P < 0.01$; *** – $P < 0.001$)

few rivers in the study area (Kalníková and Eremiášová 2013; Skokanová et al. 2015), but it was not observed on any of the four streams under study. Interestingly, this species occurs on gravel bars of the river Ostravice (not studied here) just a half kilometre from the study plots on the Čeladenka stream, its tributary that was sampled in this study (Kalníková and Eremiášová 2013). A later successional stage on gravel bars of Carpathian rivers is supposed to be a specialized willow scrub of the alliance *Salicion elaeagno-daphnoidis*, which is nowadays also very rare there (Chytrý 2013; Klečková 2013; Sochor et al. 2013). The observed juveniles of Salix sp div. (mostly *Salix euxina*) indicate that succession directs towards lowland willow vegetation (alliance *Salicion triandrae*), which is considered a natural successional stage replacing the *Phalaridion arundinaceae* vegetation (Kopecký 1961). This indicates a change in the stream dynamics, especially in the water flow regime, sediment regime and nutrient dynamics, which is no longer supporting the gravel bar habitats, like at other sites worldwide (Müller 1995; Müller and Scharm 2001; Tockner et al. 2006; Gurnell et al. 2009; Škarpich et al. 2013; Janssen et al. 2016; Gostner et al. 2017).

During the succession on the gravel bars under study, the most common species were those capable of reproducing both vegetatively and by seeds, for example the above mentioned *Phalaris arundinacea*, a frequent dominant in the later years of the study period. A combination of vegetative and generative reproduction in the same species seems to be a good adaptation to the successional habitats like gravel bars, as it both supports colonization of new sites and enhances species potential to become dominant (Prach and Pyšek 1994). The differences in representation of species with combined strategies and species dispersed only by seeds were small or non-significant in the first two years.

Some of the study plots were placed on the gravel bars that probably survived the floods whereas others were placed on newly created gravel bars. It is possible that on some old bars a few species survived, resprouted under the accumulated sediment, and perhaps also the regeneration from seed bank played a more prominent role there. By contrast, on the new gravel bars more pioneer species reproducing by seeds could occur casually in the first year and then be replaced by more specialized species (e.g. Corenblit et al. 2009). However, the history of particular gravel bars was probably not very important for vegetation succession in our case, because we found no significant effect of gravel bar age on succession. Moreover, we do not know the proportion of species established from the seed bank and those that arrived from the surroundings.

Factors influencing the succession and its speed

In general, succession speed and its direction are affected by local environmental conditions. The most important variables emphasized in various studies of gravel-bar vegetation include altitude (Šigutová 2009; Prach et al. 2014), fluctuation of river flow, elevation above the water level (Karrenberg et al. 2003; Gilvear et al. 2008; Šigutová 2009; Prach et al. 2014), substrate structure (Richards et al. 2002; Gilvear et al. 2008; Corenblit et al. 2009; Šigutová 2009; Prach et al. 2014; Bätz et al. 2015; Babej et al. 2016) and human impact on the local environment (Müller 1995; Tockner et al. 2008). Our analyses indicated that major changes and turnover in species composition were related to altitudinal variation, substrate structure and stream identity, i.e. there were specific patterns on different streams.

Most of these factors are correlated with altitude (Vannote et al. 1980). Low-altitude areas are often used for agriculture and more influenced by humans, which often results in loss of biodiversity and ecological functioning of the gravel bar habitats (Müller 1995; Muhar et al. 2007; Tockner et al. 2008). This is probably why stream identity was an important factor in our study. Major parts of the Čeladenka and Mohelnice streams flow through a forested mountain area whereas large parts of the Stonávka and Ropičanka watersheds are agricultural landscapes.

Further, at lower river courses, the current is usually slower, which affects sediment erosion and deposition (Vannote et al. 1980). Thus, river bar sediments on these sites typically consist of smaller particles (gravel) and include fine sediment fraction, which is richer in nutrients and more fertile (Richards et al. 2002; Babej 2012; Grohmanová 2012). By contrast, coarser sediments with smaller moisture availability and limited nutrient retaining capacity are increasingly more common at upper stream courses at higher altitudes (Richards et al. 2002; Grohmanová 2012). The difference in moisture and nutrient availability between gravelly bars at lower altitudes and stony bars at higher altitudes is most likely the key to understanding why succession runs faster on the former bar type. Finer substrates are important for the recruitment of plant individuals during succession, being colonized quickly by fast-growing, short-living species (Wardle 1980; Richards et al. 2002). These early successional species may then trap more sediment, thus creating a habitat that supports faster development of late-successional species (Kopecký 1961; Richards et al. 2002; Corenblit et al. 2009). In the last year of our monitoring, we observed that the vegetation in stony plots was significantly more even than the vegetation in gravelly plots. In particular, the stony plots tended to have sparser cover of perennial vascular plants and lower degree of dominance by competitive herbaceous species than the gravelly plots.

The gravelly and stony plots differed also in species richness and cover of bryophytes, both being higher in the stony plots. Stony bars have more structured microtopography, providing different microsites important for colonization and survival (Muotka and Virtanen 1995; Gilvear et al. 2008; Tockner et al. 2006).

In conclusion, our study shows that natural disturbances by floods are important triggers of vegetation succession on gravel bars. This succession is initially fast, providing temporary habitats for many different species, some of them specialists of this habitat. River regulations and other changes of the natural hydrological regime can lead to reduced flood dynamics, which can result in a loss of the remarkable and endangered habitat of river gravel bars.

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Supplementary materials (paper 1)

Table S1 Tests of differences between groups of species belonging to different vegetation types and reproduction types within individual years. H is the statistic of the Kruskal–Wallis test comparing groups of different vegetation or reproduction types. The significant results ($p<0.05$) are in bold.

	2010		2011		2012		2013	
	H	p	H	p	H	p	H	p
Vegetation type	**13.24**	**0.01**	**27.95**	**< 0.001**	**60.5**	**< 0.001**	**29.75**	**< 0.001**
Reproduction type	**3.88**	**0.048**	2	n.s.	**13.32**	**< 0.001**	**33**	**< 0.001**

Table S2 Effects of environmental factors on the succession rate expressed as the Bray-Curtis dissimilarity index between pairs of consecutive years. Significant differences ($p<0.05$) identified by the Mann-Whitney test (U) or Kruskal-Wallis test (H) are in bold.

	2010–2011		2011–2012		2012–2013	
	U	p	U	p	U	p
Substrate structure	204	0.51	**115**	**0.005**	**105**	**0.002**
Position in the channel	55	0.34	59	0.43	68	0.69
	H	P	H	p	H	p
Shading	4.24	0.11	**7.88**	**0.01**	1.12	0.56
Stream identity	0.58	0.9	3.66	0.3	3.35	0.34

Table S3 Statistics of comparisons of plot characteristics. Plots with prevailing stones or gravel were tested in each year of the study. U is the statistic of the Mann-Whitney test comparing groups of different substrate. The significant results ($p<0.05$) are in bold. In the columns G (gravel) and S (stone), there are the mean values of each of the tested category.

	2010			2011			2012			2013		
	U	p	G; S	U	p	G; S	U	p	G; S	U	p	G; S
No. of vascular plant taxa	213	0.67	8.5; 8.5	171.5	0.151	16.5; 14.7	183	0.248	23.5; 27.8	161.5	0.093	25.7; 31.5
No. bryophyte taxa	199	0.444	0.5; 0.9	**106**	**0.002**	2.1; 4.2	**84.5**	**0.0003**	2.27; 5	**128**	**0.012**	4.09; 6.7
Cover of herb layer (%)	230.5	1	4.9; 3.1	218	0.761	15.6; 6.8	185	0.268	38.6; 27.9	175.5	0.181	59.09; 47.5
Cover of moss layer (%)	216.5	0.733	0.5; 0.4	**124**	**0.009**	1.5; 1.6	**110.5**	**0.003**	2.27; 4.4	**115**	**0.005**	2.5; 4.2
Maximum height of herb layer (cm)	85	0.58	23.6; 18.2	216	0.919	42; 29.1	225.5	0.903	85.9; 84.2	211	0.644	147.3; 143.1
Evenness of herb layer	62.5	0.112	0.95; 0.96	196	0.546	0.92; 0.95	154.5	0.064	0.85; 0.94	**134**	**0.019**	0.73; 0.87

Electronic supplementary materials (paper 1)

Table S4 Table of vegetation plots.

Table S5 Localities of vegetation-plot records.

Table S6, S7 Additional information on vegetation plots.

Fig. 1S–4S Pictures of a gravel bar plots.

Paper 2

Kalníková, V. and Kudrnovsky, H. (2017) Gravel Bar Vegetation Database. *Phytocoenologia*, 47, 109–110.

Phytocoenologia Vol. 47 (2017), Issue 1, 109–110
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Section Ecoinformatics
Short Database Report

Gravel Bar Vegetation Database

Veronika Kalníková* & Helmut Kudrnovsky

Abstract

For the purpose of an ongoing research project dealing with the classification of European river gravel bar vegetation, we collected and digitized vegetation-plot data included in the Gravel Bar Vegetation Database (GIVD ID: EU-00-025, http://www.givd.info/ID/EU-00-025). The database consists of vegetation plots obtained from the literature and from our own field sampling in the countries where this vegetation has not previously been studied or is less explored, especially in southeastern and northern Europe and the Caucasus. The database currently contains 1,738 vegetation plots from 18 countries representing different types and successional stages in the range of gravel bar vegetation from the initial herbaceous stands to scrub, mainly of the order *Epilobietalia fleischeri* (class *Thlaspietea rotundifolii*) and the class *Salicetea purpureae*. Geographical coordinates are available for all plots; accuracy of those derived from the literature depends on the precision of the location descriptions. European montane and submontane gravel-bed rivers with their typical vegetation belong to most endangered habitats; thus the database should complete the information about their distribution and their typical vegetation types. It also serves as data source for studies of vegetation structure and dynamics. The database is managed by the Vegetation Science Group at the Department of Botany and Zoology, Masaryk University, Brno. It has been integrated in the European Vegetation Archive (EVA).

Keywords: database; *Epilobietalia fleischeri*; European Vegetation Archive (EVA); gravel bar; phytosociology; relevé; restoration; riverine habitat; *Salicetea purpureae;* TURBOVEG; vegetation plot; vegetation survey.

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0340-269X/2017/0177 $ 0.90

GIVD Fact Sheet

GIVD Database ID: EU-00-025			**Last update:** 2017-01-04
Gravel Bar Vegetation Database		**Web address:** [NA]	
Database manager(s): Veronika Kalníková (v.kalnikova@seznam.cz); Helmut Kudrnovsky (alectoria@gmx.at)			
Owner: Vegetation Science Group, Department of Botany and Zoology, Masaryk University			
Scope: The database contains relevés of different European and Caucasian gravel bar vegetation types. It comprises the data which were digitized from the literature and data from our own field work. Most of the relevés are not stored in any other vegetation database.			
Availability: according to a specific agreement		**Online upload:** no	**Online search:** no
Database format(s): TURBOVEG		**Export format(s):** TURBOVEG, MS Access, Excel, CSV file, plain text file	
Plot type(s): normal plots		**Plot-size range:** 4-1000 m²	
Non-overlapping plots: 1,738	**Estimate of existing plots:** 1,738	**Completeness:** 100%	**Status:** completed and continuing
Total no. of plot observations: 1,738	**Number of sources (biblio-references, data collectors):** 48		**Valid taxa:** [NA]
Countries: AL: 0.1%; AT: 10.2%; BG: 2.4%; CH: 7.0%; DE: 11.6%; FR: 0.1%; GE: 1.2%; IT: 13.8%; ME: 0.6%; MK: 0.6%; NO: 20.7%; PL: 23.7%; RO: 3.1%; RS: 0.7%; RU: 1.0%; SE: 0.4%; SI: 0.2%; UA: 1.8%			
Formations: Forest: 4 % = Terrestrial: 4 % // Non Forest: Terrestrial: 96 % (Non arctic alpine: 96 % [Natural: 96 %])			
Guilds: all vascular plants: 100%; bryophytes (terricolous or aquatic): 52%; lichens (terricolous or aquatic): 18%			
Environmental data: altitude: 90%; slope aspect: 9%; slope inclination: 9%; surface cover other than plants (open soil, litter, bare rock etc.): 1%			
Performance measure(s): presence/absence only: 20%; cover: 80%			
Geographic location: GPS coordinates (precision 25 m or less): 45%; point coordinates less precise than GPS, up to 1 km: 46%; small grid (not coarser than 10 km): 9%			
Sampling periods: 1930-1939: 0.92%; 1950-1959: 3.2%; 1960-1969: 1.3%; 1970-1979: 5.6%; 1980-1989: 5.1%; 1990-1999: 22.15%; 2000-2009: 23.0%; 2010-2019: 16.3%; unknown: 22.3%			
Information as of 2016-11-22 further details and future updates available from http://www.givd.info/ID/EU-00-025			

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Paper 3

Kalníková, V., Chytrý, K., Novák, P., Zukal, D. and Chytrý, M. (accepted) Natural habitat and vegetation types of river gravel bars in the Caucasus Mountains, Georgia. *Folia Geobotanica*.

Natural habitat and vegetation types of river gravel bars in the Caucasus Mountains, Georgia

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Abstract

River gravel-bar habitats are highly endangered. They are still well-preserved in the Caucasus, but developing conservation strategies is burdened by the lack of data from this region. We studied vegetation and habitat types on gravel bars of 22 rivers in Georgia, including successional stages from open early-successional herbaceous vegetation to scrub. We distinguished five vegetation types based on vegetation physiognomy and β-flexible clustering of species composition, and described them as phytosociological vegetation units: Early-successional herbaceous vegetation at higher altitudes was described as the new association *Epilobietum colchici* and that at lower altitudes as the *Petrorhagia saxifraga*-*Crepis foetida* community. The grassland dominated by *Calamagrostis pseudophragmites* and scrub vegetation were assigned to the associations previously described from Central Europe (*Tussilagini farfarae-Calamagrostietum pseudophragmitae*, *Salici purpureae-Myricarietum germanicae* and *Salici incanae-Hippophaëtum rhamnoidis*). We established diagnostic plant species for each type using the fidelity calculation and related these types to environmental variables. We further compared them with the previously published data on gravel-bar vegetation from the Russian part of the Caucasus and with European systems of habitat classification. This study demonstrates that vegetation and habitat types occurring in Georgia relatively correspond to those recognized earlier in Europe, and can be easily linked to the European systems of habitat classification. Unlike in other parts of Europe, these habitats are still well-preserved on rivers with natural hydrological dynamics in Georgia, but they are threatened by plans of dam building and other river regulations. Our study provides baseline data for developing conservation strategies for the Caucasian gravel-bar habitats.

Keywords

Caucasus, flooding regime, Georgia, phytosociology, riparian vegetation, river gravel bars

Introduction

River gravel bars are riparian accumulations of sedimentary gravel, which provide important habitat to various specialized species. This habitat is distributed worldwide in rugged mountain systems with easily eroded bedrock and large discharge variation, which causes natural transport of sedimentary material in river channels (e.g. Tockner et al. 2006; Hohensinner et al. 2018). It occurs in broad river valleys in piedmont and mountain areas, in the river sections where a sudden decrease of current velocity supports sedimentation. Consequently, the erosion and accumulation of bedload are balanced over a long time period, resulting in braided rivers with shifting mosaics of channels, pools, bars and islands (e.g. Müller 1995; Montgomery and Buffington 1998; Richards et al. 2002; Hohensinner et al. 2018).

River gravel bars represent a heterogeneous environment supporting a variety of plant communities dependent on the natural flooding regime (Tockner et al. 2006). Floods regularly destroy existing habitat patches and create new within periods of up to ~20 years (Kollmann et al. 1999). Malard et al. (2006) described that on the glacial Roseg River in the Swiss Alps up to 30% of river braids renewed monthly. High water levels occur especially during the snowmelt period in spring and high-rainfall periods in summer (Tockner et al. 2000). The rivers of glacier origin have discharge peaks in summer and daily flood pulses (e.g. Milner and Petts 1994; Tockner et al. 2000; Malard et al. 2006), which make the environment even more extreme for the biota.

These dynamics constantly renew vegetation succession, creating a mosaic of vegetation patches of different successional ages (e.g. Müller 1995, 1998; Tockner et al. 2000; Gilvear et al. 2008). Although the succession on river gravel bars is relatively fast (Jeník 1955; Prach et al. 2016; Kalníková et al. 2018a), it often does not reach the stage of the full-grown floodplain forest, which is often missing or restricted to more stable parts of the floodplain. In less stable parts, the oldest successional stage is usually scrub (Pettit and Froend 2001; Loučková 2012). River gravel bars are permanently supplied by propagules of various plants (Johansson et al. 1996; Tockner et al. 2006). However, most of the species persist there for a short time period only, as they are unable to cope with the fluctuating water level, surface overheating, low nutrient content (Tockner et al. 2006) or fast successional changes (Corenblit et al. 2009; Prach et al. 2014; Kalníková et al. 2018a). Still, gravel bars serve as collectors for species with different environmental requirements distributed in the surrounding landscape or upstream (Tockner et al. 2006; Uziębło and Barć 2015), including alpine species (e.g. Uziębło et al. 2018).

Gravel-bar habitats face various threats, including channel regulations and construction of water reservoirs and hydropower plants. These interventions have a strong negative impact on the whole gravel-bed rivers, as documented from the Alps, Carpathians and Balkans, where most of the mountain rivers are regulated and gravel-bar habitats highly fragmented (e.g. Müller 1995; Skoulikidis et al. 2009; Rădoane et al. 2013). Therefore, river gravel bars and floodplains are one of the most endangered habitat types world-wide (Tockner et al. 2006). In Europe, they experienced a reduction in their area by 34–36% over the last 50 years (Janssen et al. 2016).

The decline of habitat types associated with river gravel bars led to their inclusion in the European Union's Habitats Directive (92/43/EEC), which is the legal basis of the Natura 2000 Network of protected areas. Specifically, the list of natural habitat types in Annex I of the Habitats Directive includes the types 3220 Alpine rivers and the herbaceous vegetation along their banks, 3230 Alpine rivers and their ligneous vegetation with *Myricaria germanica* and 3240 Alpine rivers and their ligneous vegetation with *Salix eleagnos* (European Commission 2013). Gravel-bar habitats are also considered in the Emerald Network, which is a network of Areas of Special Conservation Interest implemented by the Council of Europe as a part of its work under the Bern Convention. This network is being implemented in European countries that are not members of the European Union. Two habitats of conservation interest related to gravel bars are recognized in the Emerald network: C3.55 Sparsely vegetated river gravel banks and C3.62 Unvegetated river gravel banks.

Georgia is one of the countries that have officially adopted the Emerald Network on its territory (since 30 November 2018). Mountainous regions of this Caucasian country still contain well-preserved gravel-bar habitats, but some of them are highly endangered, for example by the planned building of the Nenskra dam, which is a possible threat to "Svaneti 1" candidate Emerald Site (Bakhia et al. 2019). However, gravel-bar habitat types have not been sufficiently surveyed in Georgia (see Kvachakidze 2009; Nakhutsrishvili 2013), which makes conservation planning and decision making difficult. The habitats "Alpine rivers and the herbaceous vegetation along their banks " and "Alpine rivers and their ligneous vegetation" are included in the national handbook *Habitats of Georgia* (Akhalkatsi & Tarkhnishvili 2012), but their definitions encompass a broad range of contrasting habitat types, including also muddy and rocky riverbanks of lower river sections and boggy riverbanks, which belong to different types in European habitat classifications (European Commission 2013; Janssen et al. 2016). Almost no specialized plant species typical of gravel-bar vegetation are included in the habitat description provided by Akhalkatsi & Tarkhnishvili (2012).

European habitat classification is largely based on phytosociological classification of vegetation (Rodwell et al. 2018). However, gravel bar vegetation of Georgia and the Caucasus Mountains has not been classified or systematically described yet (see Kvachakidze 2009; Nakhutsrishvili 2013). There is only one study from the Greater Caucasus describing this vegetation type using the Braun-Blanquet approach, carried out in the Teberda Nature Reserve in the Russian part of this mountain range (Onipchenko 2002), and occasional reports of individual plant communities (e.g. Pietsch 1967 from the Transcaucasian lowlands or Parolly 2004 from the Turkish side of the Lesser Caucasus). Therefore we have performed habitat and vegetation survey on Georgian gravel-bar rivers, with the aim of providing basic information on gravel-bar habitat and vegetation types occurring in this country, which could be used as a scientific foundation for conservation planning and assessment.

The objectives of this study are to (i) propose a classification of the vegetation of river gravel bars in Georgia and relate it to habitat types used in European habitat classifications; (ii) identify the main ecological factors driving species composition of these vegetation and habitat types; and (iii) assess the main threats to these habitats.

Material and methods

Study area

Sampling was performed in three regions of Georgia: the Greater Caucasus, the Lesser Caucasus and the highlands of central Georgia (Fig. 1). Georgia is a mountainous country: only ~25% of its total area is classified as lowlands and plains, and only ~13% of the land area is below 200 m a.s.l. (Ketskhoveli 1959). We sampled the vegetation on gravel bars of 22 rivers, from piedmonts to the subalpine belt. The altitude of the sampling sites ranged from 16 m a.s.l. in the Chorokhi River mouth to 2419 m a.s.l. in the mountain valleys of the Greater Caucasus (Table 1). A large area in the Greater Caucasus is covered by glaciers (~1000 km^2; Forte at al. 2014), and most of the studied rivers have a glacial source. The Caucasus Mountains are geologically highly diverse. The watersheds of most of the studied rivers in the Lesser Caucasus are formed of various Tertiary volcanic rocks (e.g. andesite, basalt and dacite) and in the Greater Caucasus mainly of Cretaceous and Tertiary sediments, especially of erosion-prone turbidities with various proportions of volcanic and carbonate components. Some mountain ranges of the Svaneti Province are formed of granitoids or metamorphic rocks such as gneiss (Adamia 2010).

Fig. 1 The study sites of river gravel bars in Georgia and location of the previously published data on gravel-bar vegetation from the Russian part of the Western Greater Caucasus (black and grey dots; Onipchenko 2002). Different symbols refer to individual vegetation types.

Table 1 The climatic characteristics of the study area. The data on the total annual precipitation and mean annual temperature were taken from the WorldClim 2 database (Fick & Hijmans 2017) for all relevé sites. The regions are defined as geographical clusters of the sampling sites. Assignments of each site to a region are shown in Table S4 in Electronic supplementary material.

Region (rivers)	**Altitude** (m a.s.l.)			**Precipitation** (mm/year)			**Temperature** (°C)			**Number of**	
	mean	*min*	*max*	*mean*	*min*	*max*	*mean*	*min*	*max*	sites	rivers
Central Greater Caucasus (Adishchala, Mestiachala, Mestiachala tributary, Rioni, Dolra, Chachakhir)	1540	1280	2272	1098	1030	1180	5	1.7	7.1	27	6
Eastern Greater Caucasus (Chkheri, Andakistkali, Tergi, Tergi tributary, Kvakhidistskali, Pirikitis Alazani, Kabali, Aragvi, Aragvi tributary)	1546	402	2419	867	669	947	6	0.4	12.5	18	9
Central Georgia (Mejuda)	584	583	586	558	558	558	12	11.6	11.6	3	1
Lesser Caucasus (Postkhovi, Chachari, Kvabliani, Adjaris-Tskali, Chorokhi, Skhalta)	804	16	1215	1090	588	2215	10	7.5	14.4	22	6

Nakhutsrishvili (2013) recognized several climatic zones in Georgia, ranging from humid, almost subtropical climate, to the zones of permanent snow and glaciers in the Caucasus summit areas. Most of our sampling sites were located in the temperate mountain zone. Climate conditions of the sampling sites vary considerably, following a strong E–W gradient of increasing precipitation (Fick and Hijmans 2017). Temperature also varies significantly, generally decreasing with altitude. The total annual precipitation of sampling sites was highest near the Chorokhi River mouth. This area is also relatively warm. Another area with high precipitation is the western mountainous part of the Greater Caucasus (Upper Svaneti), which is also the coldest among the sampling sites. The lowest total annual precipitation is received at the sampling sites in Inner Kartli in central Georgia (Table 1).

Data collection

We made field surveys in summers of 2012, 2013 and 2015–2017 using vegetation plots (further called relevés) of a size of 4 m × 4 m (n = 70), in which plant species were recorded with abundance estimated using a nine-degree cover-abundance scale (Westhoff and van der Maarel 1978). We recorded all species of vascular plants and bryophytes (except for four relevés in which bryophytes were not sampled and 29 relevés where they were missing). For each relevé, we recorded coordinates (WGS 84) using a portable GPS device and estimated the cover of each vegetation layer (E_2 – shrub, E_1 – herb, E_0 – moss layer) and the maximum and mean height of the shrub and herb layers. We also recorded prevailing substrate structures according to the modified Wentworth scale (Bunte and Abt 2001) using three categories: stones (ø > 20 cm), gravel (ø < 20 cm and > 2 mm) and sand or mud (ø ≤ 2 mm). Substrates with a higher proportion of organic matter were classified as "mud". We also measured, from a map, the riverine distance of the sampling sites from the stream source. A detailed description and the location of each relevé is provided in Table S3 and S4 in Electronic supplementary material.

On each site, we sampled several physiognomically distinct vegetation types of river gravel bars. We sampled only the sites where tree layer was not developed (i.e. from initial herbaceous to scrub vegetation) and we also avoided highly human-influenced sites or those under significant grazing pressure. We preferably sampled vegetation containing the species recognized as gravel-bar specialists in Europe or in the Western Greater Caucasus (Stöcklin 1999; Onipchenko 2002; Jansen et al. 2016; Mucina et al. 2016; e.g. *Calamagrostis pseudophragmites*, *Epilobium colchicum*, *E. dodonaei*, *Hippophaë rhamnoides*, *Myricaria germanica*, *Salix purpurea*, *Scrophularia heterophylla* and *Silene compacta*).

We collected difficult-to-identify vascular plants and bryophytes for further identification or revision in the lab. The specimens of vascular plants are stored in the Herbarium of Masaryk University, Brno, Czech Republic (BRNU) and the specimens of bryophytes in the Herbarium of the Moravian Museum, Brno (BRNM). All relevés are stored in the Gravel Bar Vegetation Database (ID: EU-00-025; Kalníková and Kudrnovsky 2017), which is included in the European Vegetation Archive (Chytrý et al. 2016).

Data analysis

All the relevés sampled in the field were stored in the Turboveg 2 database (Hennekens and Schaminée 2001). Subsequently, they were processed in R software (R Core Team 2017): with the help of the *vegan* package (Oksanen et al. 2017), we calculated cluster analyses and created an ordination model. Using the *tidyverse* package (Wickham 2017), we created plots of the altitudinal distribution of vegetation types and selected species and created boxplots of different characteristics. Climatic variables for each relevé were obtained from the WorldClim 2 database (Fick and Hijmans 2017) using QGIS software (QGIS Development Team 2018). Finally, we created the synoptic table and calculated the phi coefficients of association between species and vegetation types using the JUICE software (Tichý et al. 2002).

Nomenclature was unified according to Euro+Med PlantBase (Euro+Med 2018) for vascular plants, Ehrendorfer (1973) and Danihelka et al. (2012) for vascular plant aggregates, Hill et al. (2006) for mosses, Grolle & Long (2000) for liverworts, and Mucina et al. (2016) for higher vegetation units.

Some individuals of taxonomically difficult plant groups (e.g. *Hieracium*, *Rubus* or *Taraxacum*) or juvenile individuals that could not be identified on the species level were omitted from the cluster and ordination analyses. Other difficult-to-identify vascular plant species were merged into aggregates: *Achillea millefolium* agg.: *A. millefolium* + *A. setacea*, *Agrostis stolonifera* agg.: *A. gigantea* + *A. stolonifera*, *Arenaria serpyllifolia* agg.: *A. leptoclados* + *A. serpyllifolia*, *Bromus racemosus* agg.: *B. commutatus* + *B. racemosus*, *Carex muricata* agg.: *C. divulsa* + *C. muricata* + *C. spicata*, *Festuca ovina* agg.: *F. brunnescens* + *F. ovina* + *F. saxatilis*, *Festuca rubra* agg.: *F. buschiana* + *F. rubra*, *Malus sylvestris* agg.: *M. pumila* + *M. sylvestris*, and *Myosotis scorpioides* agg.: *M. cespitosa* + *M. lithospermifolia* + *M. scorpioides*. All records of the same species occurring in different layers were combined.

Gravel bars offer a wide range of microhabitats with specific environmental conditions and different vegetation types of several successional stages ranging from the early-successional herbaceous vegetation to scrub and transitions between those. To classify so heterogeneous data, we used a combined classification approach involving formal definitions based on cover thresholds of dominant species or life forms (i.e. cover of the shrub layer) and cluster analysis based on species composition. Formal definitions were created and applied only during the data analysis, therefore, they did not influence our choice of the sampling site in the field. First, we divided the total dataset into subsets of tall grassland (n = 8) and scrub (n = 25) according to the cover of *Calamagrostis pseudophragmites* (≥ 20%) and shrubs (≥ 10%) and early-successional herbaceous vegetation (n = 37 relevés). The subsets of early-successional herbaceous vegetation and scrub were further clustered using the beta-flexible algorithm (β = -0.25) with the Bray-Curtis dissimilarity measure (Oksanen et al. 2017). To identify the diagnostic species of each cluster, we used the phi coefficient of association (Sokal and Rohlf 1995) as a measure of fidelity. We considered the species with phi coefficient higher than 0.35 and 0.45 as diagnostic and highly diagnostic, respectively, those occurring in more than 40% of relevés of the cluster as constant species, and those with a cover higher than 25% in at least 15% of relevés of the cluster as dominant species. In addition, we calculated Fisher's exact test and excluded the species with non-significant ($p > 0.05$) concentration of their occurrence in the cluster from the lists of diagnostic species (Tichý and Chytrý 2006).

We summarized the variation in plant species composition among relevés using the non-metric multidimensional scaling (NMDS). We plotted its model on an ordination diagram together with several environmental and vegetation characteristics and the best fitting species as indicated by the permutation test. These variables were passively fitted using the *envfit* function of the R package *vegan* (Oksanen et al. 2017).

We tested the differences between environmental variables (altitude, distance from the stream source, mean annual temperature and total annual precipitation) and vegetation variables (moss, herb and shrub layer cover, mean and maximal herb and shrub layer height, number of species) between the clusters using an analysis of variance and subsequent post-hoc Tukey's test using the R package *stats* (R Core Team 2017).

For naming vegetation units, we applied the rules of the International Code of the Phytosociological Nomenclature (Weber et al. 2000).

Extended dataset

To compare the species composition of the clusters identified in our study with the associations previously described from the Russian part of the Western Greater Caucasus (Onipchenko

2002), we prepared an extended dataset containing both our relevés (n = 70) and the relevés published in the original descriptions of relevant syntaxa (n = 19). Two associations of early-successional vegetation were included in the Russian data: *Scrophulario variegatae-Epilobietum dodonaei* (alliance *Murbeckiello huetii-Epilobion dodonaei*) and *Sileno compactae-Salicetum purpureae* (alliance *Epilobion fleischeri*). Both are currently classified to the order *Epilobietalia fleischeri* of the class *Thlaspietea rotundifolii* (Belonovskaya et al. 2014; Mucina et al. 2016). Nomenclature of the taxa in the extended dataset was unified. Some pairs of species were merged to avoid possible bias in the analyses caused by differences in taxonomical concepts used (*Festuca ovina* agg.: *F. ovina* + *F. vivipara*, *Luzula campestris* agg.: *L. multiflora* + *L. sudetica*, *Poa nemoralis* agg.: *P. glauca* + *P. nemoralis* and *Poa alpina*: *P. alpina* + *P. badensis*). Geographic coordinates of these relevés were assigned based on the description of their sites in the original publication with a potential location uncertainty of 2 geographical minutes.

The extended dataset was superimposed on the NMDS ordination plot together with the best fitting species and fitted environmental variables (altitude, mean annual temperature and total annual precipitation) and vegetation variables (moss, herb and shrub layer covers which were reported in the original literature).

Results and discussion

Floristic composition

In the dataset of 70 original relevés, a total of 441 plant taxa were recorded (337 not counting those determined only at the genus level), including 406 (312) vascular plants and 35 (25) bryophytes. The most frequent vascular plant taxa were *Calamagrostis pseudophragmites* (44 relevés), *Epilobium colchicum* (37), *Plantago lanceolata* (29), *Medicago lupulina* (27), *Arenaria serpyllifolia* agg. (25), *Petrorhagia saxifraga* (25), *Poa alpina* (25), *Myricaria germanica* (22), *Crepis foetida* (21) and *Trifolium repens* (20). The most frequent bryophytes were *Racomitrium canescens* (19), *Bryum caespiticium* (13), *B. argenteum* (10), *Barbula unguiculata* (8) and *Polytrichum piliferum* (7). Most of the species occurred with a very low frequency.

Some of the recorded taxa are considered endemic to the Caucasus, including *Crepis sonchifolia*, *Heracleum pubescens*, *H. scabrum*, *Scrophularia ruprechtii*, *Senecio leucanthemifolius* subsp. *caucasicus*, *Silene lacera*, *Trigonocaryum involucratum*, *Tripleurospermum caucasicum*, *Valeriana colchica* and *Veronica petraea* (Gagnidze 2005). The moss *Bryum klinggraeffii* was found during the field survey as a new species for Georgia and the whole Greater Caucasus (Kalníková et al. 2018b). Alien species (sensu Kikodze et al. 2009) spreading on Georgian gravel bars were also recorded in our relevés (e.g. *Bidens frondosus*, *Erigeron annuus*, *E. canadensis*, *Galinsoga quadriradiata*, *Juncus tenuis* and *Tagetes minuta*). Other alien species that we frequently observed on gravel bars but did not record in the relevés included *Amorpha fruticosa*, *Buddleja davidii* and *Paulownia tomentosa*.

Vegetation types

The mono-dominant tall-grass vegetation with a cover of *Calamagrostis pseudophragmites* higher than 20% was interpreted as (i) the association *Tussilagini farfarae-Calamagrostietum pseudophragmitae*. Using the cluster analysis of the relevés of herbaceous vegetation with a lower cover of *Calamagrostis pseudophragmites*, we identified two clusters of the early-successional stages of gravel-bar vegetation: (ii) the new association *Epilobietum colchici* and (iii) the *Petrorhagia saxifraga-Crepis foetida* community. Within the subset of scrub vegetation, the numerical analysis identified two clusters, which were interpreted as the associations (iv) *Salici purpureae-Myricarietum germanicae* and (v) *Salici incanae-Hippophaëtum rhamnoidis* (Table S2 in Electronic supplementary material).

Table 2 A shortened synoptic table of the Caucasian gravel-bar vegetation types: *Tussilagini farfarae-Calamagrostietum pseudophragmitae* (Tus-Cal), *Epilobietum colchici* (Epi), *Petrorhagia saxifraga-Crepis foetida* community (Pet-Cre), *Salici purpureae-Myricarietum germanicae* (Sal-Myr) and *Salici incanae-Hippophaëtum rhamnoidis* (Sal-Hip). The numbers are percentage occurrence frequencies (constancies). Shaded species are sorted by their decreasing fidelity to a particular vegetation type: dark shading indicates values of phi ≥ 0.45 and light shading those of phi ≥ 0.35. Only species reaching a constancy of at least 20% in at least one vegetation type are shown. The letter B indicates bryophytes. For the full version of this synoptic table see Table S2 in Electronic supplementary material.

Vegetation type	**Tus-Cal**	**Epi**	**Pet-Cre**	**Sal-Myr**	**Sal-Hip**
Number of relevés	8	23	14	19	6
Tussilagini farfarae-Calamagrostietum pseudophragmitae					
Equisetum arvense	50	9	7	5	.
Juncus articulatus	38	.	.	5	17
Calamagrostis pseudophragmites	100	70	.	89	50
Plantago major	50	4	14	37	.
Epilobietum colchici					
Senecio leucanthemifolius subsp. *caucasicus*	.	30	.	5	.
Poa alpina	25	65	.	42	.
Racomitrium canescens (B)	13	52	21	16	.
Rumex acetosella	.	48	14	11	17
Pinus sylvestris	.	26	.	11	.
Pilosella officinarum	.	26	.	11	.
Petrorhagia saxifraga-Crepis foetida community					
Trifolium arvense	.	9	64	16	17
Plantago lanceolata	13	4	100	42	83
Crepis foetida	.	9	79	26	50
Silene compacta	.	17	50	11	.
Petrorhagia saxifraga	.	13	86	32	67
Arenaria serpyllifolia agg.	.	22	79	37	33
Barbula unguiculata (B)	.	4	43	.	17
Daucus carota	.	.	29	5	.
Petrorhagia prolifera	.	.	21	.	.
Echium vulgare	.	.	57	21	33
Syntrichia ruralis (B)	.	4	21	.	.
Salici purpureae-Myricarietum germanicae					
Myricaria germanica	.	22	.	89	.
Trisetum rigidum	.	22	.	58	.
Gypsophila elegans	.	13	.	47	.
Equisetum variegatum	.	.	.	32	.
Silene ruprechtii	.	4	.	26	.
Lotus corniculatus	13	.	14	42	.
Vicia sosnowskyi	.	.	.	16	.
Cirsium echinus	.	13	14	37	.
Salvia verticillata	.	4	7	26	.
Salici incanae-Hippophaëtum rhamnoidis					
Hippophaë rhamnoides	.	9	7	21	100
Sonchus oleraceus	.	4	.	.	33
Paracynoglossum glochidiatum	.	9	21	.	50
Verbascum sessiliflorum	.	.	7	.	33

Vegetation type	Tus-Cal	Epi	Pet-Cre	Sal-Myr	Sal-Hip
Number of relevés	8	23	14	19	6
Elytrigia repens	.	.	7	.	33
Hypochaeris radicata	.	.	7	.	33
Poa pratensis	.	.	7	5	33
Catapodium rigidum	.	.	14	.	33
Alnus glutinosa	13	.	7	.	33
Erigeron canadensis	13	9	64	11	67
Epilobium colchicum	25	87	7	74	.
Other species occurring in at least 20% of relevés					
Setaria viridis	.	.	29	.	17
Salix caprea	.	13	14	26	.
Medicago minima	.	.	29	.	33
Euphorbia maculata	.	.	29	.	33
Bidens frondosus	25	.	.	.	17
Phalaroides arundinacea	25	.	.	.	17
Anisantha tectorum	.	4	29	.	17
Achillea millefolium agg.	.	9	21	21	.
Sedum spurium	13	22	14	11	.
Tussilago farfara	25	17	7	21	.
Alnus incana	.	17	.	21	.
Sedum pallidum	.	26	29	5	.
Ceratodon purpureus (B)	.	17	29	11	.
Vulpia myuros	.	.	21	.	17
Bromus japonicus	.	4	29	11	17
Papaver fugax	.	17	.	21	.
Seseli transcaucasicum	.	13	.	21	.
Prunella vulgaris	.	13	14	26	17
Agrostis stolonifera agg.	25	4	43	37	17
Bryum caespiticium (B)	13	17	14	26	17
Sedum album	.	4	21	.	17
Ranunculus repens	25	.	7	16	17
Bryum argenteum (B)	.	22	29	.	17
Equisetum ramosissimum	25	.	7	.	33
Tanacetum parthenium	.	13	36	16	17
Erigeron acris	.	39	7	37	.
Cerastium fontanum	.	26	7	11	17
Trifolium repens	38	9	36	42	33
Ambrosia artemisiifolia	.	.	21	.	33
Trifolium pratense	13	17	7	37	.
Poa compressa	.	.	21	26	.
Leucanthemum vulgare	13	4	21	53	33
Tortella inclinata (B)	.	9	.	21	.
Medicago lupulina	25	17	57	63	17
Poa nemoralis	13	35	.	16	.
Artemisia absinthium	.	13	7	32	17
Salix alba	25	9	14	47	33
Polytrichum piliferum (B)	.	22	.	11	.
Tripleurospermum caucasicum	13	26	.	5	.
Salix purpurea	38	13	7	42	50
Brachythecium rivulare (B)	25	.	7	.	33

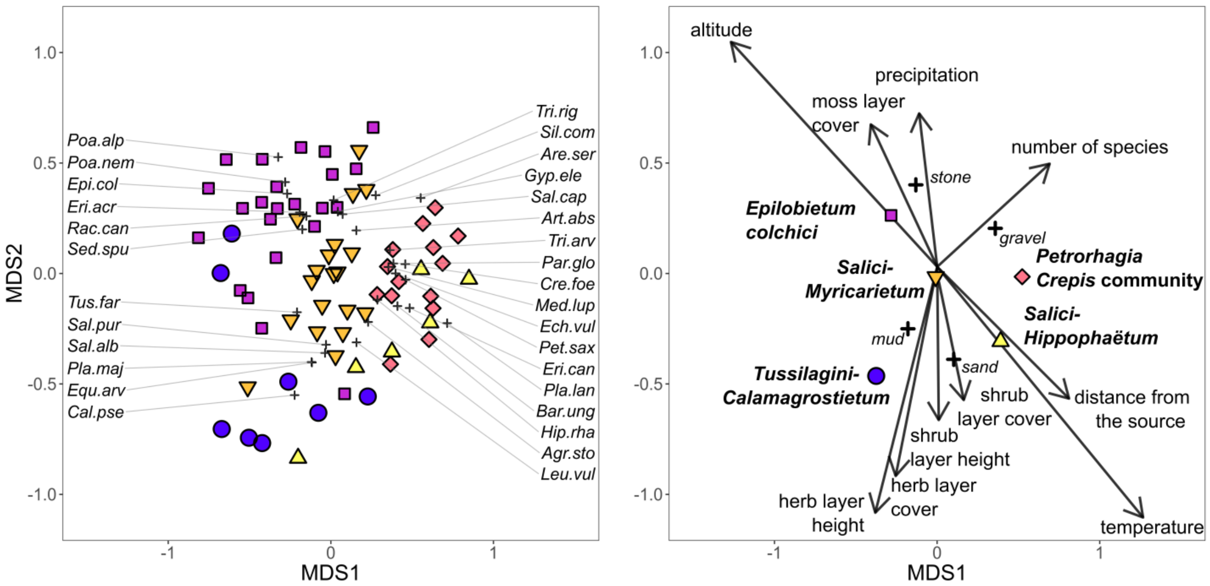

Fig. 2 NMDS ordination diagram. The left plot shows the best fitting species ($p < 0.01$) occurring in at least five relevés and individual relevés classified to vegetation types. The right plot shows the centroids of individual vegetation types and fitted vectors that include bioclimatic variables (total annual precipitation and mean annual temperature), substrate variables (gravel, mud, sand and stone), site variables (altitude and distance from the stream source) and vegetation characteristics (moss, herb and shrub layer cover, mean herb and shrub layer height and total number of species). *Agr.sto – Agrostis stolonifera*, *Are.ser – Arenaria serpyllifolia* agg., *Art.abs – Artemisia absinthium*, *Bar.ung – Barbula unguiculata*, *Cal.pse – Calamagrostis pseudophragmites*, *Cre.foe – Crepis foetida*, *Ech.vul – Echium vulgare*, *Epi.col – Epilobium colchicum*, *Equ.arv – Equisetum arvense*, *Eri.acr – Erigeron acris*, *Eri.can – E. canadensis*, *Gyp.ele – Gypsophila elegans*, *Hip.rha – Hippophaë rhamnoides*, *Leu.vul – Leucanthemum vulgare*, *Med.lup – Medicago lupulina*, *Par.glo – Paracynoglossum glochidiatum*, *Pet.sax – Petrorhagia saxifraga*, *Pla.lan – Plantago lanceolata*, *Pla.maj – Plantago major*, *Poa.alp – Poa alpina*, *Poa.nem – P. nemoralis*, *Rac.can – Racomitrium canescens*, *Sal.alb – Salix alba*, *Sal.cap – S. caprea*, *Sal.pur – S. purpurea*, *Sed.spu – Sedum spurium*, *Sil.com – Silene compacta*, *Tri.arv – Trifolium arvense*, *Tri.rig – Trisetum rigidum*, *Tuss.far – Tussilago farfara*.

The results of NMDS are summarized in an ordination diagram (Fig. 2; stress = 0.26). We found a significant relationship ($p < 0.05$) between the species composition and altitude ($r^2 = 0.67$), number of species ($r^2 = 0.3$; note that this variable is inherently dependent on species composition), distance from the stream source ($r^2 = 0.25$), mean annual temperature ($r^2 = 0.74$), total annual precipitation ($r^2 = 0.11$), herb layer cover ($r^2 = 0.22$) and mean herb layer height ($r^2 = 0.29$). Of the substrate variables, significant responses of species composition were observed for all substrate types (gravel: $r^2 = 0.18$; mud: $r^2 = 0.09$; sand: $r^2 = 0.19$; stone: $r^2 = 0.17$). Altitude, mean annual temperature, herb-layer cover and height were highly negatively correlated.

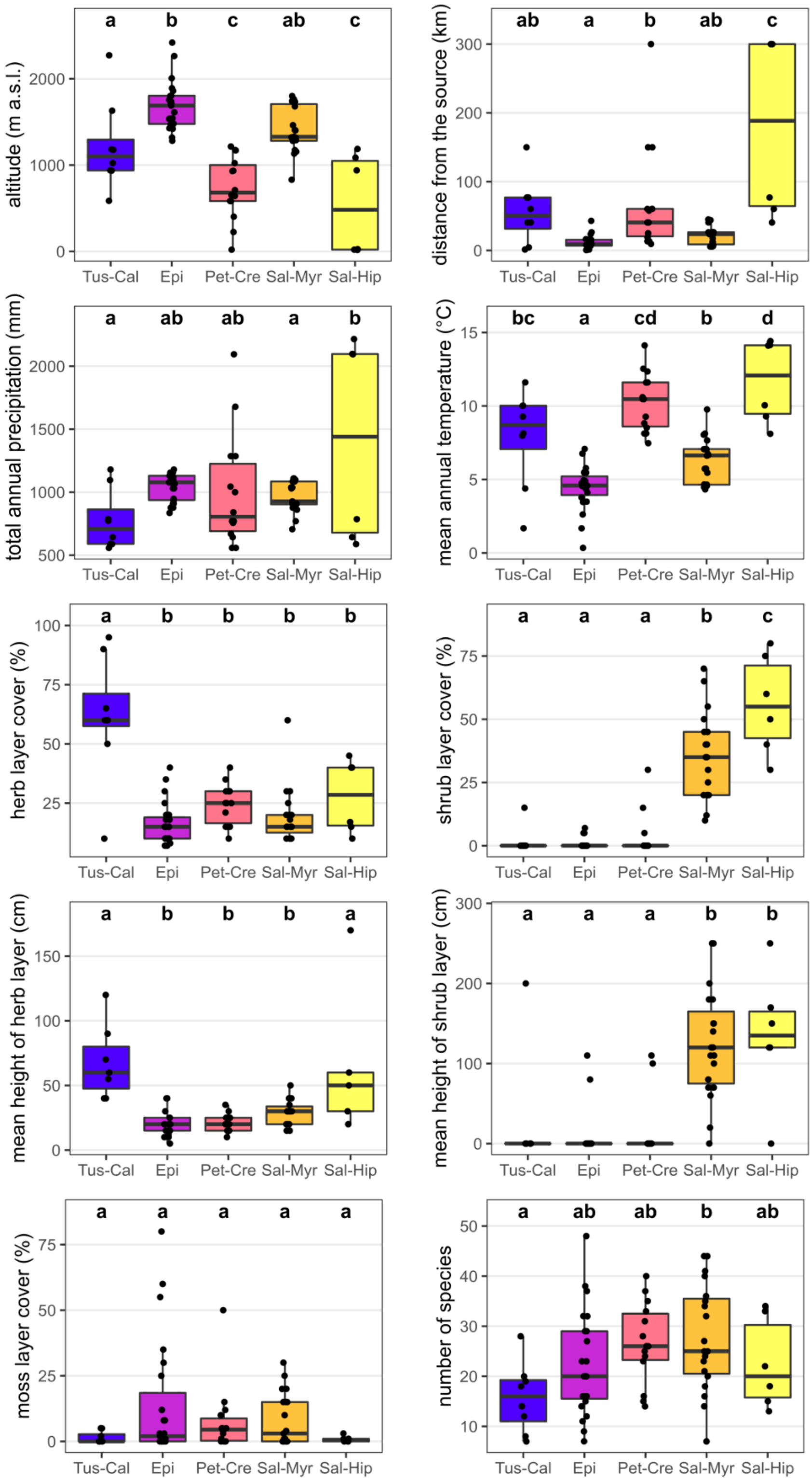

Fig. 3 Comparison of selected environmental variables and vegetation characteristics among vegetation types (Tus-Cal – *Tussilagini farfarae-Calamagrostietum pseudophragmitae*, Epi – *Epilobietum colchici*, Pet-Cre – *Petrorhagia saxifraga-Crepis foetida* community, Sal-Myr – *Salici purpureae-Myricarietum germanicae* and Sal-Hip – *Salici incanae-Hippophaëtum rhamnoidis*). Horizontal lines within the boxes indicate medians and black points indicate individual plots. The letters above the boxes indicate homogeneous groups (Tukey's test, $P < 0.05$, see Table S1 in Electronic supplementary material for details).

The results of Tukey's post-hoc test of environmental and vegetation characteristics are shown in Fig. 3; the complete statistics for all variables are in Table S1 in Electronic supplementary material. The altitudinal distribution of the gravel-bar plant communities together with selected diagnostic or frequent species is shown in Fig. 4. Other important gradients are the time period since the last severe disturbance, reflected by the shrub and herb layer cover and height, and the substrate structure, which also affects species composition and the succession pattern. These characteristics are discussed in the descriptions of particular vegetation units.

Syntaxonomical outline and description of vegetation units

Following the standard European vegetation classification (Mucina et al. 2016), the gravel-bar vegetation of Georgia is divided into sparse early-successional vegetation, tall grasslands with *Calamagrostis pseudophragmites* (order *Epilobietalia fleischeri* of the class *Thlaspietea rotundifolii*) and scrub (class *Salicetea purpureae*). We follow this scheme here, considering also other synthetic studies and national vegetation classification systems (e.g. Dierßen 1996; Valachovič et al. 1997; Schubert et al. 2001; Matuszkiewicz 2007; Chytrý 2011, 2013; Petrović et al. 2012). We propose the following syntaxonomic scheme of the vegetation types recognized on Georgian gravel bars:

Thlaspietea rotundifolii Br.-Bl. in Br.-Bl. et Jenny 1926

Epilobion fleischeri G. Br.-Bl. ex Br.-Bl. 1950 – high-mountain herbaceous gravel-bar vegetation

1. *Tussilagini farfarae-Calamagrostietum pseudophragmitae* Pawłowski et Walas 1949 – gravel-bar grasslands with *Calamagrostis pseudophragmites*
2. *Epilobietum colchici* Kalníková, K. Chytrý, Novák, Zukal et M. Chytrý 2020 – high-mountain early-successional herbaceous gravel-bar vegetation

Artemisietea vulgaris Lohmeyer et al. in Tx. ex von Rochow 1951

Dauco-Melilotion Görs ex Rostański et Gutte 1971

3. *Petrorhagia saxifraga-Crepis foetida* community – submontane early-successional herbaceous gravel-bar vegetation

Salicetea purpureae Moor 1958

Salicion eleagno-daphnoidis (Moor 1958) Grass 1993 – gravel-bar scrub

4. *Salici purpureae-Myricarietum germanicae* Moor 1958 – gravel-bar scrub with *Myricaria germanica*
5. *Salici incanae-Hippophaëtum rhamnoidis* Br.-Bl. in Volk 1939 – gravel-bar scrub with *Hippophaë rhamnoides*

1. Gravel-bar grasslands with *Calamagrostis pseudophragmites*

Tussilagini farfarae-Calamagrostietum pseudophragmitae Pawłowski et Walas 1949 (Table 1 in Supplement S1, relevés 1–8)

Diagnostic species: *Calamagrostis pseudophragmites*, ***Equisetum arvense***, *Juncus articulatus*, *Plantago major*
Constant species: *Calamagrostis pseudophragmites*, *Equisetum arvense*, *Plantago major*
Dominant species: *Calamagrostis pseudophragmites*

Fig. 5 *Tussilagini farfarae-Calamagrostietum pseudophragmitae* on the Mejuda River, Central Georgia (photo V. Kalníková, 2016).

Description: The tall-grass vegetation of this association occurs predominantly in sections with finer sediments, on sandy to muddy patches of river gravel bars. Its altitudinal distribution is relatively wide (Fig. 3). It usually occurs on moist sites in gravel bar depressions or close to water, and is inundated several times a year. Its stands are well connected with the ground or surface running water. Such environmental conditions are suitable for moisture-demanding riparian plants, e.g. *Agrostis stolonifera* agg., *Juncus articulatus* and *Ranunculus repens*. The dominant *Calamagrostis pseudophragmites* is a tall clonal grass creating dense stands, in which few other species survive. Apart from the riparian plants, ruderal species (e.g. *Equisetum arvense* and *Plantago major*), nutrient-demanding and shade-tolerant species or aliens (e.g. *Bidens frondosus*) are common in this vegetation, especially in the lower sections of mountain rivers with higher human population density. The moss layer is species-poor, composed especially of mesophilous and hygrophilous bryophytes such as *Brachythecium rivulare*, *Cratoneuron filicinum* or *Plagiomnium cuspidatum*.

Syntaxonomy: There are no local diagnostic species restricted to this vegetation in the Caucasus; therefore we identify it as *Tussilagini farfarae-Calamagrostietum psedophragmitae*, an association originally described from the Carpathians (Pawłowski and Walas 1949), which also occurs in the Alps and other parts of Central Europe (e.g. Schubert et al. 2001; Chytrý 2011). However, the position of this association in higher syntaxonomical units is unclear and inconsistent among national vegetation classifications of European countries; it is classified to the *Phalaridion arundinaceae* alliance of the *Phragmito-Magnocaricetea* class (e.g. Valachovič 2001; Chytrý 2011) or to the *Epilobion fleischeri* alliance (e.g. Schubert et al. 2001). It is herbaceous vegetation that represents both early-successional and more developed stages of vegetation. The species of more open vegetation (e.g. scree species) could be present, but the community is basically defined by the dominance of a single species, *Calamagrostis pseudophragmites*, and the presence of more nutrient- and moisture-demanding species. In this study, we assign it to *Epilobion fleischeri* because of significant representation of gravel bar specialists (mainly *Epilobium colchicum*).

Threats: The dominant species *Calamagrostis pseudophragmites*, which to a large extent defines this vegetation type, finds its optimum at oligotrophic sites. With channel regulations, reservoir constructions and consequent eutrophication of rivers in many parts of Europe, it was replaced by more mesotrophic species such as *Phalaroides arundinacea*, and it became rare in several European countries (Müller 1995; Skokanová et al. 2015; Kalníková et al. 2018a). Nevertheless, it is still relatively common in extensive mountain systems such as the Caucasus.

2. High-mountain early-successional herbaceous gravel-bar vegetation

Epilobietum colchici ass. nova hoc loco (Table S3 in Electronic supplementary material, relevés 9–31)

Nomenclature type: Relevé 19, Table S3 in Electronic supplementary material (holotypus; see below).

Diagnostic species: ***Epilobium colchicum***, *Pilosella officinarum*, *Pinus sylvestris* juv., *Poa alpina*, *Rumex acetosella*, ***Senecio leucanthemifolius* subsp. *caucasicus***; *Racomitrium canescens*
Constant species: *Calamagrostis pseudophragmites*, *Epilobium colchicum*, *Poa alpina*, *Rumex acetosella*; *Racomitrium canescens*
Dominant species: *Racomitrium canescens*

Fig. 6 *Epilobietum colchici* with scattered individuals of *Epilobium colchicum* and *Myricaria germanica* and dense moss layer dominated by *Racomitrium canescens* on the Mestiachala River, Central Greater Caucasus – the site of nomenclatural type relevé (photo V. Kalníková, 2016).

Description: The vegetation of the *Epilobietum colchici* association occurs at the highest altitudes of river gravel bar distribution in the Georgian part of the Caucasus (Fig. 3), often in the proximity of glaciers. It is found especially in precipitation-rich areas such as the Western and Central Greater Caucasus. It develops on stony to gravelly sites that are frequently flooded. During sunny days, when the glacier melting is faster, the flooding intervals can be very short.

The dynamic environmental conditions with alternating flooding and drought periods are tolerated by few species. This association is dominated by Caucasian alpine or scree species including *Papaver fugax*, *Sedum pallidum*, *S. spurium*, *Senecio leucanthemifolius* subsp. *caucasicus*, *Seseli transcaucasicum*, *Silene compacta* and *Tripleurospermum caucasicum*. Some species found in similar habitats in the Alps (e.g. *Erigeron acris*, *Poa alpina*, *Rumex acetosella* and *R. scutatus*) are also frequent in this vegetation type. Further, it also harbours species commonly occurring in other types of river gravel bars, such as *Calamagrostis pseudophragmites*, *Myricaria germanica* and *Salix* spp., but they fail to attain dominance here. Because of its occurrence at high altitudes, this vegetation usually lacks alien species. The moss layer is lacking on frequently disturbed or newly created gravel bars, but it can be well developed at some sites, containing especially species of open habitats, e.g. *Racomitrium canescens*, which can attain a high cover. Other typical bryophytes include *Pohlia filum*, *Polytrichum piliferum* and species with ruderal tendency such as *Bryum argenteum* and *B. caespiticium*.

Syntaxonomy: This association is a geographical vicariant of the *Epilobietum fleischeri* association described from the Alps (Frey 1922). These two associations differ in the presence of diagnostic species typical for the Caucasus and not occurring in the Alps, and vice versa. The key diagnostic species of both communities (*Epilobium colchicum* and *E. fleischeri*) are geographical vicariants (Stöcklin 1999). Both associations occur in similar environmental conditions, share several species of vascular plants (e.g. *Erigeron acris*, *Poa alpina* and *Rumex acetosella*) and most of the bryophyte taxa (e.g. Moor 1958; Burga et al. 2010; Leuschner and Ellenberg 2017). Consequently, we propose to classify *Epilobietum colchici* to the *Epilobion fleischeri* alliance.

Threats: *Epilobietum colchici* vegetation is threatened especially by river regulations for its high dependence on frequent floods. Longer intervals between floods, potentially caused by river regulations, allow the development of scrub and often disrupt the connectivity of stands with initial vegetation. At high altitudes of precipitation-rich areas, this vegetation type is not directly endangered, but it becomes vulnerable at middle altitudes below ~1500 m a.s.l.

Nomenclatural type relevé of the association *Epilobietum colchici – holotypus hoc loco designatus* (relevé 19 in Table S3 in Electronic supplementary material): Georgia, Upper Svaneti, Mestia, river Mestiachala, a gravel bar on the north end of the small town Mestia; altitude 1473 m a.s.l.; coordinates 43°03'58.8"N, 42°45'02.3"E; relevé area 16 m^2; slope 0°; cover of the herb layer 7%; cover of the moss layer 80%; recorded on 19 Jul 2016 by Veronika Kalníková and Kryštof Chytrý.
Herb layer: *Epilobium colchicum* 2m, *Artemisia incana* +, *Calamagrostis pseudophragmites* +, *Carex leporina* +, *Cerastium fontanum* +, *Erigeron acris* +, *Filago arvensis* +, *Silene dianthoides* +, *Taraxacum* sect. *Taraxacum* +, *Petrorhagia saxifraga* r, *Rumex acetosella* r;

Moss layer: *Racomitrium canescens* 5, *Ceratodon purpureus* +, *Polytrichum piliferum* +.

3. Submontane early-successional herbaceous gravel-bar vegetation

Petrorhagia saxifraga-Crepis foetida community (Table S3 in Electronic supplementary material, relevés 32–45)

Diagnostic species**:** ***Arenaria serpyllifolia* agg.**, ***Crepis foetida***, *Daucus carota*, *Echium vulgare*, *Petrorhagia prolifera*, ***P. saxifraga***, ***Plantago lanceolata***, ***Silene compacta***, ***Trifolium arvense***; ***Barbula unguiculata***, *Syntrichia ruralis*
Constant species: *Agrostis stolonifera* agg., *Arenaria serpyllifolia* agg., *Crepis foetida*, *Echium vulgare*, *Erigeron canadensis*, *Medicago lupulina*, *Petrorhagia saxifraga*, *Plantago lanceolata*, *Silene compacta*, *Trifolium arvense*; *Barbula unguiculata*

Fig. 7 *Petrorhagia saxifraga-Crepis foetida* community on the Kabali River, Eastern Greater Caucasus (photo V. Kalníková, 2016).

Description: The *Petrorhagia saxifraga-Crepis foetida* community represents early-successional gravel-bar vegetation at lower altitudes (Fig. 3), in warmer and precipitation-poorer areas. It occurs on gravel deposits with sand admixture and is flooded less frequently than the vegetation of *Epilobietum colchici*. Such sites are drier, and their vegetation is sparse, containing ruderal, drought-tolerant, light-demanding and also annual species such as *Bromus japonicus*, *Crepis foetida*, *Daucus carota*, *Echium vulgare*, *Medicago minima*, *Petrorhagia prolifera*, *P. saxifraga*, *Trifolium arvense* and *Vulpia myuros*. As this community predominantly occurs in the submontane areas, it is surrounded by a wider spectrum of habitat types and thus influenced by a larger species pool. Therefore it is relatively species-rich. It is also often invaded by alien species, e.g. *Erigeron annuus* and *E. canadensis*. At some sites, the moss layer is well-developed, formed especially of ruderal species capable of growing at drier sites, e.g. *Barbula unguiculata*, *Bryum argenteum*, *Ceratodon purpureus* and *Syntrichia ruralis*.

Syntaxonomy: Due to the high variability of this vegetation and the group of diagnostic species including plants from contrasting habitats, we do not formally describe this vegetation as an association. We relate it to the drought-adapted ruderal vegetation of the *Dauco-Melilotion* alliance (class *Artemisietea vulgaris*). A comparable vegetation type assigned to *Dauco-Melilotion* was described from the Carpathians (*Epilobio dodonaei-Melilotetum albi*; Slavík 1978). However, similar communities were classified to the *Epilobion fleischeri* alliance in Montenegro (*Epilobietum dodonaei* Lakušić 1999; Petrović et al. 2012). *Epilobium dodonaei* is a more thermophilous species forming communities on gravel bars at lower altitudes, but it is closely related to Caucasian *E. colchicum* and *E. stevenii* or Alpine *E. fleischeri* (Stöcklin 1999; Leuschner and Ellenberg 2017). We recorded *E. dodonaei* only in one relevé of the *Petrorhagia saxifraga-Crepis foetida* community in Georgia.

Threats: The *Petrorhagia saxifraga-Crepis foetida* community generally harbours few gravel-bar specialist species, but some alpine species can locally establish such as *Epilobium colchicum* or *Poa alpina*. It is threatened by reservoir constructions and river regulations, but also by intensive livestock grazing.

4. Gravel-bar scrub with *Myricaria germanica*

Salici purpureae-Myricarietum germanicae Moor 1958 (Table S3 in Electronic supplementary material, relevés 46–64)

Diagnostic species: *Cirsium echinus*, *Epilobium colchicum*, ***Equisetum variegatum***, ***Gypsophila elegans***, *Lotus corniculatus*, ***Myricaria germanica***, *Salvia verticillata*, *Silene ruprechtii*, ***Trisetum rigidum***, *Vicia sosnowskyi*
Constant species: *Calamagrostis pseudophragmites*, *Epilobium colchicum*, *Gypsophila elegans*, *Leucanthemum vulgare*, *Lotus corniculatus*, *Medicago lupulina*, *Myricaria germanica*, *Plantago lanceolata*, *Poa alpina*, *Salix alba*, *Salix purpurea*, *Trifolium repens*, *Trisetum rigidum*
Dominant species: *Myricaria germanica*

Fig. 8 A young stand of *Salici purpureae-Myricarietum germanicae* in gravel bar depression on the Tergi River, Eastern Greater Caucasus (photo V. Kalníková, 2015).

Description: *Salici purpureae*-*Myricarietum germanicae* is an open to closed scrub representing an older successional stage of river gravel bar vegetation. It is common at high to middle altitudes (Fig. 3). The prevailing substrate structure is fine gravel to sand. Both of these substrates are accumulated especially at the microsites with higher groundwater level, which is crucial for germination of *Myricaria germanica* seeds (Müller 1995). Thus, the community typically occupies periodically inundated depressions or margins of gravel bars. However, both of these substrate types can become very dry in summer and thus occupied also by many drought-tolerant species, e.g. *Arenaria serpyllifolia* agg., *Gypsophila elegans*, *Petrorhagia saxifraga* and *Trisetum rigidum*. *Myricaria germanica* can be accompanied by other woody species, e.g. *Alnus incana*, *Hippophaë rhamnoides* or *Salix purpurea*, if they are occurring in the nearby vegetation. *Salici*-*Myricarietum* is a relatively species-rich community with numerous Caucasian species, e.g. *Epilobium colchicum*, *Silene lacera*, *Teucrium orientale* or *Vicia sosnowskyi*, but also with species distributed in Central Europe, e.g. *Agrostis stolonifera* agg., *Equisetum variegatum*, *Erigeron acris* or *Poa alpina*. *Calamagrostis pseudophragmites* is often scattered in the community. We observed no alien species in this vegetation type. Moss layer is well developed, especially at high altitudes. Common bryophyte species include *Bryum caespiticium*, *Ceratodon purpureus*, *Racomitrium canescens* and *Tortella inclinata*.

Syntaxonomy: We identified this community type with the European association *Salici purpureae-Myricarietum germanicae* (originally described from the Alps; Moor 1958), despite the occurrence of several species restricted to the Caucasus, which however occurred sparsely. This association is defined by the presence (and usually dominance) of *Myricaria germanica* (Oriolo and Poldini 2002), accompanied by other gravel-bar specialists (*Calamagrostis pseudophragmites*, *Epilobium colchicum* or *E. dodonaei*). Cluster analysis also assigned to this group some relevés from the Central Greater Caucasus with many alpine scree species but dominated by *Hippophaë rhamnoides* or *Salix purpurea*. For the purpose of this study, we accept this assignment, but we suggest that the alpine vegetation with *Hippophaë rhamnoides* deserves further study.

Threats: Similarly to other river gravel bar communities of the Caucasus, the main threat to *Salici purpureae-Myricarietum germanicae* are river regulation and reservoir constructions. Otherwise, this community is relatively stable and frequent in Georgia, which is in contrast to the massive decline of the diagnostic species *Myricaria germanica* in last decades in Europe (e.g. Kudrnovsky 2013; Werth et al. 2014; Sitzia et al. 2016; Werner 2016; Fink et al. 2017; Marinov et al. 2017).

5. Gravel-bar scrub with *Hippophaë rhamnoides*

Salici incanae-Hippophaëtum rhamnoidis Br.-Bl. in Volk 1939 (Table S3 in Electronic supplementary material, relevés 65–70)

Diagnostic species: *Alnus glutinosa*, *Catapodium rigidum*, ***Elytrigia repens***, *Erigeron canadensis*, ***Hippophaë rhamnoides***, ***Hypochaeris radicata***, ***Paracynoglossum glochidiatum***, *Poa pratensis*, ***Sonchus oleraceus***, ***Verbascum sessiliflorum***
Constant species: *Calamagrostis pseudophragmites*, *Crepis foetida*, *Erigeron canadensis*, *Hippophaë rhamnoides*, *Paracynoglossum glochidiatum*, *Petrorhagia saxifraga*, *Plantago lanceolata*, *Salix purpurea*
Dominant species: *Hippophaë rhamnoides*, *Salix purpurea*

Fig. 9 *Salici incanae-Hippophaëtum rhamnoidis* on a sandy gravel bar on the Kvabliani River, Lesser Caucasus (photo V. Kalníková, 2017).

Description: The association *Salici incanae-Hippophaëtum rhamnoidis* occurs on gravel bars containing a variable fraction of gravel and sand. Its sites are located rather high above the water level, thus being inundated less frequently and less influenced by groundwater. In some places, this vegetation corresponds to an older successional stage of the *Petrorhagia saxifraga-Crepis foetida* community, which often occurs nearby. Both communities are floristically similar. However, the occurrence of *Salici-Hippophaëtum* is limited by the distribution of the relatively rare shrub *Hippophaë rhamnoides*. This species is able to grow under harsh conditions, probably partly due to its nitrogen-fixing ability. In the Caucasus region, it also occurs on abandoned fields, grasslands close to settlements, and at other ruderal sites (Tephnadze et al. 2014). In Europe, it also dominates shrub vegetation on coastal sand dunes (e.g. Leuschner and Ellenberg 2017). Within this study, we observed *Salici-Hippophaëtum* only at low altitudes of the piedmont of the Lesser Caucasus near to seashore (Fig. 3). *Hippophaë rhamnoides* can grow with an admixture of other shrubs, such as *Salix alba* and *S. purpurea*, or young *Alnus glutinosa* trees. The vegetation is characterized by the presence of drought-tolerant ruderal species such as *Arenaria serpyllifolia* agg., *Catapodium rigidum*, *Crepis foetida*, *Echium vulgare* and *Medicago minima*. Several alien species were also observed in this community, e.g. *Ambrosia artemisiifolia*, *Erigeron annuus*, *E. canadensis* and *Tagetes minuta*. Moss layer is sparse, consisting mostly of ruderal species such as *Barbula unguiculata* or *Bryum argenteum*.

Syntaxonomy: *Salici incanae-Hippophaëtum rhamnoidis* was originally described from the Alps (Volk 1940). It is defined by the dominance of a single species, *Hippophaë rhamnoides*, being however often accompanied by *Salix daphnoides* or *S. eleagnos* in Europe (e.g. Müller 1995; Oriolo and Poldini 2002). These two *Salix* species reach their eastern distribution limit in Turkey, being absent in Georgia (Gagnidze 2005). However, we recorded a low number of species specific to the Caucasus in this vegetation, therefore we consider it to be the same association as in the Alps.

Threats: This association is restricted to subalpine to piedmont sites with the occurrence of rare species *Hippophaë rhamnoidis*. This makes this vegetation rare and possibly threatened.

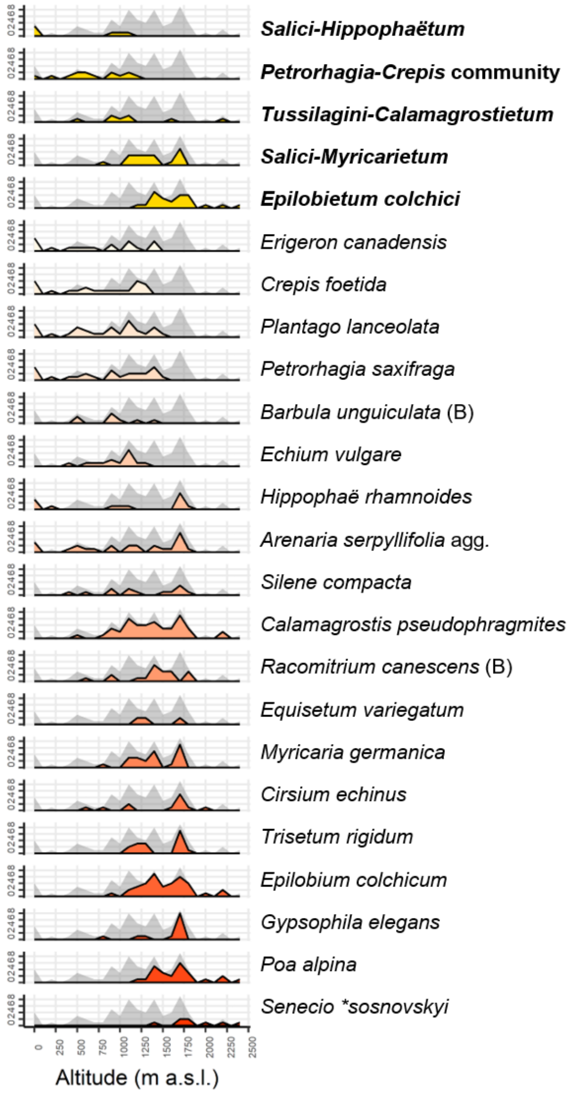

Fig. 4 Altitudinal distribution of gravel-bar vegetation types and their selected diagnostic species. Species are sorted by their means of altitudinal distribution. Numbers of relevés of a particular vegetation type or with a particular species are shown in 100-m intervals of altitude, with a grey background silhouette indicating the total number of all plots.

Successional patterns

Our results indicate that the main gradient in the species composition of the Caucasian gravel-bar vegetation is connected with the riverine altitudinal continuum (Vannote et al. 1980). This continuum summarizes the effects of several inter-correlated factors such as altitude, floodplain morphology, flooding regime, nutrient and oxygen content, species distribution and substrate structure. The studied vegetation types were well separated along the altitudinal gradient (Fig. 3, 4), which also affects their successional pattern. Similar altitudinal patterns were observed in various studies worldwide (e.g. Jeník 1955; Oriolo and Poldini 2002; Prach et al. 2014) and related to the parallel patterns of substrate structure (Fyles and Bell 1986; Richards et al. 2002; Gilvear et al. 2008; Corenblit et al. 2009; Prach et al. 2014; Kalníková et al. 2018a) and intensity and periodicity of floods (Tockner et al. 2000; Gilvear et al. 2008; Loučková 2012; Fig. 3). Our observations suggest that the successionally youngest stages on the gravelly and stony substrate, i.e. *Epilobietum colchici* and the *Petrorhagia saxifraga-Crepis foetida* community, can be both replaced by scrub: *Epilobietum colchici* more likely by *Salici purpureae-Myricarietum germanicae*, while *Petrorhagia saxifraga-Crepis foetida* community by *Salici incanae-Hippophaëtum rhamnoidis*. Both of them can be replaced also by floodplain forest dominated by *Alnus glutinosa*, *A. incana* or *Salix* spp., depending on the local species pool. Sandy to muddy gravel bars support the development of *Tussilagini farfarae-Calamagrostietum pseudophragmitae*. This vegetation is more stable as it is dense and limits the growth of juvenile shrubs, but it can also develop into the above-mentioned types of scrub. Various successional stages of vegetation modify their environment, e.g. by intercepting mud and sand (Müller 1995; Richards et al. 2002; Corenblit et al. 2009). In such a way, the development of *Epilobietum colchici* may support further succession towards *Salici purpureae-Myricarietum germanicae* or other types of scrub.

Caucasian gravel-bar scrub differs from European gravel-bar scrub by the absence or low representation of shrubby willows. Of the typical European gravel-bar *Salix* species, only *Salix purpurea* occurs there, whereas the distribution range of *Salix daphnoides* or *S. eleagnos* does not reach Georgia (Meusel et al. 1965), and there are no ecologically vicariant species (Gagnidze 2005). Other willows which we found on Georgian gravel bars (e.g. *Salix alba*, *S. caucasica*, *S. caprea* or *S. pseudomedemii*) have their ecological optimum in other habitat types. We sampled only one well-developed scrub dominated by *Salix purpurea* on the Kvabliani River in the Lesser Caucasus. This vegetation was similar to the European association *Salicetum purpureae* Wendelberger-Zelinka 1952. As it was only one relevé, we did not include it in the analysis, as well as several relevés with young stands of *Alnus incana*, which also require further study.

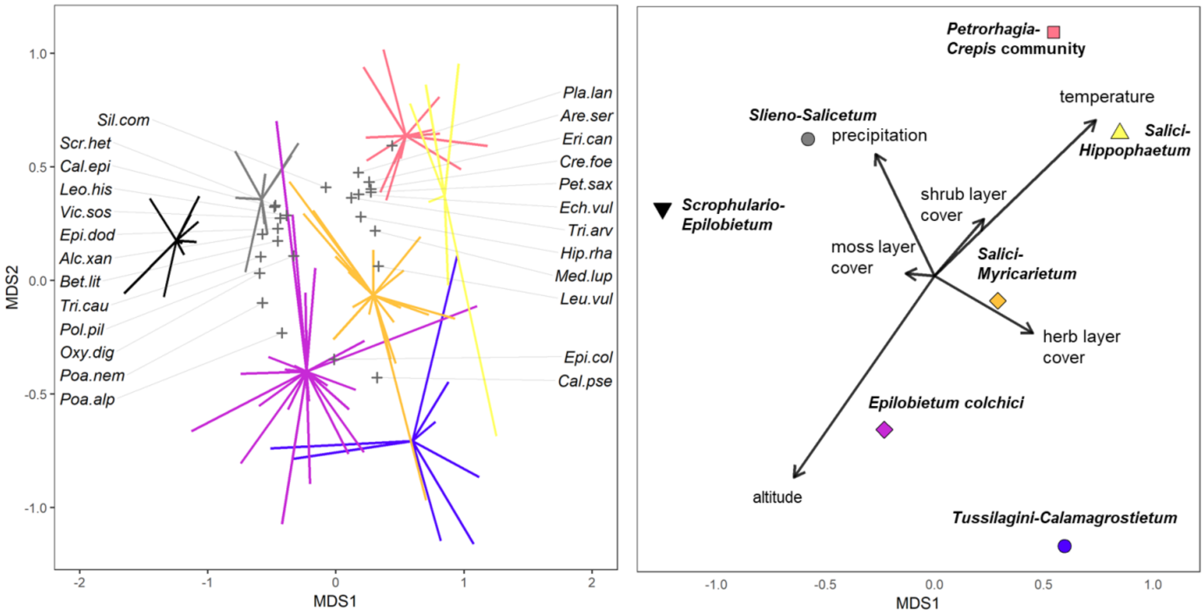

Fig. 10 NMDS ordination diagram of the vegetation of river gravel bars sampled in Georgia and the Russian part of the Western Greater Caucasus (Onipchenko 2002). The diagram includes passively fitted environmental variables. The best-fitting species ($p < 0.01$) occurring in at least five relevés are shown: *Alc.xan – Alchemilla xanthochlora*, *Are.ser – Arenaria serpyllifolia* agg., *Bet.lit – Betula litwinowii*, *Cal.epi – Calamagrostis epigejos*, *Cal.pse – C. pseudophragmites*, *Cre.foe – Crepis foetida*, *Ech.vul – Echium vulgare*, *Epi.col – Epilobium colchicum*, *Epi.dod – E. dodonaei*, *Eri.can – Erigeron canadensis*, *Hip.rha – Hippophaë rhamnoides*, *Leo.his – Leontodon hispidus*, *Leu.vul – Leucanthemum vulgare*,

Med.lup – Medicago lupulina, *Oxy.dig – Oxyria digyna*, *Pet.sax – Petrorhagia saxifraga*, *Pla.lan – Plantago lanceolata*, *Poa.alp – Poa alpina*, *Poa.nem – P. nemoralis* agg., *Pol.pil – Polytrichum piliferum*, *Scr.het – Scrophularia heterophylla*, *Sil.com – Silene compacta*, *Tri.arv – Trifolium arvense* and *Vic.sos – Vicia sosnowskyi*.

Numerical comparison with the previously distinguished Caucasian vegetation types

Ordination of the extended dataset (Fig. 10) revealed that relevés sampled in Georgia differ from those sampled on river gravel bars in the Russian part of the Western Greater Caucasus (associations *Scrophulario variegatae-Epilobietum dodonaei* and *Sileno compactae-Salicetum purpureae*). They were described by Onipchenko (2002) as open vegetation of alpine moraines and floodplain gravel bars.

The association *Scrophulario variegatae-Epilobietum dodonaei* is the typus of the alliance *Murbeckiellion huetii*, which was later renamed by Belonovskaya et al. (2014) to *Murbeckiello huetii-Epilobion dodonaei*. Belonovskaya et al. (2014) also recommended classifying this alliance to the order of gravel-bar vegetation *Epilobietalia fleischeri* (instead of the original classification to the order of scree vegetation *Androsacetalia alpinae*), which was later accepted in the European vegetation classification system by Mucina et al. (2016). The reasons for this reclassification were habitat ecology and the frequent occurrence of *Epilobium dodonaei*, which is typical of similar vegetation in Europe (e.g. Slavík 1978; Stöcklin 1999). However, the original data suffer from the fact that *Epilobium dodonaei* was not distinguished from another specialist species of this habitat, *E. colchicum* (as well as another specialist species *Calamagrostis pseudophragmites* was not distinguished from *C. epigejos*; Onipchenko, pers. comm.). The diagnostic species of *Scrophulario variegatae-Epilobietum dodonaei* are *Betula litwinowii* juv., *Poa nemoralis*, *Pohlia filum*, *Scrophularia heterophylla* and *Trifolium spadiceum* (Onipchenko 2002). We did not observe this vegetation in the Georgian part of the Greater Caucasus, and the ordination diagram indicated that it is dissimilar from the Georgian communities (Fig. 10).

The second association from the Russian Greater Caucasus, *Sileno compactae-Salicetum purpureae*, also comprises early-successional vegetation, but it is more similar to Alpine or Carpathian gravel-bar vegetation due to the occurrence of several shared species such as *Agrostis stolonifera*, *Calamagrostis epigejos*, *Epilobium dodonaei*, *Erigeron acris*, *Myricaria germanica*, *Racomitrium canescens*, *Rumex acetosella*, *Salix purpurea*, *Silene compacta* and *Trifolium repens* (Onipchenko 2002). This association is more similar in species composition to *Epilobietum colchici* (Fig. 10). However, we prefer not to include them in the same association due to uncertainty of identification of the two important diagnostic species. The environmental conditions of the *Silene compactae-Salicetum purpureae* association in Russia and the *Epilobietum colchici* association in Georgia are very similar, but Russian relevés were located on the precipitation-richer northern slopes of the Caucasus.

Habitat types and implications for conservation

The vegetation types described on river gravel bars in Georgia clearly correspond to habitats used in Natura 2000 and Emerald Network (Table 3). Our study is the first that provides detailed data on their floristic composition and distribution in Georgia, thus supporting conservation planning, habitat assessment, monitoring and decision making.

Table 3 A crosswalk between the habitat types used in European habitat classifications and vegetation types of river gravel bars in Georgia described in this study.

Emerald network (EUNIS classification)	Natura 2000 (EU Habitats Directive, Annex I)	Vegetation types described on river gravel bars in Georgia
C3.62 Unvegetated river gravel banks	–	not studied
C3.55 Sparsely vegetated river gravel banks	3220 Alpine rivers and the herbaceous vegetation along their banks	1.Gravel-bar grasslands with *Calamagrostis pseudophragmites* (*Tussilagini-Calamagrostietum*)
		2. High-mountain early-successional herbaceous gravel-bar vegetation (*Epilobietum colchici*)
		3. Submontane early-successional herbaceous gravel-bar vegetation (*Petrorhagia-Crepis* community)
	3230 Alpine rivers and their ligneous vegetation with *Myricaria germanica*	4. Gravel-bar scrub with *Myricaria germanica* (*Salici-Myricarietum*)
	3240 Alpine rivers and their ligneous vegetation with *Salix eleagnos*	5. Gravel-bar scrub with *Hippophaë rhamnoides* (*Salici-Hippophaëtum*)

The Georgian Caucasus is notable for so far almost undisturbed river network with well-preserved natural gravel-bed rivers. Local degradation of gravel-bar habitats caused by overgrazing or local gravel mining is still reversible due to the functional hydrological dynamics of these rivers. There are current plans to build river cascades and hydropower plants in the Central Greater Caucasus, including flooding of several river valleys in the Upper Svaneti, the most valuable region regarding the wild river dynamics. For instance, the Nenskra dam and the Khudoni dam projects assume flooding the valleys of the Nenskra River at about 1400 m a.s.l. and the Enguri River at about 1000 m a.s.l., respectively (SLR Consulting France SAS 2017). Both projects and regulations of the channels of gravel-bed rivers would cause a great loss of species and habitat diversity and destroy a unique wild landscape with vegetation and habitat types that are under the protection elsewhere in Europe. Water reservoirs destroy not only the habitats of the flooded river section, but also dramatically change the natural flooding and sedimentation regime for hundreds of kilometres downstream (Dai and Liu 2013). As a result, the formation of new gravel bars is prevented, and older gravel bars are being overgrown by either nutrient-demanding or moisture-demanding species, depending on the substrate (Müller 1998).

Protected areas in Georgia cover approximately 7.5% of the country, but most of them were established in the lowlands because the high-mountain areas are thought not to be directly endangered by habitat destruction (Nakhutsrishvili 2013). However, examples from many European countries clearly show that mountain gravel-bar habitats are significantly endangered by river regulations and dam building. Such habitats are still well-preserved at many sites in Georgia, and they can be saved if they receive an appropriate level of protection, for example within the Emerald Network. By providing the data on habitat types of river gravel-bar habitats in Georgia, their floristic diversity and distribution, the current study can serve as a baseline for developing conservation plans and strategies for these habitats.

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Author contributions

VK conceived the study and led the writing. Field sampling was organized by VK and PN and conducted by VK, KC, PN and DZ. Statistical analyses were performed by VK and KC. All the authors participated in the interpretation of the results and manuscript writing.

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Supplementary materials (paper 3)

Table S1 Comparison of environmental variables and vegetation characteristics among the vegetation types of Caucasian gravel bars. The letter indices next to the mean values indicate homogeneous groups (Tukey's test, $P < 0.05$). Abbreviations: Tus-Cal – *Tussilagini farfarae-Calamagrostietum pseudophragmitae*, Epi – *Epilobietum colchici*, Pet-Cre – *Petrorhagia saxifraga-Crepis foetida* comm., Sal-Myr – *Salici purpureae-Myricarietum germanicae* and Sal-Hip – *Salici incanae-Hippophaëtum rhamoidis*.

Variable		**Tus-Cal**	**Epi**	**Pet-Cre**	**Sal-Myr**	**Sal-Hip**
altitude (m a.s.l.)	*mean*	1218^{a}	1684^{c}	733^{b}	1412^{ac}	546^{b}
	max.	2272	2419	1215	1800	1187
	min.	586	1282	20	830	16
no. of species	*mean*	16^{a}	22^{ab}	26^{ab}	28^{b}	22^{ab}
	max.	28	48	40	44	34
	min.	7	7	14	7	13
shrub layer cover (%)	*mean*	1.9^{a}	0.7^{a}	3.6^{a}	35.6^{b}	55.8^{c}
	max.	15	7	30	70	80
	min.	0	0	0	10	30
herb layer cover (%)	*mean*	61.2^{a}	16^{b}	24.7^{b}	19.1^{b}	27.8^{b}
	max.	95	40	40	60	45
	min.	10	7	10	10	10
moss layer cover (%)	*mean*	1.5	14.1	7.9	8.4	0.8
	max.	5	80	50	30	3
	min.	0	0	0	0	0
mean shrub layer height (m)	*mean*	0.2^{a}	0.1^{a}	0.2^{a}	1.3^{b}	1.6^{b}
	max.	2	1.1	1.1	2.5	2.5
	min.	0	0	0	0.2	1.2
max shrub layer height (m)	*mean*	0.5^{a}	0.2^{a}	0.2^{a}	2.1^{b}	2.8^{b}
	max.	4	2	1.8	4	3.5
	min.	0	0	0	1	2
mean herb layer height (cm)	*mean*	67.9^{a}	19.8^{b}	19.3^{b}	27.6^{b}	66^{a}
	max.	120	40	35	50	170
	min.	40	5	0	0	20
max herb layer height (cm)	*mean*	112.6^{ad}	60.7^{c}	59.6^{bc}	86.1^{ad}	128^{b}
	max.	150	120	120	120	230
	min.	71	15	0	50	90

distance from the source (km)	*mean*	43[ab]	11.3[b]	68.9[a]	21.5[b]	59.3[ab]
	max.	77	43	300	45	77
	min.	1.4	0.6	9.4	5.6	40.6
annual precipitation (mm/year)	*mean*	777[a]	1042[ab]	997[ab]	966[a]	1404[b]
	max.	1180	1180	2094	1109	2215
	min.	558	835	558	706	588
mean annual temperature (°C)	*mean*	8[ab]	4[d]	10[ac]	6[b]	12[c]
	max.	12	7	14	10	14
	min.	1.6	0.3	7	4	8

Table S2 Complete synoptic table of the Caucasian gravel-bar vegetation types: *Tussilagini farfarae-Calamagrostietum pseudophragmitae* (Tus-Cal), *Epilobietum colchici* (Epil), *Petrorhagia saxifraga-Crepis foetida* comm. (Pet-Cre), *Salici purpureae-Myricarietum germanicae* (Sal-Myr) and *Salici incanae-Hippophaëtum rhamnoidis* (Sal-Hip). The numbers are percentage constancy. Shaded species are ranked by their decreasing fidelity to a particular vegetation type: dark shading for phi ≥ 0.45 and light shading for 0.45 > phi ≥ 0.35. The letter B indicates bryophytes.

Vegetation type	**Tus-Cal**	**Epil**	**Pet-Cre**	**Sal-Myr**	**Sal-Hip**
Number of relevés	8	23	14	19	6
Tussilagini farfarae-Calamagrostietum pseudophragmitae					
Equisetum arvense	**50**	9	7	5	.
Juncus articulatus	**38**	.	.	5	17
Calamagrostis pseudophragmites	**100**	70	.	89	50
Plantago major	**50**	4	14	37	.
Epilobietum colchici					
Senecio leucanthemifolius subsp. *caucasicus*	.	**30**	.	5	.
Poa alpina	25	**65**	.	42	.
Racomitrium canescens (B)	13	**52**	21	16	.
Rumex acetosella	.	**48**	14	11	17
Agrostis capillaris	.	**17**	.	.	.
Pinus sylvestris	.	**26**	.	11	.
Pilosella officinarum	.	**26**	.	11	.
***Petrorhagia-Crepis* community**					
Trifolium arvense	.	9	**64**	16	17
Plantago lanceolata	13	4	**100**	42	83
Crepis foetida	.	9	**79**	26	50
Silene compacta	.	17	**50**	11	.
Petrorhagia saxifraga	.	13	**86**	32	67
Arenaria serpyllifolia agg.	.	22	**79**	37	33
Barbula unguiculata (B)	.	4	**43**	.	17
Daucus carota	.	.	**29**	5	.
Petrorhagia prolifera	.	.	**21**	.	.
Echium vulgare	.	.	**57**	21	33
Syntrichia ruralis (B)	.	4	**21**	.	.
Salici purpureae-Myricarietum germanicae					
Myricaria germanica	.	22	.	**89**	.
Trisetum rigidum	.	22	.	**58**	.
Gypsophila elegans	.	13	.	**47**	.
Equisetum variegatum	.	.	.	**32**	.
Silene ruprechtii	.	4	.	**26**	.
Lotus corniculatus	13	.	14	**42**	.

Vegetation type Number of relevés	Tus-Cal 8	Epil 23	Pet-Cre 14	Sal-Myr 19	Sal-Hip 6
Vicia sosnowskyi	.	.	.	**16**	.
Cirsium echinus	.	13	14	**37**	.
Salvia verticillata	.	4	7	**26**	.
Salici incanae-Hippophaëtum rhamnoidis					
Hippophaë rhamnoides	.	9	7	21	**100**
Sonchus oleraceus	.	4	.	.	**33**
Paracynoglossum glochidiatum	.	9	21	.	**50**
Verbascum sessiliflorum	.	.	7	.	**33**
Hypochaeris radicata	.	.	7	.	**33**
Elytrigia repens	.	.	7	.	**33**
Poa pratensis	.	.	7	5	**33**
Catapodium rigidum	.	.	14	.	**33**
Alnus glutinosa	13	.	7	.	**33**
Erigeron canadensis	13	9	64	11	**67**
Epilobium colchicum	25	**87**	7	**74**	.
Other species occurring in at least 20% of relevés					
Setaria viridis	.	.	29	.	17
Salix caprea	.	13	14	26	.
Medicago minima	.	.	29	.	33
Euphorbia maculata	.	.	29	.	33
Bidens frondosus	25	.	.	.	17
Phalaroides arundinacea	25	.	.	.	17
Anisantha tectorum	.	4	29	.	17
Achillea millefolium agg.	.	9	21	21	.
Sedum spurium	13	22	14	11	.
Tussilago farfara	25	17	7	21	.
Alnus incana	.	17	.	21	.
Sedum pallidum	.	26	29	5	.
Ceratodon purpureus (B)	.	17	29	11	.
Vulpia myuros	.	.	21	.	17
Bromus japonicus	.	4	29	11	17
Papaver fugax	.	17	.	21	.
Seseli transcaucasicum	.	13	.	21	.
Prunella vulgaris	.	13	14	26	17
Agrostis stolonifera agg.	25	4	43	37	17
Bryum caespiticium (B)	13	17	14	26	17
Sedum album	.	4	21	.	17
Ranunculus repens	25	.	7	16	17
Bryum argenteum (B)	.	22	29	.	17
Equisetum ramosissimum	25	.	7	.	33
Tanacetum parthenium	.	13	36	16	17
Erigeron acris	.	39	7	37	.
Cerastium fontanum	.	26	7	11	17
Trifolium repens	38	9	36	42	33
Ambrosia artemisiifolia	.	.	21	.	33
Trifolium pratense	13	17	7	37	.
Poa compressa	.	.	21	26	.
Leucanthemum vulgare	13	4	21	53	33
Tortella inclinata (B)	.	9	.	21	.
Medicago lupulina	25	17	57	63	17
Poa nemoralis	13	35	.	16	.
Artemisia absinthium	.	13	7	32	17
Salix alba	25	9	14	47	33
Polytrichum piliferum (B)	.	22	.	11	.
Tripleurospermum caucasicum	13	26	.	5	.
Salix purpurea	38	13	7	42	50
Brachythecium rivulare (B)	25	.	7	.	33
Other species					
Trifolium campestre	.	.	14	.	.
Minuartia hamata	.	.	14	.	.
Chondrilla juncea	.	.	14	.	.
Scrophularia heterophylla	.	9	.	16	.
Pseudocrossidium hornschuchianum (B)	.	.	14	.	.
Barbula convoluta (B)	.	.	14	.	.
Rumex obtusifolius	.	.	14	.	.

Vegetation type	**Tus-Cal**	**Epil**	**Pet-Cre**	**Sal-Myr**	**Sal-Hip**
Number of relevés	8	23	14	19	6
Cynosurus echinatus	.	.	14	.	.
Euphorbia esula	.	.	14	.	.
Teucrium polium	.	.	7	.	.
Sedum annuum	.	4	.	11	.
Herniaria glabra	.	.	7	11	.
Anthyllis vulneraria s. l.	.	9	.	16	.
Origanum vulgare	.	.	7	11	.
Crepis sonchifolia	.	9	.	5	.
Briza media	.	.	.	5	.
Eupatorium cannabinum	.	.	.	11	.
Galium verum	.	.	.	5	.
Avenella flexuosa	.	4	.	.	.
Fimbristylis bisumbellata	.	.	7	.	.
Mentha longifolia	13	4	7	11	.
Teucrium chamaedrys	.	4	.	11	.
Crepis pulchra	.	4	.	11	.
Sanguisorba minor	.	.	14	16	.
Rumex scutatus	.	9	.	11	.
Rorippa austriaca	13	.	.	5	.
Potentilla reptans	13	.	.	5	.
Sambucus ebulus	.	.	7	.	.
Rumex acetosa	.	9	.	11	.
Phleum alpinum	.	.	.	11	.
Filago arvensis	.	17	14	11	.
Betula pendula	.	4	.	11	.
Bromopsis biebersteinii	.	4	.	11	.
Campanula sibirica	.	9	.	11	.
Euphorbia stricta	.	.	.	5	.
Heracleum pubescens	.	9	.	5	.
Veronica petraea	.	9	.	11	.
Convolvulus arvensis	.	.	.	5	.
Festuca rubra agg.	.	4	.	11	.
Pimpinella saxifraga	.	4	7	.	.
Myosotis scorpioides agg.	13	9	.	5	.
Scabiosa ochroleuca	.	.	.	11	.
Senecio viscosus	.	4	.	5	.
Koeleria eriostachya	.	.	.	5	.
Potentilla argentea	.	.	.	5	.
Phleum pratense	13	4	.	11	.
Verbascum nigrum	.	.	.	5	.
Clinopodium acinos	.	.	.	11	.
Rhinanthus minor	.	.	.	5	.
Urtica dioica	.	.	.	5	.
Lathyrus pratensis	.	9	.	5	.
Cardamine impatiens	.	.	.	5	.
Festuca karsiana	.	.	.	5	.
Salix pseudomedemii	.	4	.	5	.
Betula litwinowii	.	13	.	11	.
Agrimonia eupatoria	.	.	.	5	.
Vulpia ciliata	.	.	.	5	.
Melilotus officinalis	.	9	7	16	.
Leontodon caucasicus	.	4	.	5	.
Dorycnium pentaphyllum	.	.	.	5	.
Carpinus betulus	.	.	.	5	.
Genista suanica	.	4	.	.	.
Mirorrhinum minus	.	4	.	.	.
Taraxacum sec. *Taraxacum*	.	9	.	.	.
Heracleum scabrum	13	4	.	.	.
Carex sylvatica	.	.	.	5	.
Betula pubescens	.	.	.	5	.
Artemisia splendens	.	.	.	5	.
Cladochaeta candidissima	.	.	.	5	.
Campylium stellatum (B)	.	.	.	5	.
Euphorbia peplus	.	.	.	5	.
Scrophularia umbrosa	.	.	.	5	.

Vegetation type	**Tus-Cal**	**Epil**	**Pet-Cre**	**Sal-Myr**	**Sal-Hip**
Number of relevés	8	23	14	19	6
Linaria meyeri	.	4	.	5	.
Brachythecium salebrosum (B)	.	.	.	5	.
Inula britannica	.	.	.	5	.
Silene lacera	.	4	.	5	.
Campanula alliariifolia	.	4	.	5	.
Astrodaucus orientalis	.	9	14	5	.
Lactuca racemosa	13	.	.	5	.
Phleum phleoides	.	4	.	5	.
Populus tremula	.	.	7	5	.
Parietaria judaica	.	4	.	5	.
Poa palustris	.	.	7	5	.
Erysimum brevistylum	.	4	.	5	.
Malus sylvestris agg.	.	.	.	5	.
Veronica filiformis	.	.	7	5	.
Lapsana communis	.	4	.	5	.
Dianthus cretaceus	.	4	.	5	.
Hordeum brevisubulatum subsp. *violaceum*	.	.	.	5	.
Leontodon hispidus	.	9	7	5	.
Thymus nummularius	.	4	.	.	.
Linum catharticum	.	.	.	5	.
Hedysarum caucasicum	.	4	.	.	.
Trifolium hybridum	.	9	.	.	.
Hieracium racemosum	.	4	.	.	.
Primula luteola	.	4	.	.	.
Bunias orientalis	.	4	.	.	.
Ajuga reptans	.	4	.	.	.
Cynodon dactylon	13	.	14	5	.
Veronica peduncularis	.	4	7	16	.
Silene dianthoides	.	4	.	.	.
Anthriscus ruprechtii	.	4	.	.	.
Galium mollugo	.	.	7	16	.
Ranunculus polyanthemos	.	4	.	5	.
Gnaphalium supinum	.	4	.	.	.
Campanula rapunculoides	.	4	.	.	.
Sagina saginoides	.	9	.	.	.
Festuca ovina agg.	.	9	.	.	.
Teucrium orientale	.	.	7	5	.
Ranunculus brachylobus	.	4	.	.	.
Odontarrhena muralis	.	4	.	.	.
Epilobium angustifolium	.	4	7	.	.
Cystopteris fragilis	.	4	.	.	.
Abies nordmanniana	.	4	.	.	.
Barbarea vulgaris	.	4	.	.	.
Hypericum orientale	.	4	.	.	.
Bupleurum falcatum	.	4	.	.	.
Gnaphalium caucasicum	.	4	.	.	.
Hypericum linarioides	.	4	.	.	.
Dryopteris filix-mas	.	4	.	.	.
Antennaria caucasica	.	4	.	.	.
Minuartia recurva	.	4	.	.	.
Epilobium hirsutum	.	.	.	.	17
Nonea versicolor	.	4	.	.	.
Filago vulgaris	.	4	.	.	.
Juncus inflexus	.	.	.	.	17
Scleranthus annuus	.	.	.	5	17
Hieracium umbellatum	.	4	.	.	.
Medicago monspeliaca	.	.	7	.	.
Populus nigra	13	.	.	.	17
Galium aparine	.	.	.	.	17
Pyrus communis	.	.	.	.	17
Cardamine uliginosa	.	9	.	.	.
Lycopus europaeus	13	.	7	.	17
Cornus sanguinea	.	.	7	.	.
Centaurea iberica	.	.	.	.	17
Arrhenatherum elatius	.	9	.	.	.

Vegetation type	**Tus-Cal**	**Epil**	**Pet-Cre**	**Sal-Myr**	**Sal-Hip**
Number of relevés	8	23	14	19	6
Rumex crispus	13	.	.	.	17
Funaria hygrometrica (B)	.	4	.	.	.
Linaria genistifolia	.	.	7	.	17
Lolium perenne	.	.	7	5	17
Galinsoga quadriradiata	.	.	7	.	.
Astragalus glycyphyllos	.	.	7	.	17
Persicaria maculosa	.	.	7	.	.
Tragopogon graminifolius	.	.	7	.	.
Deschampsia cespitosa	.	9	.	.	.
Dipsacus strigosus	.	.	7	.	.
Hypericum nummularioides	.	9	.	.	.
Veronica gentianoides	.	4	.	.	.
Veronica anagallis-aquatica	13	.	.	.	.
Picris hieracioides	.	4	.	.	.
Picea orientalis	.	4	.	.	.
Salvia pratensis	.	.	7	.	.
Artemisia vulgaris	.	9	14	16	17
Valeriana alliariifolia	13	.	.	.	.
Hygroamblystegium varium (B)	.	.	.	.	17
Astragalus fragrans	.	9	.	.	.
Aconogonon alpinum	.	9	.	.	.
Oplismenus hirtellus	.	.	.	.	17
Sagina oxysepala	.	13	.	.	.
Cruciata coronata	.	13	.	.	.
Pohlia filum (B)	.	13	.	.	.
Artemisia campestris	.	4	.	.	17
Hypericum perforatum	.	9	.	11	17
Fragaria vesca	.	13	.	.	.
Myosoton aquaticum	.	.	.	.	17
Tagetes minuta	.	.	.	.	17
Bromus squarrosus	.	.	.	.	17
Alyssum alyssoides	.	.	14	5	17
Salix caucasica	.	17	7	.	.
Onobrychis viciifolia	.	.	7	.	.
Lactuca saligna	.	.	7	.	.
Sedum tenellum	.	.	.	.	17
Persicaria hydropiper	.	.	.	.	17
Carex muricata agg.	.	4	7	5	17
Schedonorus pratensis	.	.	.	.	17
Perilla frutescens	.	.	.	.	17
Euphorbia hirsuta	.	.	.	.	17
Erigeron annuus	13	.	14	11	17
Ochlopoa annua	13	4	7	5	17
Arctium lappa	.	.	7	.	.
Achillea filipendulina	.	.	7	.	.
Grimmia pulvinata (B)	.	.	7	.	.
Stachys annua	.	.	7	.	.
Rhaponticum repens	.	.	7	.	.
Anagallis arvensis	.	.	7	.	.
Clinopodium nepeta	.	.	7	.	.
Abietinella abietina (B)	.	.	7	.	.
Xeranthemum annuum	.	.	7	.	.
Bromus racemosus agg.	13	.	.	.	.
Bolboschoenus maritimus	13	.	.	.	.
Dysphania botrys	13	.	.	.	.
Cratoneuron filicinum (B)	13	.	.	.	.
Polygala alpicola	13	.	.	.	.
Gnaphalium uliginosum	13	.	.	.	.
Persicaria lapathifolia	13	.	.	.	.
Gnaphalium sylvaticum	13	.	.	.	.
Brachythecium campestre (B)	13	.	.	.	.
Clematis vitalba	.	.	7	.	.
Digitaria sanguinalis	.	.	7	.	.
Valeriana colchica	.	9	.	11	.
Cichorium intybus	.	.	7	.	17

Vegetation type	**Tus-Cal**	**Epil**	**Pet-Cre**	**Sal-Myr**	**Sal-Hip**
Number of relevés	8	23	14	19	6
Epilobium tetragonum agg.	.	.	7	.	.
Sonchus asper	.	.	.	5	.
Mentha arvensis	.	.	7	.	.
Bryum klinggraeffii (B)	13	4	7	.	.
Laserpitium hispidum	.	.	.	5	.
Gaudiniopsis macra	13	.	7	.	.
Herniaria incana	.	.	7	.	.
Juniperus communis	.	4	.	.	.
Hygrohypnum ochraceum (B)	.	.	7	.	.
Humulus lupulus	.	.	7	.	.
Crepis setosa	.	.	7	.	.
Lappula squarrosa	.	9	7	.	.
Viola kitaibeliana	.	.	7	.	.
Sedum hispanicum	.	.	7	.	.
Epilobium dodonaei	.	.	7	.	.
Artemisia incana	.	4	.	.	.
Epilobium ponticum	.	9	.	.	.
Scirpus sylvaticus	13	.	.	.	.
Trifolium spadiceum	13	4	.	.	.
Oxyria digyna	.	9	.	.	.
Carlina vulgaris	.	9	.	.	.
Vicia cracca	.	4	.	.	.
Plagiomnium cuspidatum (B)	13	.	.	.	.
Rorippa palustris	13	.	.	.	.
Silene vulgaris	13	4	.	.	.
Minuartia imbricata	.	4	.	.	.
Pohlia drummondii (B)	.	4	.	.	.
Juncus effusus	13	.	.	.	.
Trigonocaryum involucratum	.	4	.	.	.
Saxifraga paniculata	.	4	.	.	.
Moehringia trinervia	.	4	.	.	.
Murbeckiella huetii	.	4	.	.	.
Carex leporina	.	4	.	.	.
Sedum acre	.	4	.	.	.
Saxifraga flagellaris	.	4	.	.	.
Lactuca serriola	.	4	7	.	.
Luzula spicata	.	4	.	.	.
Rubus idaeus	.	4	.	.	.
Rostraria cristata	.	.	7	.	.
Medicago sativa agg.	.	.	7	.	.
Saxifraga sibirica	.	4	.	.	.
Sedum sexangulare	.	4	.	.	.
Scrophularia ruprechtii	.	4	.	.	.
Cerastium arvense	.	4	.	.	.
Pohlia wahlenbergii (B)	13	.	.	.	.
Poa trivialis	13	.	.	.	.
Rumex alpinus	.	4	.	.	.
Papaver oreophilum	.	4	.	.	.
Geranium ibericum	.	4	.	.	.
Sedum caespitosum	.	4	.	.	.
Scrophularia olympica	.	4	.	.	.
Echinochloa crus-galli	13	.	.	.	.

Electronic supplementary materials (paper 3)

Table S3 Table of vegetation plots.

Table S4 Vegetation-plot data and environmental variables.

Fig 1S–7S Gravel-bar habitats – additional pictures.

Paper 4

Kalníková, V., Chytrý, K., Biţa-Nicolae, C., Bracco, F., Font, X., Iakushenko, D., Kącki, Z., Kudrnovsky, H., Landucci, F., Lustyk, P., Milanović, D., Šibík, J., Šilc, U., Uziębło A.K., Villani, M. and Chytrý, M. (manuscript) Vegetation of the European mountain river gravel bars: a formalized classification.

Vegetation of the European mountain river gravel bars: a formalized classification

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Abstract

Aims: River gravel bars belong to endangered habitats in Europe. However, classification schemes of their vegetation and habitat types differ among European countries, and they are even ignored in some national schemes. This causes problems in conservation planning, monitoring and management. Hence we aimed at building the first unified vegetation classification for river gravel-bar habitats across European mountain systems.
Location: Europe.
Methods: In total 4769 vegetation-plot records of river gravel bar plant communities were collected from national, regional or private databases, digitized from the literature and newly collected in the field. A hierarchical classification expert system with formal definitions of vegetation types was created. The formal definitions combined the criteria of presence or cover of groups of species with similar ecology or single species narrowly specialized to a particular gravel-bar habitat. The TWINSPAN classification was applied to early-successional vegetation types to check whether the classification based on formal definitions is supported by the results of unsupervised classification. Similarity patterns among vegetation types were visualized using the DCA ordination.
Results: Early-successional and scrub gravel-bar vegetation types were respectively classified to two classes: *Thlaspietea rotundifolii* and *Salicetea purpureae*. Two subassociations, eleven

associations and four alliances (*Calamagrostion pseudophragmitae*, *Epilobion fleischeri*, *Salicion cantabricae* and *Salicion eleagni*) were defined formally. Based on a critical revision, some associations or alliances defined in the previous literature were merged or discarded. The main variability within the gravel-bar vegetation is connected with the altitudinal gradient, biogeographical variation, local hydro-morphological processes and various successional changes.

Conclusions: The first unified and formalized classification system of the European mountain river gravel-bar vegetation was created, and species composition, ecology and distribution of these types were characterized. The syntaxonomical nomenclature of these types was checked and revised. This study provides a base for conservation planning of these threatened and rapidly disappearing habitats.

Keywords: Association; Europe; Phytosociology; Riparian vegetation; River gravel bars; Syntaxonomy; Threatened habitat; Vegetation classification; Vegetation database; Vegetation succession

1 Introduction

Gravel bars of mountain stream beds and banks are azonal habitats dependent on hydro-morphological conditions, which host specialized flora and specific vegetation types. They are typical of wandering or braided river systems occurring from glacial river floodplains in the alpine belt to broad floodplains in the piedmonts. They develop on rivers with significant variation in discharge and are maintained by torrents that are bringing new sediments and disturbing or rearranging river banks. Gravel bars occur preferably in places where the strong current suddenly slows down, allowing the deposition of the particles released by bank erosion in the upstream sections (Montgomery and Buffington, 1998; Tockner *et al.*, 2006; Galia and Škarpich, 2013; Škarpich *et al.*, 2013; Hohensinner *et al.*, 2018). The erosion-accumulation processes and fluctuating water level, including periods of submersion, cause continuous instability and spatio-temporal habitat heterogeneity (Junk et al., 1989; Tockner *et al.*, 2000; Ward et al. 2002). As a result, single gravel bars often support vegetation types in different successional stages to occur next to each other (Richards *et al.*, 2002; Karrenberg *et* al., 2003; Gilvear *et al.*, 2008; Corenblit *et al.*, 2009; Prach *et al.*, 2014).

Vegetation succession on river gravel bars is very fast (Jeník, 1955; Prach *et al.*, 2016; Kalníková *et al.*, 2018; Caponi *et al.*, 2019). Frequent disturbances support the development of pioneer early-successional vegetation, which subsequently develops into denser vegetation with shade-tolerant species if the frequency of disturbances decreases (Tockner *et al.*, 2006). On the active gravel bars of natural and unregulated rivers, forest vegetation is often lacking, while scrub is the oldest successional stage (Nilsson *et al.*, 1989; Pettit and Froend, 2001; Loučková, 2011). The successional gradient is also reflected in the classification of the gravel-bar vegetation. In the EuroVegChecklist (Mucina *et al.*, 2016) the early-successional plant communities are assigned to the order *Epilobietalia fleischeri* of the class *Thlaspietea rotundifolii*, while scrub vegetation of more developed successional stages is assigned to the alliances *Salicion eleagno-daphnoidis* and *Salicion cantabricae* of the order *Salicetalia purpureae*, class *Salicetea purpureae*.

Gravel-bar habitats are strongly affected by human activities. In Europe, they are quickly disappearing, while their remnants experience a considerable decline in biological quality of their natural vegetation (Müller, 1995; Tockner *et al.*, 2006; Muhar *et al.*, 2007; Gurnell *et al.*, 2009; Skoulikidis *et al.*, 2009; Rădoane *et al.*, 2013; Janssen *et al.*, 2016). They are classified as vulnerable in the European Red List of Habitats, based on the criterion of a large reduction in the habitat area over the last 50 years (about 35%; Janssen *et al.*, 2016). The main pressures include increasing regulation of gravel-bar channels, sediment extraction and construction of dams, weirs and hydropower plants (Müller, 1995; Kondolf, 1997; Lytle and Poff, 2004; Dai and Liu, 2013). The damage to the natural hydro-morphological regime leads to a change from the multi-thread to the single-thread channels, faster pedogenesis and homogenization of gravel-bar microtopography, transformation of the gravelly beds to bedrock beds and channel incision (Kondolf, 1997; Škarpich *et al.*, 2013; Hajdukiewicz and Wyżga; 2019). Moreover, gravel bars with disturbed natural flooding regime are prone to invasion by alien plants (e.g. Smale, 1990; Meier *et al.*, 2013; Wilczek *et al.*, 2015; Brummer *et al.*, 2016). The habitat destruction and fragmentation also have a significant impact on populations of specialized gravel-bar species, which are included on the national Red Lists in many European countries (e.g. Sochor *et al.*, 2013; Werth *et al.*, 2014; Skokanová *et al.*, 2015; Sitzia *et al.*, 2016; Werner, 2016; Fink *et al.*, 2017). Three habitat types of river gravel bars are listed in Annex I of the European Habitats Directive, which is the legal basis of the Natura 2000 network (3220 Alpine rivers and the herbaceous vegetation along their banks, 3230 Alpine rivers and their ligneous vegetation with *Myricaria germanica*, and 3240 Alpine rivers and their ligneous vegetation with *Salix eleagnos*; European Commission 2013). In the European countries that are not members of the European Union, the habitat is encompassed in the Emerald Network, which is a network of Areas of Special Conservation Interest implemented by the Council of Europe (C3.55 Sparsely vegetated river gravel banks and C3.62 Unvegetated river gravel banks). However, in many European countries, there are insufficient or no data available on these habitats, which makes it difficult to assess their distribution, quality and trends (Janssen *et al.*, 2016).

European classification of terrestrial habitats is largely based on phytosociological classification of vegetation (Rodwell *et al.*, 2018). However, a critical international revision of the classification of gravel-bar vegetation is still missing, although there has been a long history of gravel-bar vegetation studies, and consolidated international information on this habitat complex is much needed for effective conservation planning. This vegetation was most studied in the Alps, starting with pioneering studies from Switzerland (Rübel, 1912; Siegrist, 1913; Hager, 1916; Lüdi, 1921; Gams, 1927) and continuing with more comprehensive local phytosociological surveys (Aichinger, 1933; Volk, 1939; Braun-Blanquet, 1948; Moor, 1958). Several studies of this vegetation were also performed in the Carpathians (Sillinger, 1933; Klika, 1936; Pawłowski and Walas, 1949; Jeník, 1955; Jurko, 1964; Kopecký, 1968; Pázmány, 1969) and other parts of Europe such as Croatia (Trinajstić, 1964), France (Tchou, 1948; Vanden Berghen, 1963), Norway (Klokk, 1978), Spain (Rivas-Martínez *et al.*, 1984) and other countries (the most important studies for each European country are listed in Appendix S2). Despite the long history of the gravel-bar research, there are still many unexplored areas in Europe, especially the Balkans, some parts of the Carpathians, Eastern European countries, Scandinavia and the Caucasus, although new phytosociological studies from some of such white spots have appeared recently (e.g. Milanović and Stupar, 2017; Drescher, 2018; Nuță and Niculescu, 2019; Kalníková *et al*., 2020).

Classification schemes of the gravel-bar vegetation in various European countries vary due to diverse classification approaches. Studies were usually done within restricted mountain regions, and researchers sometimes described the same vegetation type in different regions under different association names. The concepts of higher vegetation units also varied considerably. Such differences are apparent when comparing national vegetation overviews (e.g. Kojić, 1998;

Valachovič and Kliment, 1995; Valachovič, 2001; Schubert *et al.*, 2001; Matuszkiewicz, 2007; Sanda *et al.*, 2008; Trinajstić, 2008; Chytrý, 2011, 2013). On the European scale, Valachovič *et al.* (1997) reviewed the herbaceous scree vegetation of the *Thlapietea rotundifoliae* class (including river gravel-bar vegetation) to the association level. Recent syntaxonomical overview of European vegetation (Mucina *et al.*, 2016) classified gravel bar vegetation to the alliance level. However, both of these overviews are incomplete and based only on a review of the existing literature and expert knowledge rather than data analysis. The need for a unified critical overview of the gravel-bar vegetation and its current state in Europe led to the establishment of the European Gravel Bar Vegetation Survey project in 2012 as one of the pilot projects of the European Vegetation Archive (EVA; Chytrý *et al.*, 2016). Cooperation within this project included collecting existing data from vegetation plots (Kalníková and Kudrnovsky, 2017), filling gaps in these data by targeted field research and nomenclature revision of the relevant previously described syntaxonomical units. The last stage of the project, presented in this paper, is the development of a pan-European vegetation classification system for gravel-bar habitats complemented with formal definitions of individual vegetation types summarized in a classification expert system (Bruelheide, 1997; 2000; Kočí *et al.*, 2003; Landucci *et al.*, 2015; Tichý *et al.*, 2019).

The aims of this paper are to (1) revise and unify previous classification systems of river gravel-bar vegetation in European mountain systems; (2) define vegetation types using the formal language for vegetation classification expert systems to the association level; (3) describe species composition, ecology and distribution of these types; and (4) revise phytosociological nomenclature of target vegetation types.

2 Methods

2.1 Study habitat

Gravel-bar habitats are highly variable in their topography, lithology and sediment particle size (Müller, 1995; Montgomery and Buffington, 1998; Richards *et al.*, 2002; Gilvear *et al.*, 2008; Corenblit *et al.*, 2009). They occur on streams with either spring or glacier source, which is reflected by differences in the frequency and duration of floods (Milner and Petts, 1994; Tockner *et al.*, 2000; Malard *et al.*, 2006). Substrate and soil reaction may vary in the local habitat micromosaics as the substrate of different origin can be transported by the river from distant parts of the valley. Due to this habitat diversity, river gravel bars are characterized by high species richness and beta-diversity (Malanson and Butler, 1991; Tabacchi *et al.*, 1998; Tockner and Malard, 2003; Tockner *et al.*, 2006; Chytrý *et al.*, 2015).

Several plant species are considered as gravel-bar specialists. Their key functional traits are the high dispersibility of diaspores, fast, often clonal growth, adaptation to disturbances, and the ability to grow on poor substrates with periods of drought stress (Jeník, 1955; Stöcklin, 1999; Karrenberg *et al.*, 2003; Oishi *et al.*, 2010; Yoishkawa *et al.*, 2012; Leuschner and Ellenberg, 2017). Such adaptations have evolved in several shrub species (e.g. *Hippophaë rhamnoides*, *Myricaria germanica* or *Salix* spp.; Jeník, 1955; Skogen, 1972; Karrenberg *et al.*, 2003; Francis *et al.*, 2005; Leuschner and Ellenberg, 2017), herbaceous species (e.g. *Epilobium* and *Petasites* species; Stöcklin and Zoller, 1991; Stöklin and Favre, 1994; Stöcklin, 1999; Uziębło, 2011), bryophytes (e.g. *Dichodontium pellucidum* or *Racomitrium canescens*; Vitt *et al.*, 1986; Muotka and Virtanen, 1995; Kalníková *et al.*, 2017) and lichens (*Stereocaulon* species; Vančurová *et al.*, submitted).

The gravel-bar specialists are often accompanied by a variety of species of different habitats occurring upstream or next to the floodplain (Tockner *et al.*, 2006; Uziębło and Barć, 2015). Early-successional stages of gravel bars serve as refugia for light-demanding and drought-adapted species (Jankovská, 2008). It is possible that they represent the primary habitat of some weed and ruderal communities (Slavík, 1978). However, many species occur on gravel bars in low population densities and survive there only for a short period (Müller and Sharms, 2001; Tockner *et al.*, 2006; Corneblit *et al.*, 2009; Prach *et al.*, 2014; Kalníková *et al.*, 2018).

The composition of river gravel-bar vegetation is influenced by the spatial mass effect, containing many species of adjacent and upstream non-floodplain habitats, and is characterized by a large degree of randomness, especially in the early-successional stages (Jeník, 1955; Malanson and Butler, 1991; Uziębło, 2011; Uziębło and Barć, 2015; Egger *et al.*, 2019). Therefore, some authors questioned whether they could be described as distinct plant community types (Jeník, 1955). Nevertheless, certain patterns of species composition in river gravel-bar habitats are characteristic for the mountain streams all over the world (e.g. Fyles and Bell, 1986; Prach, 1994; Onipchenko, 2002; Hussain *et al.*, 2012; Prach *et al.*, 2014). Gravel-bar vegetation contains specialist species of this habitat as a whole, and of its particular successional stages or microhabitats (Fig. 1). However, the number of such species in Europe is small, depending on the biogeography and altitude. The most typical specialists species are *Calamagrostis pseudophragmites*, *Chondrilla chondrilloides*, *Epilobium colchicum*, *E. dodonaei*, *E. fleischeri*, *Hippophaë rhamnoides*, *Myricaria germanica*, *Salix cantabrica*, *S. daphnoides*, *S. eleagnos* and *S. purpurea* (e.g. Jeník, 1955; Moor, 1958; Müller, 1995; Oriolo and Poldini, 2002; Kalníková *et al.*, 2020).

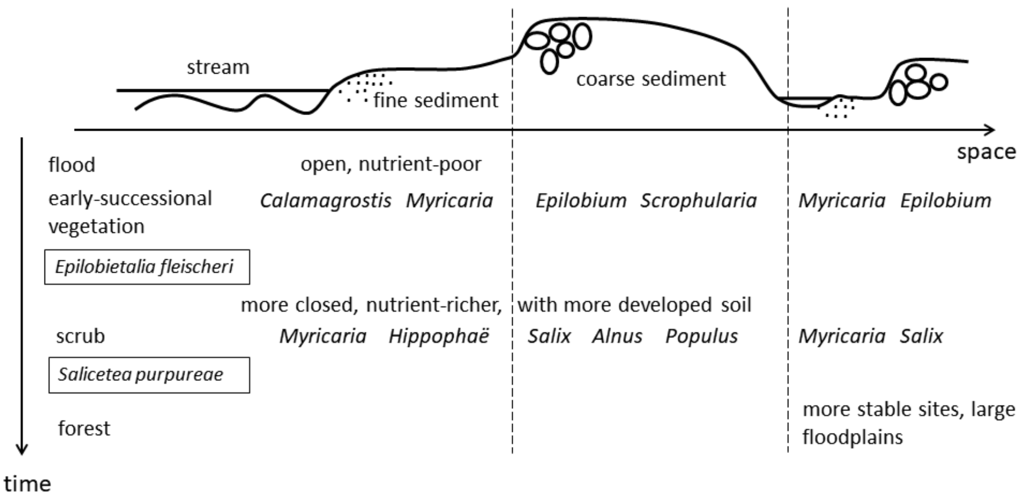

Fig. 1 A scheme of the spatial zonation and succession in river gravel-bar habitats.

2.2 Data collection and filtering

The study area includes the whole of Europe, but the studied vegetation is restricted to mountain systems and their foothills (64°N–39° N, 7°W–41°E; Fig. 2). The object of the study is the cool-temperate and boreal gravel-bar vegetation belonging to the phytosociological order *Epilobietalia fleischeri* (class *Thlaspietea rotundifolii*) and the alliances *Salicion eleagno-daphnoidis* and *Salicion cantabricae* of the order *Salicetalia purpureae* (class *Salicetea purpureae*). Excluded is the vegetation of gravel bars in beds of periodically dry Mediterranean rivers (so-called "fiumare") belonging to *Andryetalia ragusinae*, *Scrophulario-Helichrysetalia*, *Nerio-Tamaricetea*, *Salicion triandro-neotrichae* and *Salicion salviifoliae*. To properly delimit the types of the focal vegetation, our data selection also included non-target riparian vegetation types (e.g. *Petasites* stands or some types of ruderal and scree vegetation).

We collected vegetation plots stored in various European national, regional or private vegetation databases which (i) belonged to the habitat types 3220, 3230 and 3240 of Natura 2000 (Annex I of the EU Habitats Directive) or (ii) contained information on the origin on a river gravel bar or (iii) were assigned to the predefined vegetation types (belonging to *Epilobietalia fleischeri* order or *Salicion eleagno-daphnoidis* alliance) or (iv) contained at least one of the diagnostic species of gravel-bar vegetation listed in the literature (*Calamagrostis pseudophragmites*, *Epilobium dodonaei*, *E. fleischeri*, *Erucastrum nasturtiifolium*, *Hippophaë rhamnoides*, *Chondrilla chondrilloides*, *Myricaria germanica*, *Petasites kablikianus*, *Salix daphnoides*, *S. eleagnos*, *S. purpurea*, *Silene tatarica* and *Trifolium saxatile*). In doubtful cases, data were verified in the original literature, or the location of vegetation plots was checked with the help of aerial photographs (www.google.com/earth). As there was an overlap between some databases, duplicates were eliminated. In total, 2707 vegetation plots were assembled. Missing geographic coordinates of vegetation plots were assigned based on the description of their sites in the original publication. To fill the obvious data gaps, we digitized vegetation plots from several literature sources and performed field sampling in the countries or regions where the gravel-bar vegetation had not been sufficiently explored (mainly in Bulgaria, France, Georgia, Montenegro, North Macedonia, Norway, Poland, Serbia, Sweden and Switzerland). Thus, further 2385 vegetation plots were collected, which are stored in the Gravel Bar Vegetation Database established for this purpose (GIVD ID: EU-00-025; Kalníková and Kudrnovsky, 2017). The plots contained data on species cover-abundance, mostly estimated on the Braun-Blanquet scales (Westhoff and van der Maarel, 1973). They were stored in the TURBOVEG 2 database software (Hennekens and Schaminée, 2001). Detailed information about the data sources is in Appendix S3.

The raw dataset used for the analysis included 4942 vegetation plots. Since it contained records from plots of variable size, which may affect the results (Otýpková and Chytrý, 2006; Dengler *et al.*, 2009; but see Peterka *et al.*, 2020), we removed plots of the size <4 m^2 or >200 m^2. The plots with missing size information were preserved in the dataset, assuming that most of them were within this range of plot sizes. The 4769 vegetation plots collected on gravel bars remained in the data set and were used for analysis. Records of the same species in different layers were merged so that each species was represented by a single row in the data matrix.

2.3 Nomenclature

The taxonomic concepts and nomenclature of vascular plants were unified according to the Euro+Med PlantBase (Euro+Med; accessed in May 2019), and some missing synonyms were verified in The Plant List (The Plant List; accessed in May 2019). Nomenclature for mosses follows Hill *et al.* (2006), for liverworts Grolle and Long (2000), and for lichens the Mycobank Database (Mycobank Database; accessed in April 2018). However, in the majority of the plots, bryophytes and lichens were not recorded. Taxa determined only to the genus level were omitted. Subspecies records were merged to the species level. Taxa of problematic, unstable or ambiguous status (usually not equally differentiated in all the data sources) were merged into aggregates or species sensu lato (Ehrendorfer, 1973; Appendix S4) to minimize the taxonomic bias (Jansen and Dengler, 2010). After taxonomic standardization and reduction, 2729 taxa remained. Names of alliances and higher syntaxonomic units follow EuroVegChecklist (Mucina *et al.*, 2016). Names of associations and subassociations were critically revised following the 4th edition of the International Code of Phytosociological Nomenclature (Theurillant *et al.*, 2020).

2.4 Classification expert system

Our aim was to develop an expert system for automatic supervised vegetation classification following the principles outlined by Bruelheide (2000), Kočí *et al.* (2003), Landucci *et al.* (2015) and Tichý *et al.* (2019). We used an expert system with a hierarchical structure including the syntaxonomical levels of the orders, alliances and associations, which classifies in the bottom-up direction, i.e. associations (in two cases with subassociations) are classified first, then the plots not assigned to any association are classified to alliances, and then the plots not assigned to any alliance are classified to the order.

The expert system comprises a set of logical definitions of vegetation types (subassociations, associations, alliances and order). These definitions combine criteria based on a threshold cover or presence of functional species groups (Landucci *et al.*, 2015, Tichý *et al.*, 2019), which in this case comprise species narrowly specialized to a particular habitat, minimum cover or presence of a single specialist species, and the presence of sociological groups of species with a statistical tendency of co-occurrence in vegetation plots. The sociological species groups were developed using the Cocktail method (Bruelheide, 1997; 2000; Kočí *et al.*, 2003) with the *phi* coefficient as a measure of interspecific association (Chytrý *et al.*, 2002). In the logical definitions, individual criteria were combined using the logical operators AND, OR and NOT (Bruelheide, 1997).

The development of classification criteria reflected various physiognomy and structure of gravel-bar vegetation. To distinguish the gravel-bar vegetation from other vegetation types, we created a group of specialized gravel-bar species ("Gravel-bar specialists") with the help of literature. Subsequently, to separate early-successional herbaceous vegetation from the scrub, functional groups of species typical of different successional stages were created ("Gravel-bar herbs" and "Gravel-bar shrubs"). These groups were set against each other using their covers. This method was chosen because most of the collected vegetation plots missed the information on vegetation layers, or the information was recorded inconsistently. If the vegetation consists mainly of the gravel-bar specialists of early-successional stages, scrub species are not dominant (although they can be present as juveniles or solitary adult species which survived the flood). Increasing cover of scrub species and competitive herbaceous species results in the disappearance of light-demanding a competitively weak herbaceous gravel-bar specialists.

Two different approaches to logical definitions of vegetation types were used, one for early-successional vegetation and the other for scrub and tall grassland with *Calamagrostis pseudophragmites*. Early-successional vegetation, which usually lacks distinct dominant species, was classified based on sociological species groups. Criteria were defined based on literature search and expert knowledge. In contrast, scrub and tall grassland with *Calamagrostis pseudophragmites* were defined based on their physiognomy characterized through the dominance or codominance of single species. The gravel-bar vegetation types were also delimited against other vegetation types using functional species groups, e.g. sandy-silt substrate herbs, mire species, or forest herbs. These groups were compiled partly based on the literature (e.g. Janssen *et al.*, 2016; Mucina *et al.*, 2016), partly on our field experience. The definitions used the following terms (with specific examples):

• <#TC Other shrubs and trees GR 50> – The total cover of the functional species group "Other shrubs and trees" is greater than 50%.

• <#TC Gravel-bar herbs GR #TC Gravel-bar shrubs> – The total cover of the functional species group "Gravel-bar herbs" is greater than the total cover of the functional species group "Gravel-bar shrubs".

• <Calamagrostis pseudophragmites GR 25> – The cover of the species Calamagrostis pseudophragmites is greater than 25%.

• <Calamagrostis pseudophragmites GR #$$> – The cover of the species Calamagrostis pseudophragmites is greater than the cover of any other species in the vegetation plot.

• <#02 Epilobium fleischeri group> – At least two species of the sociological species group "Epilobium fleischeri group" must be present.

• <#TC Other shrubs and trees GR 50> – The total cover of the functional species group "Other shrubs and trees" is greater than 50%.

The diagnostic species of associations and subassociations were calculated using the *phi* coefficient of association for the virtually equalized size of all groups of plots that represented associations and subassociations (Tichý and Chytrý, 2006). We considered the species with a *phi* coefficient value higher than 0.4 and 0.5 as diagnostic and highly diagnostic, respectively; those occurring in more than 25% of plots of the cluster as constant species; and those with a cover higher than 25% in at least 5% of plots of the cluster as dominant species. The significance of fidelity was tested using Fisher's exact test ($P < 0.05$). Diagnostic species were calculated using a stratified-resampled dataset of vegetation plots. The stratification was based on criteria combining spatial distance among vegetation plots and similarity in their species composition according to Divíšek and Chytrý (2018). The similarity between each pair of plots within a single association or subassociation was measured using the β_{sim} index (Lennon *et al.*, 2001). If two plots were closer than 1000 m in space and their compositional similarity was 0.4 or higher at the same time, then just one plot from the pair was selected randomly. We applied resampling separately to the plots of each association as classified by the expert system that was represented by at least 35 plots. However, despite this limitation, some diagnostic species may show local or specific validity, that can be applied within certain vegetation type only, not in general.

The expert system, classification and determination of diagnostic species were processed in the JUICE 7.0 program (Tichý, 2002), and the stratification was calculated in R (R Core Team, 2019). Boxplots comparing climatic affinity of associations and subassociations used the Bioclim dataset of CHELSA (Karger *et al.*, 2017), from which we extracted values with the help of the raster package (Hijmans *et al.*, 2020). The distribution maps of associations were prepared in QGIS 3.10 (QGIS Development Team, 2020). All other graphics were prepared in R with the help of *tidyverse* package (Wickham, 2017).

2.5 Evaluation of the expert system using unsupervised classification and ordination

We visualized the variation in plant species composition among the formally defined associations using detrended correspondence analysis (DCA; Hill and Gauch, 1980) from the *vegan* package in R (Oksanen *et al.*, 2017).

To evaluate the expert system classification of the difficult-to-classify early-successional vegetation, we performed an unsupervised classification on the data subset containing the early-successional stages of the order *Epilobietalia fleischeri*. We selected the *Epilobietalia fleischeri* plots using the formulas from the expert system classification (E000 *Epilobietalia* vs. SSA0 *Salicion eleagno-daphnoidis*; see the expert system in Appendix S5) from the whole dataset of 4769 plots. We performed the hierarchical divisive classification of TWINSPAN (Hill, 1979) with four pseudo-species cut levels for species covers (0%, 2%, 5%, 10% and 20%) using the R package *twinspan* (Oksanen and Hill, 2019). The classification results were summarized in a dendrogram and plotted on the DCA ordination diagram, where they were compared with the results of classification by the expert system containing formal definitions.

In addition, the functionality of the expert system was tested on the whole European dataset using the EUNIS habitat classification (Chytrý *et al.*, submitted), in order to guarantee that the formal definitions of gravel-bar vegetation would not misidentify plots of other vegetation types as gravel-bar vegetation. This test (results not shown) indicated that misclassification cases are very rare.

3 Results

3.1 Syntaxonomical outline and descriptions of vegetation types

In total, 1365 plots were assigned by formal definitions to a single vegetation type on some level of the syntaxonomical hierarchy (i.e. they met the criteria of just one formal definition), of which 1177 plots were assigned to the association or subassociation level. The rest of the plots remained unclassified or were classified to more than one unit. As a result, 11 associations, 2 subassociations, 4 alliances of 2 classes of gravel-bar vegetation were formally defined. The diagnostic species were identified from 904 geographically stratified vegetation plots assigned to the associations and subassociations (Table 1 and 2). The classification scheme with distinguishing features of vegetation types and proposed syntaxonomy for associations and associations are given in Appendix S1. The geographic distribution of these types is presented in Fig. 2, and a detailed overview of the distribution of gravel-bar vegetation associations in Europe with the most important literature references is in Appendix S2.

Table 1 A shortened synoptic table of the early-successional gravel-bar communities: *Tussilagini farfarae-Calamagrostietum pseudophragmitae typicum* (TusTyp), *Tussilagini farfarae-Calamagrostietum pseudophragmitae phalaridetosum arundinaceae* (TusPha), *Epilobietum fleischeri* (EpiFle), *Epilobietum colchici* (EpiCol), *Myricario-Chondrilletum chondrilloidis* (MyrCho), *Epilobio dodonaei-Scrophularietum caninae* (EpiScr) and *Epilobietum dodonaei* (EpiDod). The classification is based on the expert system. The numbers are percentage occurrence frequencies (constancies). Other species are sorted by decreasing frequencies. Shaded species are sorted by their decreasing fidelity to a particular vegetation type: dark shading indicates values of *phi* ≥ 0.5 and light shading those of *phi* ≥ 0.4. Only species reaching a constancy of at least 20% in at least one vegetation type are shown. The letter B indicates bryophytes. See Appendix S6 for the full version of this synoptic table.

Vegetation type	TusTyp	TusPha	EpiFle	EpiCol	MyrCho	EpiScr	EpiDod
Number of plots	52	122	105	19	32	34	31
Tussilagini farfarae-Calamagrostietum pseudophragmitae							
Calamagrostis pseudophragmites	100	100	5	63	28	21	6
Ranunculus repens	2	45	2	.	3	3	6
Mentha longifolia	21	71	2	5	.	9	32
Phalaroides arundinacea	10	41	.	.	3	.	10
Myosotis scorpioides agg.	.	30	.	11	.	.	.
Rumex obtusifolius	.	26	.	.	.	.	6
Epilobietum fleischeri							

Epilobium fleischeri	.	.	100	.	.	.	.
Trifolium pallescens	.	.	35	.	.	3	.
Saxifraga aizoides	6	.	48	.	28	.	.
Rumex scutatus	4	2	40	11	3	3	.
Sempervivum arachnoideum	.	.	22	.	.	.	.
Saxifraga paniculata	.	.	22	.	.	.	.
Anthyllis vulneraria	2	1	49	11	22	3	6
Larix decidua	.	.	19	.	.	.	.
Linaria alpina	.	.	37	.	25	.	.
Epilobietum colchici							
Epilobium colchicum	.	.	.	100	.	.	.
Racomitrium canescens (B)	.	1	8	53	.	.	6
Silene compacta	.	.	.	37	.	.	.
Trisetum rigidum	.	.	.	37	.	.	.
Rumex acetosella	.	2	1	32	.	.	.
Senecio leucanthemifolius	.	.	.	26	.	.	.
Tripleurospermum caucasicum	.	.	.	26	.	.	.
Poa alpina	2	.	43	68	28	3	.
Petrorhagia saxifraga	.	.	1	26	.	3	.
Papaver fugax	.	.	.	21	.	.	.
Bryum caespiticium (B)	.	.	.	21	.	.	.
Sedum pallidum	.	.	.	21	.	.	.
Sedum spurium	.	.	.	21	.	.	.
Tanacetum parthenium	.	1	.	21	.	.	.
Myricario-Chondrilletum chondrilloidis							
Chondrilla chondrilloides	.	.	.	.	100	.	3
Dryas octopetala	2	.	8	.	50	.	.
Carex flacca	2	1	3	.	44	3	.
Campanula cochleariifolia	4	.	30	.	50	6	.
Carex ornithopoda	2	.	1	.	25	.	.
Salix purpurea	29	43	19	16	81	32	13
Myricaria germanica	33	11	17	16	63	3	6
Epilobio dodonaei-Scrophularietum caninae							
Scrophularia canina	4	.	.	.	.	100	.
Echium vulgare	2	7	9	11	3	71	48
Melilotus albus	13	25	6	.	.	65	35
Euphorbia cyparissias	.	1	18	.	3	59	42
Populus nigra agg.	21	7	6	.	.	53	16
Reseda lutea	.	.	7	.	.	41	19
Oenothera biennis agg.	4	5	.	.	.	32	6
Epilobietum dodonaei							
Epilobium dodonaei	6	4	2	.	19	56	100
Daucus carota	8	15	4	.	3	41	71
Verbascum nigrum	.	2	1	.	.	.	23
Arenaria serpyllifolia agg.	2	7	1	32	.	9	48
Other species occurring in at least 20% in at least one vegetation type							
Agrostis stolonifera agg.	33	68	31	11	53	38	55
Salix eleagnos	42	10	21	.	50	71	39
Tussilago farfara	27	34	42	11	34	26	39
Galium mollugo agg.	19	12	10	5	19	59	42
Silene vulgaris	13	6	30	.	13	56	45
Artemisia vulgaris agg.	8	30	3	11	3	50	55
Medicago lupulina	10	20	5	26	13	32	48
Plantago lanceolata	8	26	2	16	6	47	42
Sanguisorba minor	4	4	8	11	13	47	52
Taraxacum sect. *Taraxacum*	17	25	7	5	22	32	29
Hypericum perforatum	2	9	3	16	3	50	42
Gypsophila repens	4	.	50	.	47	21	3
Tolpis staticifolia	10	.	54	.	53	6	.
Achillea millefolium agg.	8	15	10	16	25	15	29
Alnus incana	13	16	7	21	38	6	16
Poa compressa	12	14	7	11	.	21	48
Lotus corniculatus agg.	10	11	22	11	13	12	26
Dactylis glomerata	2	23	8	.	9	26	35
Plantago major	10	41	2	5	3	15	23
Elymus caninus	12	20	4	.	9	29	23
Trifolium pratense	8	16	19	26	3	9	16
Leucanthemum vulgare agg.	13	11	6	11	9	12	35
Trifolium repens	12	29	1	5	16	6	26
Cerastium fontanum	4	21	3	32	6	.	29
Equisetum arvense	27	38	3	5	.	6	16
Erigeron acris	4	2	24	37	16	6	.

Deschampsia cespitosa agg.	15	10	9	5	28	21	.
Leontodon hispidus s. l.	6	2	31	11	16	18	3
Erigeron canadensis	6	11	2	16	.	15	35
Pinus sylvestris	4	1	5	21	41	6	6
Petasites paradoxus	2	.	15	.	31	32	3
Erigeron annuus	4	10	.	.	.	41	26
Barbarea vulgaris	4	22	1	5	.	24	23
Poa nemoralis agg.	2	5	24	32	.	.	16
Eupatorium cannabinum	4	16	1	5	6	18	26
Tanacetum vulgare	6	22	.	.	.	9	35
Geranium robertianum agg.	2	7	1	.	3	29	29
Vicia cracca agg.	12	17	1	5	.	3	29
Picris hieracioides	2	2	5	5	.	29	23
Achnatherum calamagrostis	.	.	11	.	16	29	10
Saponaria officinalis	.	14	2	.	.	24	23
Salix daphnoides	13	2	12	.	28	3	.
Urtica dioica	2	25	3	.	.	3	23
Carduus defloratus	4	.	20	.	22	9	.
Clematis vitalba	.	5	1	.	.	32	16
Thymus praecox agg.	.	.	14	.	31	6	3
Petasites hybridus	8	23	1	.	13	6	3
Microrrhinum minus	.	.	.	.	3	26	23
Erucastrum nasturtiifolium	2	.	20	.	6	18	6
Salix euxina agg.	8	28	.	.	.	3	13
Myosoton aquaticum	4	23	.	.	.	6	19
Juncus articulatus	6	21	2	.	19	3	.
Sesleria caerulea	2	.	9	.	31	3	6
Pilosella piloselloides agg.	4	1	7	.	9	26	3
Impatiens parviflora	4	8	.	.	.	15	23
Bryum argenteum (B)	4	6	.	21	.	.	16
Lapsana communis	.	4	1	11	.	.	29
Centaurea paniculata agg.	2	4	1	.	3	12	23
Cichorium intybus	2	8	.	.	.	12	23
Sonchus oleraceus	2	9	.	5	.	6	23
Poa trivialis agg.	6	23	1	.	.	.	13
Holcus lanatus	.	16	1	.	.	.	23
Galeopsis speciosa	.	3	.	.	.	26	10
Diplotaxis tenuifolia	4	2	.	.	.	26	6
Pilosella officinarum	2	1	2	26	.	6	.
Lycopus europaeus	4	23	.	.	.	3	6
Pastinaca sativa	.	2	1	.	.	9	23
Prunella grandiflora	2	.	.	.	22	3	3
Polytrichum piliferum (B)	.	.	4	21	.	.	.
Peucedanum altissimum	.	.	.	.	.	21	3

Table 2 A shortened synoptic table of the scrub gravel-bar communities: *Salicetum cantabricae* (SalCan), *Epilobio dodonaei-Myricarietum germanicae* (EpiMyr), *Salicetum eleagno-purpureae* (SalEle), *Salici incanae-Hippophaëtum rhamnoidis* (SalHip) and *Saponario officinalis-Salicetum purpureae* (SapSal). The classification is based on the expert system. The numbers are percentage occurrence frequencies (constancies). Other species are sorted by decreasing frequencies. Shaded species are sorted by their decreasing fidelity to a particular vegetation type: dark shading indicates values of *phi* ≥ 0.5 and light shading those of *phi* ≥ 0.4. Only species reaching a constancy of at least 20% in at least one vegetation type are shown. See Appendix S7 for the full version of this synoptic table.

Vegetation type	SalCan	EpiMyr	SalEle	SalHip	SapSal
Number of plots	22	200	184	24	97
Salicetum cantabricae					
Salix cantabrica	100	.	.	.	.
Salix cinerea	55	.	3	.	.
Salix triandra	41	6	3	4	11
Epilobio dodonaei-Myricarietum germanicae					
Myricaria germanica	.	100	17	13	5
Saxifraga aizoides	.	24	3	.	.
Salicetum eleagno-purpureae					
Salix eleagnos	32	54	98	29	47

Salici incanae-Hippophaëtum rhamnoidis					
Hippophaë rhamnoides	.	3	3	100	3
Other species occurring in at least 20% in at least one vegetation type					
Salix purpurea	64	69	72	46	100
Agrostis stolonifera agg.	.	50	33	21	39
Galium mollugo agg.	.	26	39	42	28
Tussilago farfara	.	54	30	21	29
Populus nigra agg.	14	12	23	33	23
Mentha longifolia	32	17	21	.	32
Alnus incana	.	41	27	.	25
Brachypodium sylvaticum	18	5	20	17	23
Taraxacum sect. *Taraxacum*	.	37	23	8	14
Achillea millefolium agg.	.	33	11	21	14
Lotus corniculatus agg.	.	35	19	17	8
Calamagrostis pseudophragmites	9	38	11	13	5
Dactylis glomerata	.	15	23	8	29
Artemisia vulgaris agg.	.	10	21	17	25
Deschampsia cespitosa agg.	.	36	17	4	14
Salix daphnoides	.	23	15	25	7
Plantago lanceolata	.	20	11	21	18
Ranunculus repens	9	16	17	.	25
Trifolium repens	.	29	14	13	10
Eupatorium cannabinum	.	11	26	4	23
Medicago lupulina	.	21	16	17	9
Petasites paradoxus	.	12	23	17	10
Salix euxina agg.	27	7	11	.	16
Fraxinus excelsior	36	2	15	.	8
Clematis vitalba	5	3	29	8	15
Equisetum arvense	14	8	20	.	18
Petasites hybridus	.	15	14	.	27
Angelica sylvestris	.	9	20	4	22
Gypsophila repens	.	23	11	21	.
Anthyllis vulneraria	.	17	5	29	1
Calamagrostis epigejos	.	4	6	33	8
Rubus caesius	.	4	21	13	13
Trifolium pratense	.	24	15	4	6
Saponaria officinalis	5	3	13	4	23
Euphorbia cyparissias	.	6	9	25	6
Prunella vulgaris	.	20	13	4	9
Leucanthemum vulgare agg.	.	20	12	8	4
Tanacetum vulgare	.	12	10	.	21
Filipendula ulmaria	27	1	3	.	7
Poa alpina	.	14	2	21	.
Erigeron acris	.	7	3	25	1
Erucastrum nasturtiifolium	5	2	3	25	.
Epilobium fleischeri	.	7	1	25	.

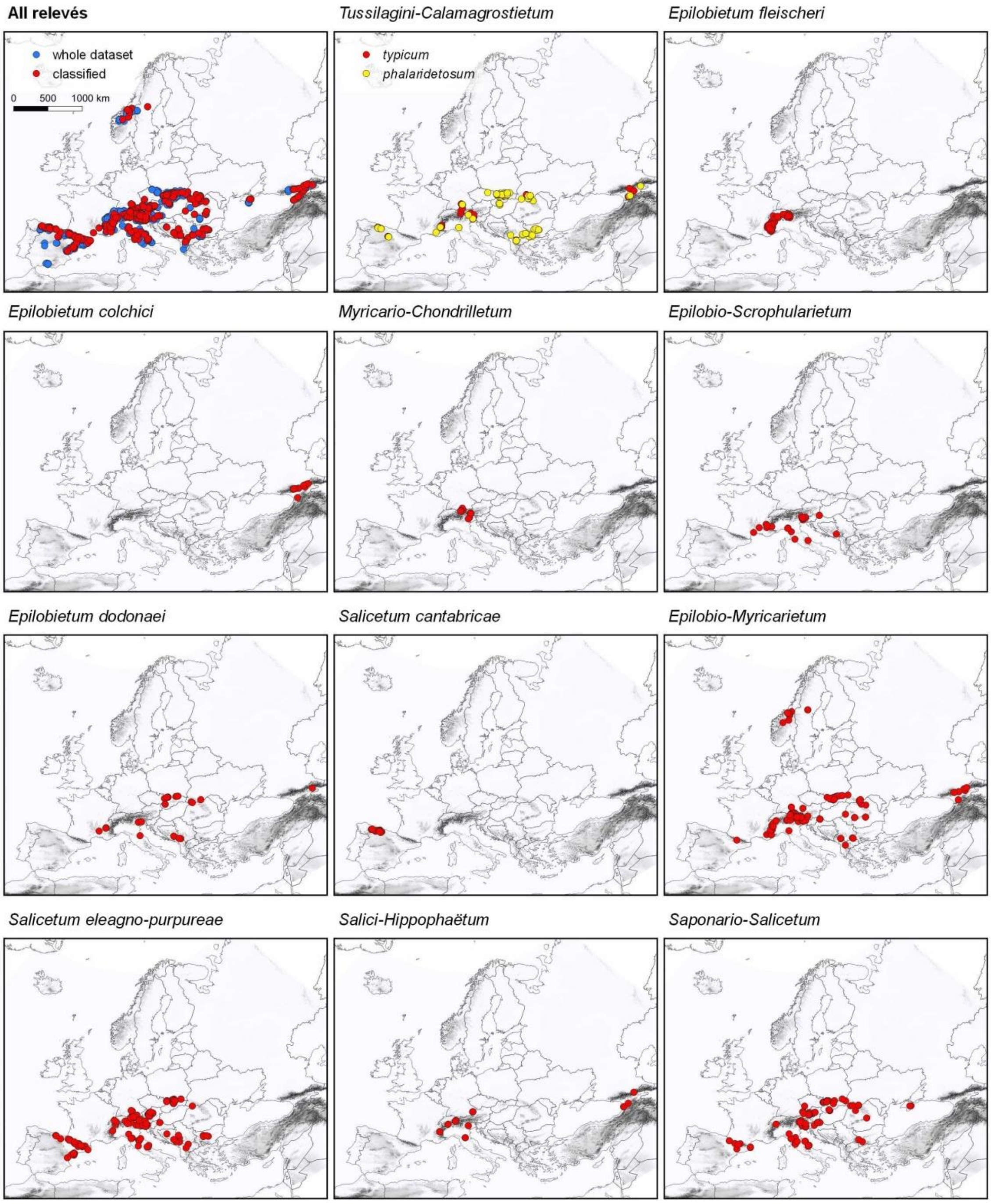

Fig. 2 Distribution of vegetation plots classified to associations and subassociations by the expert system.

The large-scale distribution of herbaceous and scrub gravel-bar pioneer communities is mainly defined by biogeography and altitudinal zonation (Fig. 3a). Climatic variables, in most cases correlated with altitude, are shown in Fig. 3b. The river gravel-bar communities are locally determined especially by hydro-morphological processes and vegetation succession. Related environmental characteristics (e.g. different microhabitats within individual gravel bars) and species composition are listed in the descriptions of particular vegetation units.

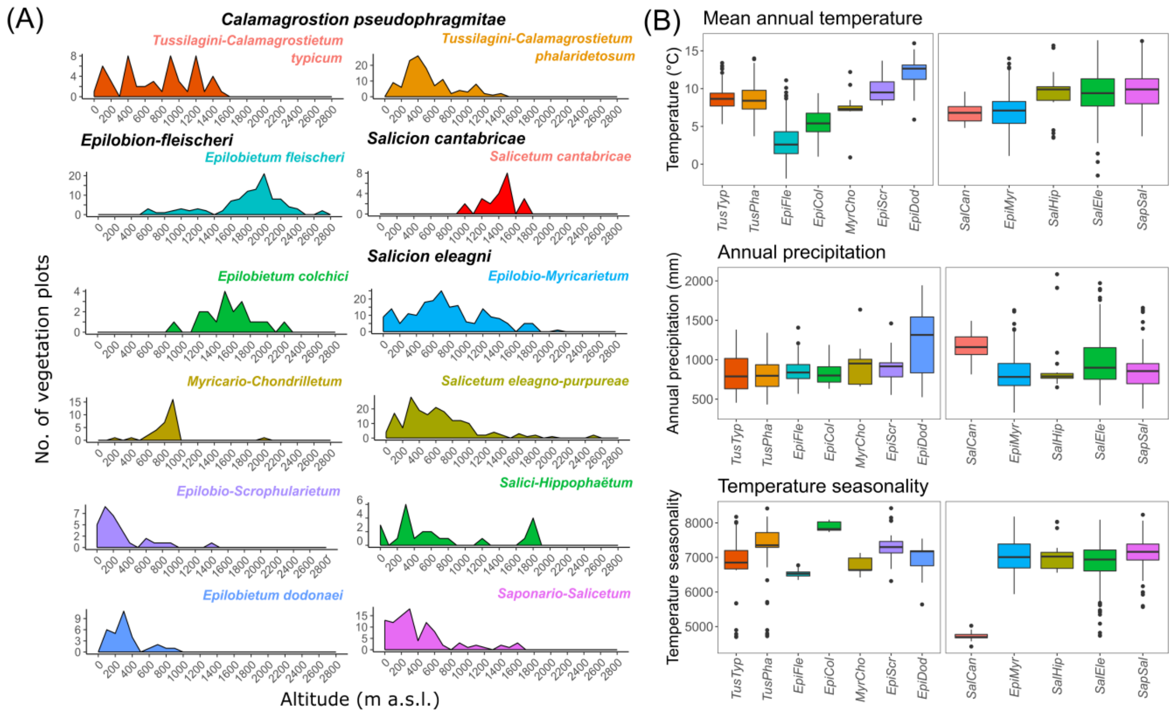

Fig. 3 A comparison of (a) altitudinal distribution and (b) selected climatic of the gravel-bar associations and subassociations. In (a), numbers of vegetation plots of particular vegetation types are shown in 100-m altitudinal bins. In (b), horizontal lines within the boxes indicate medians. Abbreviations are the same as in Tables 1 and 2.

3.2 Syntaxonomical synopsis

Thlaspietea rotundifolii Br.-Bl. 1948

Epilobietalia fleischeri Moor 1958
Herbaceous vegetation on gravel bars of alpine to submontane rivers in the temperate and boreal Eurasian mountains

Calamagrostion pseudophragmitae Rivas-Martínez et al. 1984
Gravel-bar grasslands with *Calamagrostis pseudophragmites* of alpine to submontane river gravel bars of the temperate European mountains and the Caucasus

• *Tussilagini farfarae-Calamagrostietum pseudophragmitae* Pawłowski et Walas 1949

• *Tussilagini farfarae-Calamagrostietum pseudophragmitae typicum*
Oligotrophic gravel-bar grasslands with *Calamagrostis pseudophragmites*
• *Tussilagini farfarae-Calamagrostietum pseudophragmitae phalaridetosum arundinaceae* (Kopecký 1968) Kalníková et al. 2020
Eutrophic gravel-bar grasslands with *Calamagrostis pseudophragmites*

Epilobion fleischeri G. Br.-Bl. ex Br.-Bl. 1950
Herbaceous early-successional vegetation of alpine to submontane river gravel bars of the temperate and boreal European mountains and the Caucasus

• *Epilobietum fleischeri* Lipmaa 1933
Alpine to montane early-successional herbaceous gravel-bar vegetation of the Alps
• *Epilobietum colchici* Kalníková et al. 2020
Alpine to montane early-successional herbaceous gravel-bar vegetation of the Caucasus
• *Myricario-Chondrilletum chondrilloidis* Br.-Bl. in Volk et Br.-Bl. 1939
Montane early-successional herbaceous gravel-bar vegetation of the Alps
• *Epilobio dodonaei-Scrophularietum caninae* W. Koch et Br.-Bl. ex Müller 1974
Montane to submontane early-successional herbaceous gravel-bar vegetation of South-Western Europe
• *Epilobietum dodonaei* Vanden Berghen 1963
Montane to submontane early-successional herbaceous gravel-bar vegetation of Central- and South-Eastern Europe

Salicetea purpureae Moor 1958

Salicetalia purpureae Moor 1958
Willow scrub and low open forests of riparian habitats in the temperate to arctic zones of Europe

Salicion cantabricae Rivas-Martínez, T.E. Díaz et Penas in Rivas-Martínez et al. 2011
Cantabrian subalpine to montane willow-scrub vegetation of river gravel bars

• *Salicetum cantabricae* Rivas-Martínez et al. 1984

Salicion eleagni Aichinger 1933
Scrub vegetation of subalpine to submontane river gravel bars of the temperate and boreal European mountains and the Caucasus

• *Epilobio dodonaei-Myricarietum germanicae* Aichinger 1933
Subalpine to montane river gravel-bar scrub with *Myricaria germanica*
• *Salicetum eleagno-purpureae* Sillinger 1933
Subalpine to montane river gravel-bar willow scrub with *Salix eleagnos* of Central and Southern Europe
• *Salici incanae-Hippophaëtum rhamnoidis* Br.-Bl. in Volk et Br.-Bl. 1939
Subalpine to montane river gravel-bar scrub with *Hippophaë rhamnoides*
• *Saponario officinalis-Salicetum purpureae* Tchou 1948
Montane to submontane river gravel-bar willow scrub of European mountains and the Caucasus

3.3 Descriptions of vegetation types

Tussilagini farfarae-Calamagrostietum pseudophragmitae

The *Tussilagini farfarae-Calamagrostietum pseudophragmitae* is montane to submontane tall-grass community of predominantly sandy to muddy sediments in depressions or on margins of gravel bars, i.e. sites inundated several times a year. The dominant *Calamagrostis pseudophragmites* creates dense stands that suppress other species. Site conditions are suitable for moisture-demanding riparian plants (e.g. *Agrostis stolonifera* agg., *Mentha longifolia* and *Myosotis scorpioides* agg.) and species with a ruderal tendency (e.g. *Equisetum arvense*, *Erucastrum nasturtiifolium* and *Tussilago farfara*). In lower sections of mountain rivers, this

vegetation contains nutrient-demanding (e.g. *Phalaroides arundinacea*, *Rumex conglomeratus* and *R. obtusifolius*) and alien species (e.g. *Bidens frondosus* and *Impatiens glandulifera*). However, the association finds its optimum at oligotrophic sites, and thus it is threatened by eutrophication. The moss layer is species-poor but can reach a high cover. It is composed especially of mesophilous and hygrophilous bryophytes such as *Brachythecium rivulare*, *Plagiomnium cuspidatum* or *Platyhypnidium riparioides*. Ruderal species such as *Barbula unguiculata*, *Bryum pseudotriquetrum* and *Ceratodon purpureus* occur at open sites.
The association is common in European mountains except for northern Europe, which is outside the distribution range of *Calamagrostis pseudophragmites* (Meusel *et al.*, 1965).
Kopecký (1968) described two well-defined subassociations within this community, *Tussilagini farfarae-Calamagrostietum pseudophragmitae phalaridetosum arundinaceae* and *Tussilagini farfarae-Calamagrostietum pseudophragmitae typicum*. The former occurs at lower altitudes on nutrient-rich substrates, is co-dominated by *Phalaroides arundinacea* and contains nutrient-demanding species. The latter subassociation occurs at higher altitudes on oligotrophic substrates and is species-poor with *Calamagrostis pseudophragmites* being the only dominant species. Both subassociations occur throughout the total distribution range of the association.

Epilobietum fleischeri

This association comprises alpine to montane early-successional vegetation of the Alps. It colonizes gravel bars of alpine streams, glacial forelands and occasionally wet screes, preferring gravelly to stony substrate. The community consists mainly of alpine species and scree specialists, resistant to frequent flooding and mechanical disturbances, e.g. *Achillea erba-rotta*, *Campanula cochleariifolia*, *Epilobium fleischeri*, *Gypsophila repens*, *Rumex scutatus*, *Saxifraga aizoides*, *Tolpis staticifolia* and *Trifolium pallescens*. The moss layer tends to be well developed at more stable sites, containing mainly species of open habitats, e.g. *Racomitrium canescens*, which can attain a high cover. Other typical bryophytes include *Polytrichum piliferum* and species with ruderal tendency such as *Barbula unguiculata* and *Ceratodon purpureus*. It hosts numerous lichens, e.g. *Acarospora nitrophila*, *Cladonia fimbriata*, *Peltigera didactyla* and *Stereocaulon alpinum*.

Epilobietum colchici

This is alpine to montane early-successional sparse vegetation of the Caucasus Mountains. It develops on frequently flooded gravelly to stony sites, often at high altitudes and in the proximity of glaciers. It is composed mostly of Caucasian alpine or scree species such as *Epilobium colchicum*, *Papaver fugax*, *Senecio leucanthemifolius*, *Seseli transcaucasicum*, *Silene compacta* and *Tripleurospermum caucasicum*. The community also shares species with the gravel-bar communities of the Alps, e.g. *Erigeron acris*, *Poa alpina*, *Rumex acetosella* and *R. scutatus*. The moss layer is lacking on newly created or frequently disturbed gravel bars, but it can be well-developed at more stable sites. It contains mainly species of open habitats, e.g. *Racomitrium canescens*. Other typical bryophytes include *Pohlia filum*, *Polytrichum piliferum* and species with ruderal tendency such as *Bryum caespiticium* or *Tortella inclinata*.
The community was described from the Greater and Lesser Caucasus in Georgia. It likely occurs in the adjacent high-mountain areas of Armenia, Russia and Turkey (compare Parolly, 2004). This association is a geographical vicariant of the association *Epilobietum fleischeri* from the Alps. Two associations of gravel-bar vegetation, *Scrophulario variegatae-Epilobietum dodonaei* Onipchenko ex Belonovskaya, Mucina et Theurillat 2014 and *Sileno compactae-Salicetum purpureae* Onipchenko 2002, were described from the Russian part of the Greater Caucasus. However, because the original data (Onipchenko 2002) suffers from inconsistencies

in taxonomic identification of diagnostic species (Kalníková *et al.*, 2020), we do not consider them in this overview, although they may correspond to *Epilobietum colchici*.

Myricario-Chondrilletum chondrilloidis

This association represents montane early-successional sparsely vegetated herbaceous gravel-bar vegetation restricted to the Alps. It replaces *Epilobietum fleischeri* in lower river sections in the valleys and mountain foothills. It prefers fresh, coarse sandy sediments, which are situated just above the mean water level, thus inundated and covered up by gravel several times a year. The characteristic species is *Chondrilla chondrilloides,* and the species composition is dynamic and variable. The community hosts high-mountain and scree species or gravel-bar specialists such as *Anthyllis vulneraria*, *Calamagrostis pseudophragmites*, *Campanula cochleariifolia*, *Epilobium fleischeri*, *Gypsophila repens*, *Saxifraga caesia*, *S. paniculata* and *Tolpis staticifolia*. Juvenile individuals of *Alnus incana, Myricaria germanica*, *Salix eleagnos* and *S. purpurea* occur frequently. Moss layer contains mostly light-demanding ruderal bryophytes such as *Syntrichia ruralis* and *Tortella inclinata*.

Epilobio dodonaei-Scrophularietum caninae

The *Epilobio dodonaei-Scrophularietum caninae* is montane to submontane early-successional gravel-bar vegetation of warm and precipitation-poor areas. It alternates with *Myricario-Chondrilletum chondrilloidis* at higher altitudes. It occurs on gravel bars with high sand content, often base-rich, located farther from the water level. The association is characterized by the presence of *Epilobium dodonaei* and *Scrophularia canina*. Other typical species are *Achnatherum calamagrostis*, *Daucus carota*, *Diplotaxis tenuifolia*, *Erucastrum gallicum*, *Gypsophila repens* and *Reseda lutea*. Juveniles of *Populus nigra*, *Salix eleagnos* and *S. purpurea* are also common. The moss layer contains mainly ruderal species such as *Barbula convoluta*, *Didymodon ferrugineus*, *Tortella inclinata* and *T. tortuosa*.
The community is reported from south-western and south-eastern calcareous Alps, northern Apennines and Montenegro. Similarly to *Epilobietum dodonaei*, it contains mountain species and pioneer ruderal species, but it differs by the presence of the species with south-western European and southern Alpine distribution and submediterranean species.

Epilobietum dodonaei

Vegetation of this association includes montane to submontane sparse early-successional vegetation of relatively warm and precipitation-poor areas. It occurs on gravel bars with a high sand content, located farther from the water level. Its sites are dry, hosting vegetation of pioneer ruderal, drought-tolerant and light-demanding species, such as *Arenaria serpyllifolia*, *Crepis foetida*, *Daucus carota*, *Echium vulgare*, *Epilobium dodonaei*, *Galeopsis angustifolia*, *Medicago minima*, *Melilotus albus*, *Poa compressa* and *Silene vulgaris*. The community is species-rich, containing many species from surrounding habitats. The moss layer is formed especially of ruderal species of drier sites, e.g. *Bryum argenteum*, *Ceratodon purpureus*, *Syntrichia ruralis* and *Tortella tortuosa*. This community is most common in the Carpathians, but it is also documented from the Balkans and the Alps.
Epilobietum dodonaei is highly variable as it consists of plants from contrasting habitats. It was described from the Western Carpathians, where it contains many drought-adapted ruderal species assigned to the *Dauco-Melilotion* alliance (class *Artemisietea vulgaris*), which otherwise comprises ruderal vegetation of anthropogenic habitats (Slavík, 1978). Similar communities were classified to the *Epilobion fleischeri* alliance in Montenegro (*Epilobietum dodonaei*; Petrović *et al.*, 2012). It is well distinguished from the other early-successional vegetation types

by the occurrence of mountain species and the presence of a number of warm-demanding and drought-adapted species. Very similar vegetation with *Epilobium dodonaei* also occurs outside gravel bars in man-made or strongly disturbed habitats with accumulated grave, e.g. in stone quarries, gravel deposits at constructions sites or on railways.

Salicetum cantabricae

This subalpine to montane pioneer scrub occurring mainly on sand and gravel is restricted to north-western Spain. It preferably occurs on sandy to gravelly substrates. The association is characterized by the endemic willow *Salix cantabrica* and its hybrids, often accompanied by *S. caprea*, *S. cinerea*, *S. eleagnos*, *S. euxina*, *S. purpurea*, *S. triandra* and *Fraxinus excelsior*. The herb layer contains nitrophilous and moisture-demanding species, such as *Equisetum palustre*, *Filipendula ulmaria* and *Mentha longifolia*. The frequent occurrence of *Calamagrostis pseudophragmites* represents a remnant from previous successional stages. No bryophytes were recorded in the analysed plots or mentioned in the literature.

The community is restricted to the Cantabrian Mountains in north-western Spain.

Salicetum cantabricae was previously assigned to *Salicion eleagni* (Rivas-Martínez *et al.*, 1984; Rivas-Martínez *et al.*, 2001), but currently, it is classified to a separate alliance *Salicion cantabricae*, which is considered as a geographical vicariant of *Salicion eleagni* (Rivas-Martínez *et al.*, 2011, Mucina *et al.*, 2016) and was also well distinguished in our analysis.

Epilobio dodonaei-Myricarietum germanicae

This is alpine to submontane, open to close, early-successional scrub with *Myricaria germanica*. It mainly occurs in periodically inundated depressions or at margins of gravel bars on the nutrient-poor sandy to fine-gravelly substrate. *Myricaria germanica* requires moist substrate to germinate, while adult plants are drought-tolerant and light-demanding. Different shrubby willows (e.g. *Salix eleagnos*, *S. myrsinifolia, S. daphnoides* and *S. purpurea*) also occur in this vegetation and can replace *Myricaria* in vegetation succession. The herb layer includes gravel-bar specialists (e.g. *Calamagrostis pseudophragmites*, *Chondrilla chondrilloides*, *Epilobium colchicum*, *E. dodonaei* and *E. fleischeri*), drought-tolerant species, some of them typical of scree habitat (e.g. *Arenaria serpyllifolia*, *Arabis alpina*, *Campanula carpatica*, *C. cochleariifolia*, *Gypsophila elegans*, *G. repens*, *Oxyria digyna* and *Petrorhagia saxifraga*) and moisture-demanding species (e.g. *Equisetum variegatum*, *Saxifraga aizoides* and *Tolpis staticifolia*). The number of mesophilous species (e.g. *Achillea millefolium* agg., *Angelica sylvestris* and *Plantago lanceolata*) increases with successional age. The moss layer is well-developed, and it can be very dense, especially in humid regions. Bryophyte species include *Bryum caespiticium, Pohlia filum*, *Polytrichum juniperinum*, *P. piliferum, Racomitrium canescens*, *R. ericoides* and *Tortella inclinata*.

The distribution of this association is related to the distribution of its characteristic species *Myricaria germanica* (Meusel *et al.*, 1978). The association is well documented from the Alps and Carpathians. It is also reported from the Caucasus, Balkans, Pyrenees, Scandinavia, and from the Drava River in Croatia and Hungary.

In the literature, this association is frequently reported as *Salici purpureae-Myricarietum germanicae* Moor 1958, but the earlier described *Epilobio dodonaei-Myricarietum germanicae* Aichinger 1933 is the correct name for this association. Some authors (e.g. Valachovič, 1995) consider *Epilobio dodonaei-Myricarietum germanicae* as an early-successional vegetation of *Epilobion fleischeri* alliance, while others understand it as a developed scrub community (e.g. Jeník, 1955; Lakušić, 1974). The original plots of Aichinger (1933) represent a scrub with a high cover of *Salix* species. Therefore we assign this association to the *Salicion eleagni* alliance, within which it is the successionally youngest community type. The associations we synonymize with *Epilobio dodonaei-Myricarietum germanicae* (e.g. *Racomitrio ericoidis-Myricarietum*, *Agrostio-Myricarietum germanicae*) are lacking unique diagnostic species, or the taxonomy of the main diagnostic species is unclear (*Myricarietum ernesti-mayeri*; Trinajstić, 1992; Božović, 2011).

Salicetum eleagno-purpureae

This subalpine to submontane, sparse to dense willow scrub is characterized by *Salix eleagnos*, co-dominated by *S. purpurea* and locally by *S. daphnoides*. In contrast to *Epilobio dodonaei-Myricarietum germanicae*, it occupies sites with coarse-gravelly to stony substrate, usually located higher above the water level. Other common woody species are *Alnus glutinosa*, *A. incana*, *Fraxinus excelsior*, *Pinus sylvestris* or *Salix euxina. Hippophaë rhamnoides* could be another, even rarer, accompanying species (Jeník, 1955; Moor, 1958; Coldea, 2015). The herb layer lacks diagnostic species and is composed mainly of riparian species. If the shrub layer is dense, the herb layer has a low cover and contains more mesophilous species, e.g. *Agrostis stolonifera*, *Clematis vitalba*, *Galium aparine* and *Petasites* spp. The moss layer is dense, containing moisture-demanding species *Brachytecium rivulare*, *Oxyrrhynchium hians* and *Sciuro-hypnum plumosum*, but also ruderal species such as *Babula unguiculata* and *Tortella tortuosa*.
Distribution of *Salicetum eleagno-purpureae* follows the distribution of *Salix eleagnos* and *S. daphnoides* (Meusel *et al.*, 1965). The community is well-documented from the Alps, Apennines, Carpathians and the Balkans.
Some vegetation plots originally described from Spain as *Saponario officinalis-Salicetum purpureae* fall within this association as delimited by our formal definition. These plots contain some thermophilous submediterranean species (e.g. *Ostrya carpinifolia*, *Polypogon viridis* and *Populus alba*; e.g. Tchou, 1948), but their frequency is low. Transitions between the types with and without these species were also reported from Italy (Oriolo and Poldini, 2002). The initial successional stages with *Salix eleagnos* on gravel bars, described by Jeník (1955) as the association *Salicetum eleagni*, are included here in *Salicetum eleagno-purpureae*.

Salici incanae-Hippophaëtum rhamnoidis

This association comprises alpine to submontane scrub dominated by *Hippophaë rhamnoides.* It occurs on partially stabilized, rather dry sites of gravel bars with coarse debris, sometimes covered by sand. It occurs on substrates of variable reaction but seems to have an affinity to calcareous sites (e.g. Biondi *et al.*, 2014). Typical subdominant shrubs are *Alnus glutinosa*, *A. incana*, *Populus nigra*, *Salix daphnoides*, *S. eleagnos* and rarely also *Myricaria germanica*. The herb layer is sparse, mostly formed of *Achillea millefolium* agg., *Galium mollugo* agg., *Sanguisorba minor* and scree species (e.g. *Gypsophila repens* or *Petrorhagia saxifraga*), and on stabilized sites, by meadow species. The community is also characterized by the presence of drought-tolerant ruderal species such as *Arenaria serpyllifolia*, *Crepis foetida*, *Echium vulgare* and *Melilotus albus*. Moss layer has a low cover, consisting mostly of small ruderal species such as *Barbula unguiculata*, *Bryum argenteum* or *Syntrichia ruralis*.
Hippophaë rhamnoides is a glacial relict, nowadays occurring in coastal habitats and floodplains of mountain streams in the Alps, Carpathians, Pyrenees and Caucasus (e.g. Bartish *et al.*, 2006; Franjić *et al.*, 2016). The vegetation of *Salici incanae-Hippophaëtum rhamnoidis* is scattered in the Alps, Pyrenees and Caucasus, rare in the Carpathians (only Romania), and it also occurs on the Drava River in Croatia, Hungary and Slovenia.

Altitudinal distribution of this community is wide, which is reflected in considerable species turnover. Especially at lower altitudes, there are transitions into more thermophilous vegetation types, e.g. *Tamarici-Hippophaëtum* Pietsch 1967, *Berberido seroi-Hippophaëtum fluviatilis* Rivas-Martínez et al. 1991 or *Spartio juncei-Hippophaëtum fluviatilis* Biondi et al. 1997 (e.g. Rivas-Martínez *et al.*, 2001; Biondi *et al.*, 2003; Viciani *et al.*, 2011; Franjić *et al.*, 2016). Some authors synonymize *Salici incanae-Hippohaëtum rhamnoidis* with *Hippophaëo-Berberidetum* Moor 1958. However, these associations differ in floristic composition and ecological requirements, and we consider them as separate syntaxa (see also Rivas-Martínez *et al.*, 2001; Oriolo and Poldini, 2002).

Saponario officinalis-Salicetum purpureae

This montane to submontane riparian scrub is characterised by the dominant *Salix purpurea*, accompanied by other willows. It occurs on gravelly and sandy accumulations with a high amount of organic matter. The typical co-occurring shrub species are *S. euxina* and *S. triandra*, rarely also *Alnus glutinosa*, *A. incana*, *Populus nigra*, *Salix alba* and *S. viminalis.* The herb layer consists of moisture-demanding species (e.g. *Chaerophyllum hirsutum*, *Myosoton aquaticum*, *Petasites hybridus*, *P. kablikianus*, *Phalaroides arundinacea* and *Stellaria alsine*), ruderal (e.g. *Artemisia vulgaris*, *Saponaria officinalis* and *Tanacetum vulgare*), forest (e.g. *Alliaria petiolata*, *Brachypodium sylvaticum* and *Festuca gigantea*) and meadow species (e.g. *Galium mollugo* agg., *Poa trivialis* and *Vicia* spp.). The most common bryophytes are the moisture-demanding *Brachytecium rivulare*, *Hylocomium splendens* and *Sciuro-hypnum plumosum*.

Distribution of this community is less known or overlooked, although it is probably relatively common. The distribution range of *Salix purpurea* covers a major part of Europe except for Scandinavia (Meusel *et al.*, 1965). The association was recorded from Austria, Belarus, Bosnia and Herzegovina, Croatia, Czech Republic, France, Germany, Hungary, Italy, Kosovo, Montenegro, Romania, Serbia, Slovakia, Slovenia, Spain and Ukraine (only the Carpathians and Crimea).

There are two similar associations described based on the dominance of *Salix purpurea*: *Salicetum purpureae* and *Saponario officinalis-Salicetum purpureae*. The former is more often reported from Central Europe (e.g. Chytrý, 2013), while the latter is more often reported form Southern Europe, where some stands contain submediterranean species (e.g. Tchou, 1948). There are inconsistencies in the understanding of these associations across European countries; however, on the European scale, they lack diagnostic species that would allow to separate them.

Ordination and unsupervised classification

The first axis of DCA (Fig. 4a) of early-successional river gravel-bar vegetation stretches from submontane and montane (e.g. *Tussilagini-Calamagrostietum*, *Epilobietum dodonaei*) to alpine (e.g. *Epilobietum fleischeri*) associations. The second axis reflects especially the biogeographical gradient from the Alps (e.g. *Epilobio dodonaei-Scrophularietum caninae*) through the Carpathians and the Balkans to the Caucasus (*Epilobietum colchici*). The first axis of DCA of scrub vegetation (Fig. 4b) also reflects the altitudinal gradient from submontane *Saponario officinalis-Salicetum purpureae* to alpine *Epilobio dodonaei-Myricarietum germanicae*. The association *Salicetum cantabricae* is differentiated mainly due to different biogeographical influences.

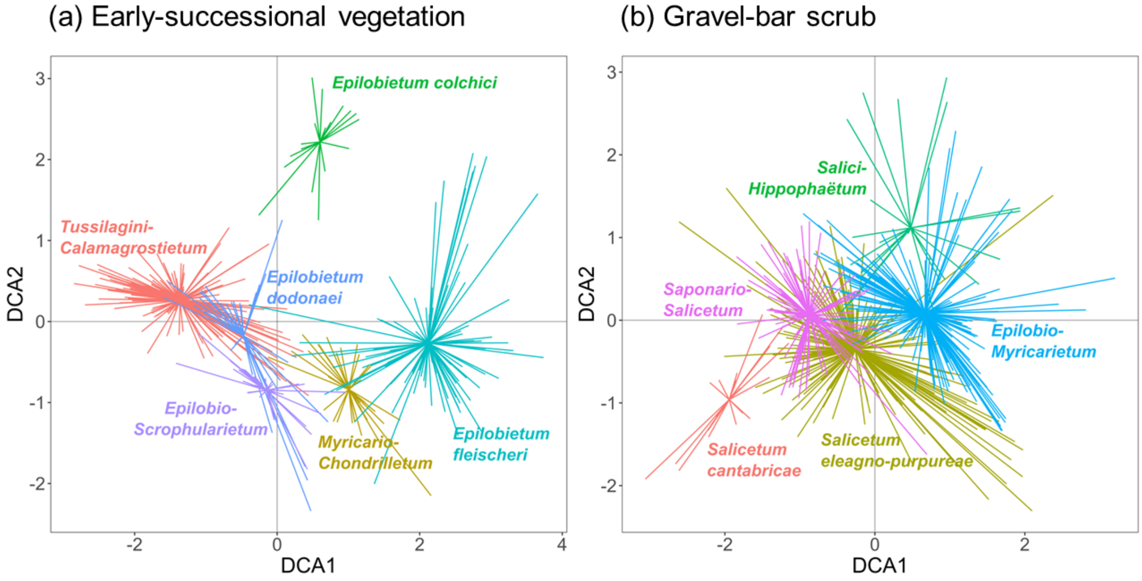

Fig. 4 DCA of vegetation plots of (a) early successional vegetation and (b) gravel-bar scrub formally assigned to associations by the expert system. The lines connect individual vegetation plots with centroids of particular associations. The diagrams come from two separate DCA ordinations.

Unsupervised TWINSPAN classification, which was applied to the set of early-successional gravel-bar vegetation plots, corresponded to the formally defined associations (Fig. 5). The classification with four hierarchical levels produced 16 terminal clusters. The marginal clusters consisting of few vegetation plots and very similar sister clusters were merged. The first division produced one cluster of plots restricted to the Alps, and another cluster consisting of plots from the Alps, Balkans and Caucasus. Apart from the clusters which largely overlap with those described by the formal definition, TWINSPAN classification recognized two regional groups of plots. The first group was from North-Western Caucasus (Onipchenko, 2002; for details see the *Epilobietum colchici* description above), while the second was from the calcareous submontane belt of more thermophilous vegetation of the South-Eastern Alps.

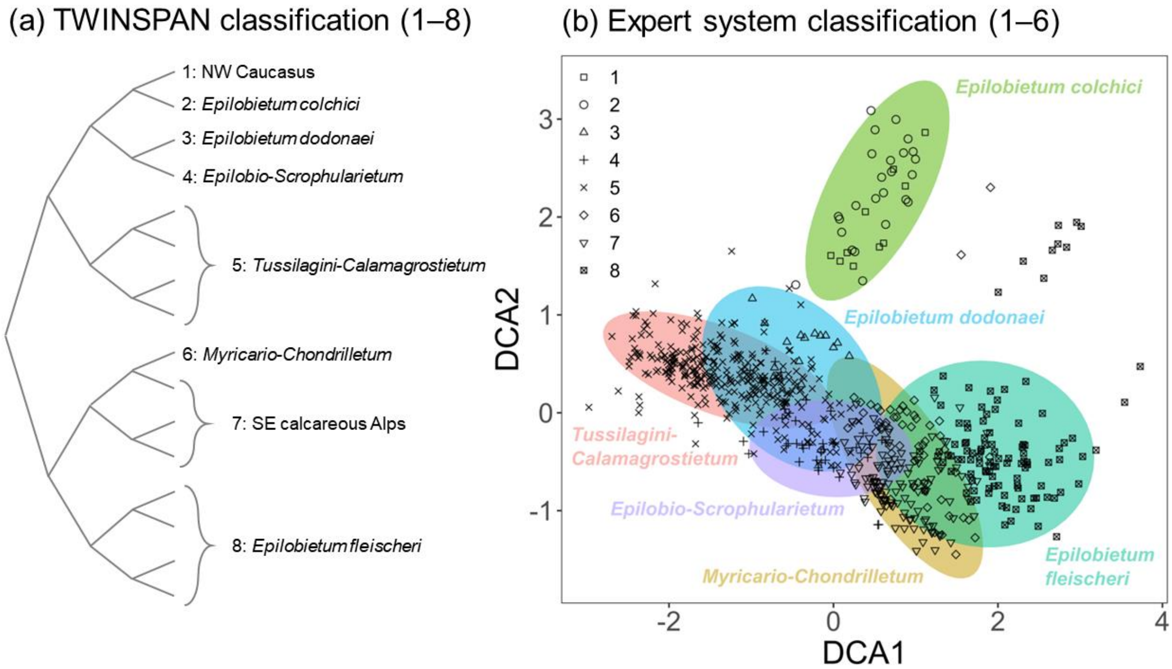

Fig. 5 TWINSPAN dendrogram with syntaxonomic interpretation of the clusters (a) and a DCA ordination diagram of plots with the indication of their classification by TWINSPAN and the expert system (b). The symbols in the DCA diagram refer to the partly merged TWINSPAN clusters (see the numbers in the dendrogram) while the colour envelopes indicate the plots classified by formal definitions.

4 Discussion

4.1 Properties of the new classification system of European gravel-bar vegetation

The vegetation-plot data of natural and near-natural mountain river gravel-bar habitats were synthesized to create the first unified classification scheme of this vegetation across Europe. The proposed scheme divides the river gravel-bar vegetation into two groups based on its physiognomy: early-successional herbaceous vegetation (order *Epilobietalia fleischeri*, class *Thlaspietea rotundifolii*) and scrub vegetation (order *Salicetalia purpureae*, class *Salicetea purpureae*). Although the first group represents initial successional stages, both of these groups should be considered as pioneer vegetation as they are shaped by morphodynamic processes and exist only as long as disturbance occurs (e.g. Müller, 1995; Egger *et al.*, 2019).

Of the total dataset, 28.6% of plots met the criteria of the formal definitions and were classified to a syntaxon at some level of our classification scheme (subassociation, association or alliance). The high proportion of unclassified plots reflects the fact that the data set also included many plots from non-target riparian vegetation types. Although these vegetation types may occur on gravel bars, they are not restricted to this habitat. Nevertheless, their inclusion helped us to properly delimit the types of focal vegetation using the formal definitions. For this reason, the percentage of classified plots cannot be used as a measure of success or quality of the classification or compared with the percentage of classified plots from other studies.

As in case of any classification, the proposed classification suffers from the lack of data from some vegetation types and areas. This specifically applies to more thermophilous early-successional vegetation types and to northern Europe.

In the case of thermophilous vegetation types, a group of vegetation plots related to the south-eastern calcareous Alps was recognized with the help of the unsupervised classification. However, this group was too variable and ambivalent, partly including basiphilous scree vegetation of the alliance *Stipion calamagrostis*, partly some ruderal communities, and partly gravel-bar vegetation of *Myricario-Chondrilletum chondrilloidis*. It also included some plots originally classified as *Leontodonto berinii-Chondrilletum* (Wraber, 1965). *Leontodon berinii*, the most indicative species of this community, is endemic to the south-eastern Alps (Wraber, 1965; Poldini and Martini, 1993; Čusin and Šilc 2006; Pignatti and Pignatti, 2014) but very rare in vegetation plots related to this association (Pignatti and Pignatti, 2014). Based on the results of unsupervised classification and the absence of other differential species, we synonymized *Leontodonto berinii-Chondrilletum* with *Myricario-Chondrilletum chondrilloidis*

In the case of northern Europe, vegetation data from river gravel bars are rare in general. Moreover, the available plots hardly met the classification criteria developed and tested using the data from Central and Southern European mountain ranges. They often lack gravel-bar specialist species, being composed only of species of the surrounding habitats (e.g. Klokk, 1980; Odland *et al.*, 1991). In Iceland, the northern part of the Scandinavian Peninsula and Russia, vegetation with *Epilobium latifolium* (Fyles and Bell, 1986; Daniëls, 1994) could be possibly recognized as an independent association within early-successional vegetation *Epilobion fleischeri* alliance. Unfortunately, there are no vegetation data available so far. More research in Northern Europe is needed in the future.

4.2 Novelties in the proposed classification system

The most remarkable change introduced in this study, with respect to previous vegetation classifications (Pawłowski and Walas, 1949; Beldie, 1967; Kornaś and Medwecka-Kornaś, 1967; Kopecký, 1968; Rivas-Martínez *et al.*, 1984; Poldini and Martini, 1993), concerns the tall-grass vegetation dominated by *Calamagrostis pseudophragmites*. This vegetation is generally classified into two associations in Europe (e.g. Rivas-Martínez *et al.*, 2001; Chytrý, 2011). In Spain, it is *Erucastro nasturtiifolii-Calamagrostietum pseudophragmitae* (alliance *Calamagrostion pseudophragmitae*), while in the rest of Europe it is *Tussilagini farfarae-Calamagrostietum pseudophragmitae* (reported under various synonyms and classified to various alliances). Both associations are similar, and consequently, we propose their merging into *Tussilagini farfarae-Calamagrostietum pseudophragmitae*, originally described from the Carpathians, within the alliance *Calamagrostion pseudophragmitae*, originally described from Spain. The latter alliance is, however, considered very broadly in the recent Spanish literature, as it comprises three associations (Rivas-Martínez *et al.*, 2001) of which two are typical of screes and periodically drying rivers of warmer areas (*Conopodio-Laserpitietum gallici* O. Bolòs 1967, *Galeopsio angustifoliae-Ptychotidetum saxifragae* O. Bolòs and Vives in O. Bolòs 1956). The third association, *Erucastro nasturtiifolii-Calamagrostietum pseudophragmitae* (which is the nomenclature type of the alliance *Calamagrostion pseudophragmitae*; Rivas-Martínez *et al.*, 1984), has very similar species composition as *Tussilagini farfarae-Calamagrostietum pseudophragmitae* with no unique differential species that would allow keeping it as a separate association. Considering its species composition and ecology, the alliance *Calamagrostion pseudophragmitae* should belong to the *Epilobietalia fleischeri* alliance of the *Thlaspietea rotundifolii* class (e.g. also Pawłowski and Walas, 1949; Julve, 1993; Malinovsky and Kricsfalusy, 2000; Schubert *et al.*, 2001; Matuszkiewicz, 2007), although it shares some species with other alliances to which the vegetation with *Calamagrostis pseudophragmites* was classified too: *Phalaridion arundinaceae* alliance of the *Phragmito-Magnocaricetea* class (e.g. Kopecký, 1968; Valachovič, 2001; Chytrý, 2011) and the *Dauco-Melilotion* alliance of the *Artemisietea vulgaris* class (Poldini and Martini, 1993).

Some other associations which lack specific diagnostic species and are mainly composed of common generalist species that have their main distribution in other vegetation types were also synonymized with the associations accepted here. This is the example of the association *Salicetum purpureae*, which we included into *Saponario-Salicetum purpureae*, or the association *Racomitrio ericoidis-Myricarietum*, described from central Norway (Klokk, 1980), which we included into *Epilobio dodonaei-Myricarietum germanicae*.

4.3 Habitat conservation

An important aim of vegetation classification is delivering clearly defined objects for conservation planning, monitoring and management (Janssen *et al.*, 2016; Rodwell *et al.*, 2018). The gravel-bar vegetation types described here are all restricted to well-preserved natural or near-natural river sections (e.g. Müller 1995; Egger *et al.* 2019). Most of the gravel-bar specialist species are sensitive to anthropogenic interferences into river hydro-morphology (Sochor *et al.*, 2013; Werth *et al.*, 2014; Skokanová *et al.*, 2015; Sitzia *et al.*, 2016; Werner, 2016; Fink *et al.*, 2017), and also the whole plant communities are at the risk of vanishing (Oriolo and Poldini, 2002; Egger *et al.*, 2019). The main causes are the habitat destruction or changes in environmental conditions that lead to eutrophication and subsequent transition to vegetation types of lowland river sections.

The knowledge on the distribution of the gravel-bar vegetation types was significantly improved by this study. However, the current state could differ in many European countries, as some of the processed data were already from the 1930s, and riverine habitats have distinctly changed since then. Dramatic hydro-morphological alterations in the active zone of wandering or braided rivers are evident, e.g. from the studies comparing current and historical remote sensing data (e.g. Grabowski *et al.*, 2014; Heckmann *et al.*, 2017; Hajdukiewicz and Wyżga, 2019). Habitat loss is illustrated, for example, by the fact that the cumulative length of the braided reaches of Austrian rivers decreased by 95% during the 20^{th} century (Muhar *et al.*, 2007), and nowadays 41% of all rivers in the Alps can be considered as altered due to hydrological and morphological pressure (Muhar *et al.*, 2019). Considering all the floodplain habitat types in the European Union, it becomes clear that their status is rather unfavourable and future prognoses are negative (Janssen *et al.*, 2016; Muhar *et al.*, 2019). The current status of gravel-bar habitats in the Balkans and the Caucasus is distinctly better (e.g. Drescher, 2018; Kalníková *et al.*, 2020) as there are still many so far almost undisturbed river networks with well-preserved natural gravel-bed rivers and diverse vegetation. Nevertheless, some of them are at risk due to existing plans of building new river cascades and hydropower plants, e.g. in Albania, Bosnia and Herzegovina (Schwarz, 2015, 2019; Drescher, 2018; Milanović and Stupar, 2017), or Georgia (Kalníková et al. 2020). Future vegetation surveys should focus on these less explored riverine systems and gather the information that could help protect them. Unfortunately, even the better explored river-bed habitats that are already included in protected areas (including the Natura 2000 and Emerald networks) are endangered, e.g. by hydropower development (Schwarz, 2015, 2019).

The last natural or near-natural European river courses should be consistently protected and restored. To improve the current unfavourable situation of gravel-bar habitats, natural river dynamics needs to be recreated, including restoration of natural flood pulses, allowing rivers to access their flood plains, reducing rates of water extraction and dependence on hydropower, and removal of selected dams (Stromberg, 2001; Egger *et al.*, 2019). The removal of dams is a possible conflict of interest as they control floods. Nevertheless, there are examples of successful riparian restoration projects from Western and Central Europe, North America and Japan, including the partial removal of bank protection, reactivation of the ancient river channels, reintroduction of sedimentation in a river system, clearing riparian forest and removal of the accumulated nutrient-rich substrate (e.g. Kondolf, 1997; Stormberg *et al.*, 2001; Binder, 2005; Maeno and Watanabe, 2008; Gaeuman *et al.*, 2017; Heckmann *et al.*, 2017).

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Author contributions

VK and MC conceived the idea; VK prepared the dataset, expert system and synoptic tables; VK and KC performed the other statistical analyses; VK wrote the paper and MC and KC participated in the interpretation of the results and manuscript improvements; all the authors provided vegetation-plot data and commented on the expert system, results and the text of the paper.

Data availability statement

The final dataset of vegetation plots used in this study is available in the repository of the European Vegetation Archive (EVA) under the project "European gravel bar vegetation survey".

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Supplementary materials (paper 4)

S1 Syntaxonomical outline and nomenclature of European gravel-bar vegetation types.

The names and concepts of alliances and higher syntaxonomical units follow Mucina et al. 2016. The only exception is the alliance name *Salicion eleagni* Aichinger 1933, which replaces the name *Salicion eleagno-daphnoidis* (Moor 1958) Grass 1993 used by Mucina et al. (2016). The codes of the syntaxa follow the expert system.

THLASPIETEA ROTUNDIFOLII Br.-Bl. 1948

E000 *EPILOBIETALIA FLEISCHERI* Moor 1958

Herbaceous vegetation on gravel bars of alpine to submontane rivers in the temperate and boreal Eurasian mountains

ECA0 *CALAMAGROSTION PSEUDOPHRAGMITAE* Rivas-Martínez et al. 1984

Gravel-bar grasslands with *Calamagrostis pseudophragmites* of alpine to submontane river gravel bars of the temperate European mountains and the Caucasus

Tussilagini farfarae-Calamagrostietum pseudophragmitae Pawłowski et Walas 1949

Original name (Pawłowski & Walas 1949): Association à *Tussilago farfara* – et *Calamagrostis pseudophragmites* (= *Tussilagineto-Pseudophragmitetum*)
Syn.: *Calamagrostietum pseudophragmitae* Beldie 1967 (nomen nudum), Zbior. *Calamagrostis pseudophragmites-Festuca rubra* Kornaś et Medwecka-Kornaś 1967 (the rank does not correspond to ICPN), *Calamagrostietum pseudophragmitae* Kopecký 1968 (syntax. syn.), *Erucastro nasturtiifolii-Calamagrostietum pseudophragmitae* Rivas-Martínez et al. 1984 (syntax. syn.), Fitocenon a *Calamagrostis pseudophragmites* Poldini et Martini 1993 (the rank does not correspond to ICPN)

ECA1 *Tussilagini farfarae-Calamagrostietum pseudophragmitae typicum*

Oligotrophic gravel-bar grasslands with *Calamagrostis pseudophragmites*

Diagnostic species: *Calamagrostis pseudophragmites*
Constant species: *Agrostis stolonifera* agg., *Equisetum arvense*, *Myricaria germanica* juv., ***Salix eleagnos* juv.**, *Salix purpurea* juv., *Tussilago farfara*
Dominant species: *Calamagrostis pseudophragmites*

ECA2 *Tussilagini farfarae-Calamagrostietum pseudophragmitae phalaridetosum arundinaceae* (Kopecký 1968) Kalníková et al. 2020

Eutrophic gravel-bar grasslands with *Calamagrostis pseudophragmites*

Original name (Kopecký 1968): *Calamagrostidetum pseudophragmitis phalaridetosum*

Diagnostic species: *Calamagrostis pseudophragmites*, *Glyceria fluitans* agg., *Mentha longifolia*, *Myosotis scorpioides* agg., *Phalaroides arundinacea*, *Ranunculus repens*, *Rumex conglomeratus*, *Rumex obtusifolius*
Constant species: *Agrostis stolonifera* agg., *Artemisia vulgaris* agg., ***Equisetum arvense***, *Plantago lanceolata*, ***Plantago major* agg.**, *Salix euxina* agg. juv., ***Salix purpurea* juv.**, *Trifolium repens*, *Tussilago farfara*
Dominant species: *Calamagrostis pseudophragmites*, *Phalaroides arundinacea*

EEP0 *EPILOBION FLEISCHERI* G. Br.-Bl. ex Br.-Bl. 1950
Herbaceous early-successional vegetation of alpine to submontane river gravel bars of the temperate and boreal European mountains and the Caucasus

EEP1 *Epilobietum fleischeri* Lippmaa 1933
Alpine to montane early-successional herbaceous gravel-bar vegetation of the Alps

Original name (Lippmaa 1933): Association à *Epilobium fleischeri*
Syn.: *Myricarietum germanicae* Rübel 1912 (nomen nudum), *Epilobietum fleischeri* Lüdi 1921 (nomen nudum), *Epilobium fleischeri*-Ass. Frey 1922 (nomen nudum), *Epilobietum dodonaei* ssp. *fleischeri* Br.-Bl. 1923 (nomen nudum), *Petasitetum paradoxi epilobietosum fleischeri* Jenny-Lips 1930 (syntax. syn.)

Diagnostic species: *Anthyllis vulneraria*, ***Epilobium fleischeri***, *Larix decidua* juv., *Linaria alpina*, *Rumex scutatus*, *Saxifraga aizoides*, *Saxifraga paniculata*, *Sempervivum arachnoideum*, ***Trifolium pallescens***
Constant species: *Agrostis stolonifera* agg., *Campanula cochleariifolia*, *Gypsophila repens*, *Leontodon hispidus* s. l., *Poa alpina*, *Silene vulgaris* agg., *Tolpis staticifolia*, *Tussilago farfara*
Dominant species: *Epilobium fleischeri*, *Racomitrium canescens*

EEP2 *Epilobietum colchici* Kalníková et al. 2020
Alpine to montane early-successional herbaceous gravel-bar vegetation of the Caucasus

Original name (Kalníková et al. 2020): *Epilobietum colchici*

Diagnostic species: ***Epilobium colchicum***, *Papaver fugax*, *Petrorhagia saxifraga*, *Poa alpina*, *Rumex acetosella*, *Sedum pallidum*, *Sedum spurium*, *Senecio leucanthemifolius* subsp. *caucasicus*, ***Silene compacta***, *Tanacetum parthenium*, *Tripleurospermum caucasicum*, ***Trisetum rigidum***; *Bryum caespiticium*, ***Racomitrium canescens***
Constant species: *Arenaria serpyllifolia* agg., ***Calamagrostis pseudophragmites***, *Cerastium fontanum* agg., *Erigeron acris* agg., *Medicago lupulina*, *Pilosella officinarum*, *Poa nemoralis* agg., *Trifolium pratense*
Dominant species: *Epilobium colchicum*, *Racomitrium canescens*

EEP3 *Myricario-Chondrilletum chondrilloidis* Br.-Bl. in Volk et Br.-Bl. 1939
Montane early-successional herbaceous gravel-bar vegetation of the Alps

Nomen mutatum/ineptum propositum

Original name (Volk & Braun-Blanquet 1939): *Myricaria=Chondrilla prenanthoides=*Assoziation J. Braun=Blanquet 1939
Syn. *Myricaria-Chondrilla prenanthoides*-Assoziation Br.-Bl. et Flütsch 1938 (syntax syn.), *Chondrilletum chondrilloidis* Moor 1958 (syntax. syn.), *Leontodonto berinii-Chondrilletum* Wraber 1965 (syntax. syn.)

Diagnostic species: *Campanula cochleariifolia*, ***Carex flacca***, *Carex ornithopoda*, ***Dryas octopetala***, ***Chondrilla chondrilloides***, *Myricaria germanica* juv., *Salix purpurea* juv.
Constant species: *Agrostis stolonifera* agg., *Alnus incana* juv., *Calamagrostis pseudophragmites*, *Deschampsia cespitosa*, *Gypsophila repens*, *Petasites paradoxus*, *Pinus sylvestris* juv., *Poa alpina*, *Salix daphnoides* juv., *Salix eleagnos* juv., *Saxifraga aizoides*, *Sesleria caerulea*, *Thymus praecox* agg., *Tolpis staticifolia*, *Tussilago farfara*
Dominant species: –

EEP4 *Epilobio dodonaei-Scrophularietum caninae* W. Koch et Br.-Bl. ex Müller 1974

Montane to submontane early-successional herbaceous gravel-bar vegetation of South-Western Europe

Original name (Müller 1974): *Epilobio dodonaei-Scrophularietum caninae* W. Koch et Br.-Bl. apud Br.-Bl. 49
Syn. *Epilobio dodonaei-Scrophularietum caninae* W. Koch et Br.-Bl. in Br.-Bl. 1949 (nomen nudum)

Diagnostic species: *Echium vulgare*, *Euphorbia cyparissias*, *Melilotus albus*, *Oenothera biennis* agg., *Populus nigra* agg. juv., *Reseda lutea*, ***Scrophularia canina***
Constant species: *Agrostis stolonifera* agg., *Achnatherum calamagrostis*, *Artemisia vulgaris* agg., *Clematis vitalba*, *Dactylis glomerata*, *Daucus carota*, *Diplotaxis tenuifolia*, *Elymus caninus*, *Epilobium dodonaei*, *Erigeron annuus*, *Galeopsis speciosa*, *Galium mollugo* agg., *Geranium robertianum* agg., *Hypericum perforatum*, *Medicago lupulina*, *Microrrhinum minus*, *Petasites paradoxus*, *Picris hieracioides*, *Pilosella piloselloides* agg., *Plantago lanceolata*, ***Salix eleagnos* juv.**, *Salix purpurea* juv., *Sanguisorba minor*, *Silene vulgaris* agg., *Taraxacum* Sec. *Taraxacum*, *Tussilago farfara*
Dominant species: –

EEP5 *Epilobietum dodonaei* Vanden Berghen 1963

Montane to submontane early-successional herbaceous gravel-bar vegetation of Central- and South-Eastern Europe

Nomen mutatum/ineptum propositum

Original name (Vanden Berghen 1963): *Chamaenerietum rosmarinifolii*
Syn.: *Epilobio dodonaei-Melilotetum albae* Slavík 1978 (syntax. syn.), *Epilobietum dodonaei* Lakušić 1999 (nomen ineditum, nomen nudum)

Diagnostic species: *Arenaria serpyllifolia* agg., ***Daucus carota***, ***Epilobium dodonaei***, *Verbascum nigrum*
Constant species: *Agrostis stolonifera* agg., *Achillea millefolium* agg., *Artemisia vulgaris* agg., *Cerastium fontanum* agg., *Dactylis glomerata*, *Echium vulgare*, *Erigeron annuus*, *Erigeron canadensis*, *Eupatorium cannabinum*, *Euphorbia cyparissias*, *Galium mollugo* agg., *Geranium robertianum* agg., *Hypericum perforatum*, *Lapsana communis*, *Leucanthemum vulgare* agg., *Medicago lupulina*, *Melilotus albus*, *Mentha longifolia*, *Plantago lanceolata*, *Poa compressa*, *Salix eleagnos* juv., *Sanguisorba minor*, *Silene vulgaris* agg., *Tanacetum vulgare*, *Taraxacum* Sec. *Taraxacum*, *Trifolium repens*, *Tussilago farfara*, *Vicia cracca* agg.
Dominant species: *Festuca stricta*

SALICETEA PURPUREAE Moor 1958

SALICION CANTABRICAE Rivas-Martínez, T.E. Díaz et Penas in Rivas-Martínez et al. 2011

Cantabrian subalpine to montane willow-scrub vegetation of river gravel bars

SSA1 *Salicetum cantabricae* Rivas-Martínez et al. 1984

Cantabrian subalpine to montane willow-scrub vegetation of river gravel bars

Original name (Rivas-Martínez et al. 1984): *Salicetum cantabricae*

Diagnostic species: ***Salix cantabrica***, ***Salix cinerea***, *Salix triandra*
Constant species: *Filipendula ulmaria*, *Fraxinus excelsior*, *Mentha longifolia*, *Salix eleagnos*, *Salix euxina agg.*, ***Salix purpurea***
Dominant species: *Salix cantabrica*

SSA0 *SALICION ELEAGNI* Aichinger 1933

Scrub vegetation of subalpine to submontane river gravel bars of the temperate and boreal European mountains and the Caucasus

Original name (Aichinger 1933): *Salicion incanae*
Syn.: *Salicion eleagno-daphnoidis* (Moor 1958) Grass 1993 (syntax. syn.)

SSA2 *Epilobio dodonaei-Myricarietum germanicae* Aichinger 1933 nom. invers.

Subalpine to montane river gravel-bar scrub with *Myricaria germanica*

Original name (Aichinger 1933): *Myricarieto-Epilobietum*
Syn.: *Myricarietum* Hager 1916 (nomen nudum), *Myricario germanicae-Epilobietum dodonaei* Klika 1936 (younger homonym), *Myricarietum germanicae* Jeník 1955 (syntax. syn.), Stadium *Myricaria germanica-Salix incana* Zarzycki 1956 (the rank does not correspond to ICPN), *Salici purpureae-Myricarietum germanicae* Moor 1958 (syntax. syn.), *Myricario germanicae-Astragaletum alpini* Höfler 1964 (syntax. syn.), *Myricarietum ernesti-mayerii* Lakušić, Pavlović et Međedović 1974 (nomen nudum), *Racomitrio ericoidis-Myricarietum* Klokk 1980 (syntax. syn.), *Agrostio-Myricarietum germanicae* Romo 1989 (syntax. syn.), *Salici amplexicaulis-Myricarietum* Vukićević, Mijanović et Žujović 1992 prov. (nomen nudum)

Diagnostic species: ***Myricaria germanica,*** *Saxifraga aizoides*
Constant species: *Agrostis stolonifera* agg., *Achillea millefolium* agg., *Alnus incana*, *Calamagrostis pseudophragmites*, *Deschampsia cespitosa*, *Galium mollugo* agg., *Lotus corniculatus* agg., *Salix eleagnos*, ***Salix purpurea***, *Taraxacum* Sec. *Taraxacum*, *Trifolium repens*, *Tussilago farfara*
Dominant species: *Myricaria germanica*

SSA3 *Salicetum eleagno-purpureae* Sillinger 1933

Subalpine to montane river gravel-bar willow scrub with *Salix eleagnos* of Central and Southern Europe

Original name (Sillinger 1933): *Salicetum incano-purpureae*
Syn.: *Salicetum incanae* Hager 1916 (nomen nudum), *Salicetum incanae* Hager ex Jeník 1955 (syntax. syn.), *Salicetum incano-purpureae* Jeník 1955 (syntax. syn.), *Salicetum eleagno-daphnoidis* (Br.-Bl. in Volk 1939) Moor 1958 (syntax. syn. pro parte), *Salicetum incanae* Jovanović et Tucović 1965 prov. (nomen nudum)

Diagnostic species: *Salix eleagnos*
Constant species: *Agrostis stolonifera* agg., *Alnus incana*, *Clematis vitalba*, *Eupatorium cannabinum*, *Galium mollugo* agg., ***Salix purpurea***, *Tussilago farfara*
Dominant species: *Salix eleagnos*, *Salix purpurea*

SSA4 *Salici incanae-Hippophaëtum rhamnoidis* Br.-Bl. in Volk et Br.-Bl. 1939

Subalpine to montane river gravel-bar scrub with *Hippophaë rhamnoides*

Original name (Volk & Braun-Blanquet 1939): *Salix incana=Hippophaë*=Assoziation (Br. =Bl. 1933 n.n.) J. Braun=Blanquet 1939
Syn.: *Hippophaëtum* Hager 1916 (nomen nudum), *Hippophaëtum* Issler 1924 (nomen nudum), *Hippophaë*-Stadium Br.-Bl. 1926 (the rank does not correspond to ICPN), *Hippophaëtum rhamnoides* Borza 1931 (nomen nudum), *Salici incanae-Hippophaëtum rhamnoidis* Wendelberger-Zelinka 1952 (younger homonym), *Salicetum eleagno-daphnoidis* (Br.-Bl. in Volk 1939) Moor 1958 (syntax. syn.)

Diagnostic species: ***Hippophaë rhamnoides***
Constant species: *Anthyllis vulneraria*, *Calamagrostis epigejos*, *Galium mollugo* agg., *Populus nigra* agg., *Salix eleagnos*, *Salix purpurea*

Dominant species: *Hippophaë rhamnoides*

SSA5 *Saponario officinalis-Salicetum purpureae* Tchou 1948

Montane to submontane river gravel-bar willow scrub of European mountains and the Caucasus

Original name (Tchou 1948): *Saponarieto-Salicetum purpureae* (Br.-Bl. 1930) Tchou (1946)
Syn.: *Salicetum purpureae* Wendelberger-Zelinka 1952 (syntax. syn.), *Agrostio-Salicetum purpureae* Jurko 1964 (syntax. syn.), *Salicetum lambertiano-angustifoliae* Rivas-Martínez et al. 1991 (nomum nudum), *Rumici crispi-Salicetum purpureae* Kevey in Borhidi 1996 (syntax. syn.)

Diagnostic species: –
Constant species: *Agrostis stolonifera* agg., *Dactylis glomerata*, *Galium mollugo* agg., *Mentha longifolia*, *Petasites hybridus*, *Phalaroides arundinacea*, *Salix eleagnos*, ***Salix purpurea***, *Tussilago farfara*, *Urtica dioica*
Dominant species: *Salix purpurea*

Table S2 Distribution of the accepted gravel-bar vegetation associations in Europe with references to the most important literature.

	Tussilagini farfarae-Calamagrostietum pseudophragmitae	***Epilobietum fleischeri***	***Epilobietum colchici***	***Myricario-Chondrilletum chondrilloidis***	***Epilobio dodonaei-Scrophularietum caninae***	***Epilobietum dodonaei***	***Salicetum cantabricae***	***Epilobio dodonaei-Myricarietum germanicae***	***Salicetum eleagno-purpureae***	***Salici incanae-Hippophëtum rhamnoidis***	***Saponario officinalis-Salicetum purpureae***
Albania	**probably occurring but no data or report**	*no record*	*no record*	*no record*	**probably occurring but no data or report**	Drescher, 2018	*no record*	new field data or classification result	Dring *et al.*, 2002; Drescher, 2018	**probably occurring but no data or report**	**probably occurring but no data or report**
Austria	Müller, 1991; Müller *et al.*, 1992; Grabherr and Mucina, 1993	Ellmauer, 2005	*no record*	Müller *et al.*, 1992; Werhoning, 1997; Essl *et al.*, 2002	**probably occurring but no data or report**	**probably occurring but no data or report**	*no record*	Aichinger, 1933; Höfler, 1964; Müller *et al.*, 1992; Petutschnig, 1994; Werhoning, 1997; Essl *et al.*, 2002; Schletterer and Scheiber, 2008; Kudrnovsky, 2013a, b	Prack, 1985; Müller, 1991; Fisher, 1997; Werhoning, 1997; Essl, 1998; Essl *et al.*, 2002; Ellmauer, 2005; Willner and Grabherr, 2007	Essl *et al.*, 2002; Ellmauer, 2005	Wendelberger-Zelinka, 1952; Müller *et al.*, 1992; Mucina *et al.*, 1993; Essl *et al.*, 2002; Willner and Grabherr, 2007
Belarus	*no record*	*no record*	*no record*	*no record*	*no record*	*no record*	*no record*	*no record*	*no record*	*no record*	Stepanovich, 2006
Bulgaria	new field data or classification result	*no record*	*no record*	*no record*	**probably occurring but no data or report**	**probably occurring but no data or report**	*no record*	*no record* (*Myricaria germanica* disappeared from natural habitats (Gussev and Dmitrov, 1997); now only secondary in quarry (Marinov *et al.*, 2017))	new field data or classification result	*no record*	new field data or classification result

	Tussilagini farfarae-Calamagrostietum pseudophragmitae	***Epilobietum fleischeri***	***Epilobietum colchici***	***Myricario-Chondrilletum chondrilloidis***	***Epilobio dodonaei-Scrophularietum caninae***	***Epilobietum dodonaei***	***Salicetum cantabricae***	***Epilobio dodonaei-Myricarietum germanicae***	***Salicetum eleagno-purpureae***	***Salici incanae-Hippophëtum rhamnoidis***	***Saponario officinalis-Salicetum purpureae***
Bosnia and Herzegovina	Đorđije Milanović – unpublished data	*no record*	*no record*	*no record*	*no record*	**new field data or classification result**	*no record*	*no record*	Milanović and Stupar, 2017	*no record*	Lakušić *et al.*, 1977
Croatia	**probably occurring but no data or report**	*no record*	*no record*	*no record*	**probably occurring but no data or report**	**probably occurring but no data or report**	*no record*	Trinajstić, 1964, 1992, 2008; Vukićević *et al.*, 1992; Antonić *et al.*, 2005; Vukelić, 2012	Trinajstić, 1964; Trinajstić and Franjić, 1994; Antonić *et al.*, 2005	Müller-Schneider, 1964; Antonić *et al.*, 2005; Franjić *et al.*, 2016	Trinajstić, 1964, 2008; Antonić *et al.*, 2005
Czech Republic	Kopecký, 1968, 1969; Adámková, 1998; Chytrý, 2011; Kalníková and Eremiášová, 2013; Skokanova *et al.*, 2015	*no record*	*no record*	*no record*	*no record*	Kolbek, 1985 (secondary habitat in a quarry); Slavík, 1978, 1986; Šigutová, 2008	*no record*	Staněk, 1954; Popelářová, *et al.* 2011; Chytrý, 2013; Banaš *et al.*, 2015	Šigutová, 2008; Klečková, 2010; Chytrý, 2013; Kalníková, *et al.* 2018	*no record*	Sofron and Štěpán, 1971; Albrechtová *et al.*, 1987; Šigutová, 2009; Chytrý, 2013; Kalníková *et al.*, 2018
France	Julve, 1993	Julve, 1993	*no record*	Julve, 1993	Julve, 1993	Berghen, 1963	*no record*	Julve, 1993; Gégout *et al.*, 2008	Julve, 1993; Gégout *et al.*, 2008; Ferrez *et al.*, 2009	Issler, 1924; Julve, 1993; Bardat *et al.*, 2004; Abdulhak and Sanz, 2012	Tchou, 1948; Berghen, 1963; Gégout *et al.*, 2008; Ferrez *et al.*, 2009
Georgia	Kalníková *et al.*, 2020	*no record*	Kalníková *et al.*, 2020	*no record*	*no record*	**probably occurring but no data or report**	*no record*	Kolakovskii, 1961; Kalníková *et al.*, 2020	*no record*	Seifriz, 1931; Kalníková *et al.*, 2020	**probably occurring but no data or report**

	Tussilagini farfarae-Calamagrostietum pseudophragmitae	*Epilobietum fleischeri*	*Epilobietum colchici*	*Myricario-Chondrilletum chondrilloidis*	*Epilobio dodonaei-Scrophularietum caninae*	*Epilobietum dodonaei*	*Salicetum cantabricae*	*Epilobio dodonaei-Myricarietum germanicae*	*Salicetum eleagno-purpureae*	*Salici incanae-Hippophëtum rhamnoidis*	*Saponario officinalis-Salicetum purpureae*
Germany	Müller and Bürger, 1990; Oberdofer, 1993; Pott, 1995; Schubert *et al.*, 2001	Oberdörfer, 1993; Pott, 1995; Schubert *et al.*, 2001	*no record*	Müller, 1988; Müller and Bürger, 1990; Pott, 1995; Schubert *et al.*, 2001; Harzel, 2016	Müller, 1974; Pott, 1995; Griese and Kleinsteuber, 1996; Schubert *et al.*, 2001	**probably occurring but no data or report**	*no record*	Müller, 1988; Müller and Bürger, 1990; Pott, 1995; Bill *et al.*, 1997	Müller and Bürger, 1990; Müller *et al.*, 1992; Pott, 1995	Pott, 1995; Schubert *et al.*, 2001	Pott, 1995; Schubert *et al.*, 2001
Hungary	*no record*	*no record*	*no record*	*no record*	*no record*	*no record*	*no record*	Kevey, 2008; Purger, 2008	*no record*	Borhidi, 1996; Kevey, 2008; Purger, 2008	Kárpáti and Tóth, 1961; Kevey, 2008; Borhidi *et al.*, 2012
Italy	Poldini and Martini, 1993; Lippert *et al.*, 1995; Francescato, 2012	Bachmann, 1997; Caccianiga and Andreis, 2004	*no record*	Poldini & Martini, 1993; Poldini & Vidali, 1995; Lippert *et al.*, 1995; Bachmann, 1997; Francescato, 2012; Pignatti and Pignatti, 2014	Poldini and Martini, 1993; Lippert *et al.*, 1995; Biondi *et al.*, 1997, 2003; Vagge, 2001; Francescato, 2012	**probably occurring but no data or report**	*no record*	Bachmann, 1997; Kiem, 1992; 1997; Oriolo and Poldini, 2002; Francescato, 2012; Biondi *et al.*, 2003; Michielon and Sitzia, 2010; Müller, 2005	Oriolo and Poldini, 2002; Biondi *et al.* 2003, 2009, 2012; Francescato 2012; Pignatti and Pignatti, 2014	Oriolo and Poldini, 2002; Francescato, 2012; Biondi *et al.*, 2014; Pignatti and Pignatti, 2014	Biondi *et al.*, 2009; Lastrucci *et al.*, 2010
North Macedonia	new field data or classification result	*no record*	*no record*	*no record*	*no record*	**probably occurring but no data or report**	*no record*	**probably occurring but no data or report**	new field data or classification result	*no record*	**probably occurring but no data or report**
Montenegro	new field data or classification result	*no record*	*no record*	*no record*	new field data or reclassification result	Lakušić, 1999; Petrović *et al.*, 2012	*no record*	Lakušić *et al.*, 1974; Božović, 2011; Petrović *et al.*, 2012	Petrović *et al.*, 2012	*no record*	Blečić and Lakušić, 1976; Božović, 2011

	Tussilagini farfarae-Calamagrostietum pseudophragmitae	*Epilobietum fleischeri*	*Epilobietum colchici*	*Myricario-Chondrilletum chondrilloidis*	*Epilobio dodonaei-Scrophularietum caninae*	*Epilobietum dodonaei*	*Salicetum cantabricae*	*Epilobio dodonaei-Myricarietum germanicae*	*Salicetum eleagno-purpureae*	*Salici incanae-Hippophëtum rhamnoidis*	*Saponario officinalis-Salicetum purpureae*
Norway	*no record*	*no record*	*no record*	*no record*	*no record*	*no record*	*no record*	Klokk, 1978, 1980; Fremstad, 1981; Odland, 1991; Dierßen, 1996	*no record*	*no record*	*no record*
Poland	Kornaś and Medwecka-Kornaś, 1967; Matuszkiewicz, 2007	*no record*	*no record*	*no record*	*no record*	**probably occurring but no data or report**	*no record*	Zarzycki, 1956; Dubiel *et al.*, 1999; Matuszkiewicz, 2007; Koczur, 2012	Mróz, 2012; Koczur, 2012	*no record*	new field data or classification result
Romania	Beldie, 1967; Dihoru, 1975; Pop *et al.*, 1986; Coldea, 1996; Popescu *et al.*, 1996; Gafta and Mountford, 2008	*no record*	*no record*	*no record*	*no record*	**probably occurring but no data or report**	*no record*	Pázmány, 1969; Ardelan, 1981; Coldea, 1991; Costicâ *et al.*, 2010; Doniţă, 2005; Sanda, 2008; Danci, 2014; Neblea, 2016; Vinţan, 2016; Nuţă and Niculescu, 2019	Coldea, 1991, 2015; Doniţă, 2005	Borza, 1931; Donita *et al.*, 2005; Gafta and Mountford, 2008; Paucă-Comănescu *et al.*, 2008	Csürös *et al.*, 1968; Dihoru, 1975; Raţiu *et al.*, 1984; Doniţă *et al.*, 1992, Doniţă *et al.*, 2005; Sanda *et al.*, 2008; Paucă-Comănescu *et al.*, 2008
Russia	**probably occurring but no data or report**	*no record*	**probably occurring but no data or report** (similar comunity Onipchenko 2002)	*no record*	*no record*	**probably occurring but no data or report**	*no record*	**probably occurring but no data or report**	*no record*	Seifriz, 1931	**probably occurring but no data or report**
Serbia and Kosovo	new field data or classification result	*no record*	*no record*	*no record*	**probably occurring but no data or report**	**probably occurring but no data or report**	*no record*	Vukićević *et al.*, 1992; Lakušić *et al.*, 2007	Jovanović et Tucović, 1965; Kojić *et al.*, 1998; Tomić and Rakonjac, 2013	Kojić *et al.*, 1998	Jovanoivić and Tucović, 1965; Kojić *et al.*, 1998; Rexhepi, 2007; Tomić and Rakonjac, 2013

	Tussilagini farfarae-Calamagrostietum pseudophragmitae	*Epilobietum fleischeri*	*Epilobietum colchici*	*Myricario-Chondrilletum chondrilloidis*	*Epilobio dodonaei-Scrophularietum caninae*	*Epilobietum dodonaei*	*Salicetum cantabricae*	*Epilobio dodonaei-Myricarietum germanicae*	*Salicetum eleagno-purpureae*	*Salici incanae-Hippophëtum rhamnoidis*	*Saponario officinalis-Salicetum purpureae*
Slovakia	Šomšák, 1972; Zaliberová, 1982; Urbanová and Zaliberová, 1996; Valachovič, 2001	*no record*	*no record*	*no record*	*no record*	Slavík, 1978	*no record*	Klika, 1936; Jeník, 1955; Jurko and Májovský, 1956; Urbanová, 1977; Zaliberová, 1982; Jarolímek and Šibík, 2008	Sillinger, 1933; Jeník, 1955; Jurko, 1964; Stanová and Valachovič, 2002; Jarolímek and Šibík, 2008; Benčaťová *et al.*, 2014	*no record*	Jurko, 1964; Stanová and Valachovič, 2002; Jarolímek and Šibík, 2008
Slovenia	**probably occurring but no data or report**	*no record*	*no record*	Wraber, 1965; Šilc & Čarni, 2012; Jogan *et al.*, 2004	Čusin, 2001; Šilc and Čarni, 2012	**probably occurring but no data or report**	*no record*	Dakskobler, 2004; Šilc and Čušin, 2004; Čušin and Šilc, 2006; Šilc and Čarni, 2012	Čušin and Šilc, 2006; Šilc and Čarni, 2012	Jogan *et al.*, 2004; Šilc and Čarni, 2012	Šilc and Čarni, 2012
Spain	Rivas-Martínez *et al.*, 1984, 2001	*no record*	*no record*	*no record*	**probably occurring but no data or report**	*no record*	Rivas-Martínez *et al.*, 1984, 2001, 2011; Loidi *et al.*, 2015; Loidi, 2017	Romo, 1989; Cambra *et al.*, 2008; Rivas-Martínez *et al.*, 2001; Toro, 2009	new field data or classification result	Toro, 2009	Díaz and Penas, 1987; Rivas-Martínez *et al.*, 1991, 2001; García, 2002; Toro, 2009
Sweden	*no record*	*no record*	*no record*	*no record*	*no record*	*no record*	*no record*	new field data or classification result	*no record*	*no record*	*no record*

	Tussilagini farfarae-Calamagrostietum pseudophragmitae	*Epilobietum fleischeri*	*Epilobietum colchici*	*Myricario-Chondrilletum chondrilloidis*	*Epilobio dodonaei-Scrophularietum caninae*	*Epilobietum dodonaei*	*Salicetum cantabricae*	*Epilobio dodonaei-Myricarietum germanicae*	*Salicetum eleagno-purpureae*	*Salici incanae-Hippophëtum rhamnoidis*	*Saponario officinalis-Salicetum purpureae*
Switzerland	**probably occurring but no data or report**	Lüdi, 1921; Frey, 1922; Jenny-Lips, 1930; Moor, 1958; Werner, 1985; Reinalter, 2004; 2007; Burga *et al.*, 2010; Klötzli, 2010	*no record*	Volk, 1939; Moor, 1958; Müller-Schneider, 1964	Moor, 1958	**probably occurring but no data or report**	*no record*	Rübel, 1912; Hager, 1916; Lüdi, 1921; Gams, 1927; Moor, 1958; Endress, 1975; Werner, 1985; Tinner and Waldburger, 2008; Werner, 2016	Hager, 1916; Volk, 1939; Moor, 1958; Roulier, 1998	Siegrist, 1913; Hager, 1916; Lüdi, 1921; Gams, 1927; Volk, 1939; Moor, 1958; Müller-Schneider, 1964; Roulier, 1998	new field data or classification result
Ukraine – Carpathians	Pawłowski and Walas, 1949; Malinovsky, 2000; Solomakha, 2010; Iakushenko *et al.*, 2011	*no record*	*no record*	*no record*	*no record*	Iakushenko *et al.,* 2011	*no record*	Iakushenko *et al.*, 2005, 2006, 2011	new field data or classification result	**probably occurring but no data or report**	new field data or classification result
Ukraine – Crimea	*no record*	*no record*	*no record*	*no record*	*no record*	*no record*	*no record*	*no record*	*no record*	*no record*	Didukh, 2016

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Table S3 Sources of data used in this study.

Data from the following vegetation databases, with IDs according to the Global Index of Vegetation-Plot Databases (GIVD; Dengler *et al.*, 2011), were made available for the present study: Alpine Botanical National Conservatory Database (CBN Alpin database), Austrian Vegetation Database, Czech National Phytosociological Database, Croatian Vegetation Database, German Vegetation Reference Database (GVRD), Polish Vegetation Database, Slovak Vegetation Database, Vegetation Database of Slovenia, VegItaly, Iberian and Macaronesian Vegetation Information System (SIVIM) and SOPHY. Almost half of the vegetation plots come from the gap-oriented Gravel Bar Vegetation Database which was created specifically for the purpose of this project. The database consists of vegetation plots digitalized from the literature or sampled during our fieldwork especially in the countries where this vegetation had not been studied before. Vegetation plots from several private databases were added.

Country	GIVD database name	GIVD database code	Reference or database custodians	No. of plots of analysed dataset	No. of classified plots	No. of classified plots after geographical stratification
Albania	Gravel Bar Vegetation Database	EU-00-025	Kalníková and Kudrnovsky, 2017	3	1	1
Austria	Austrian Vegetation Database	EU-AT-001	Willner *et al.*, 2012	274	88	80
	Gravel Bar Vegetation Database			313	204	169
Bulgaria	Gravel Bar Vegetation Database			43	28	27
Bosnia and Herzegovina	Gravel Bar Vegetation Database			2	1	1
	Private data		Đorđije Milanović	28	4	3
Croatia	Croatian Vegetation Database	EU-HR-002	Željko Škvorc, Daniel Krstonošić	18	8	8
Czech Republic	Czech National Phytosociological Database	EU-CZ-001	Chytrý and Rafajová, 2003	532	57	50
	Private data		Martin Kočí, Pavel Lustyk, Karel Prach	111	27	26
France	SOPHY	EU-FR-003	Garbolino *et al.*, 2012	7	6	6
	CBN Alpin database		Jean-Michel Genis	322	115	96
	Gravel Bar Vegetation Database			22	14	12

Georgia	Gravel Bar Vegetation Database			85	49	48
Germany	German Vegetation Reference Database (GVRD)	EU-DE-014	Jandt and Bruelheide, 2012	48	9	8
	Gravel Bar Vegetation Database			199	47	35
Italy	VegItaly	EU-IT-001	Landucci *et al.*, 2012	320	45	41
	Gravel Bar Vegetation Database			319	152	101
	Private data		Michela Tomasella, Mariacristina Villani and Francesco Bracco	70	8	7
Macedonia	Gravel Bar Vegetation Database			11	6	6
Montenegro	Gravel Bar Vegetation Database			12	10	10
Norway	Gravel Bar Vegetation Database			274	40	18
Poland	Polish Vegetation Database	EU-PL-001	Kącki and Śliwiński, 2012	38	4	4
	Slovak Vegetation Database	EU-SK-001	Šibík, 2012	13	0	0
	Gravel Bar Vegetation Dat.			460	67	59
Romania	Gravel Bar Vegetation Database			51	16	9
	Private data		Claudia Biţă-Nicolae, Valeriu Vintan	14	3	3
Russia	Gravel Bar Vegetation Database			19	10	10
Serbia	Gravel Bar Vegetation Database			13	7	7
Slovakia	Slovak Vegetation Database	EU-SK-001	Šibík, 2012	278	51	38
Slovenia	Vegetation Database of Slovenia	EU-SI-001	Šilc, 2006	262	49	38
	Gravel Bar Vegetation Database			5	5	1
Spain	Gravel Bar Vegetation Database			6	3	3

	SOPHY	EU-FR-003	Garbolino *et al.*, 2012	5	0	0
	Iberian and Macaronesian Vegetation Information System (SIVIM)	EU-00-004	Xavier Font	279	92	83
Sweden	Gravel Bar Vegetation Database			2	2	2
	Private data		Kerstin Worler	3	3	3
Switzerland	Gravel Bar Vegetation Database			133	72	44
	Swiss Biodiversity Monitoring Program BDM		Tobias Roth	7	1	1
	Private data		Thomas Wohlgemuth	48	1	1
	SOPHY	EU-FR-003	Garbolino *et al.*, 2012	40	25	23
Ukraine	Gravel Bar Vegetation Database			40	20	16
	Private data		Yulia Mala, Dmytro Iakusenko, Roman Kish	40	15	12

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Electronic supplementary materials (paper 4)

S4 Taxonomical aggregates and *sensu lato* species used in this study.

S5 Expert system for classification of European gravel-bar vegetation plots that can be run in the JUICE program.

Table S6, S7 Full synoptic tables of European gravel-bar vegetation types.

Paper 5

Kalníková, V., Palpurina, S., Peterka, T., Kubešová, S., Plesková, Z. and Sabovljević, M. (2017) Bryophytes on river gravel bars in the Balkan Mountains: New records and insights into ecology. *Herzogia*, 30, 370–386.

Bryophytes on river gravel bars in the Balkan mountains: new records and insights into ecology

Veronika Kalníková*, Salza Palpurina, Tomáš Peterka, Svatava Kubešová, Zuzana Plesková & Marko Sabovljević

Abstract: Kalníková, V., Palpurina, S., Peterka, T., Kubešová, S., Plesková, Z. & Sabovljević, M. 2017. Bryophytes on river gravel bars in the Balkan mountains: new records and insights into ecology. – Herzogia **30**: 370–386.

Gravel bars are a heterogeneous habitat on the border between the aquatic and terrestrial environments that can maintain a high diversity of bryophyte species. However, the bryoflora of river gravel bar habitats has rarely been explored, particularly in Southeastern Europe. We therefore carried out a two-year field survey on river gravel bars in selected mountains and foothills in the Balkan Peninsula, recording all bryophytes in 4×4 or 3×5 m plots. In total, we sampled 59 vegetation plots on 30 streams and rivers and recorded 85 bryophyte taxa. Here we report *Bryum klinggraeffii* (a new species for the floras of Albania, Montenegro and Serbia) and five data-deficient or vulnerable species. We found several drought-tolerant bryophytes on gravel bars, e.g. *Barbula convoluta*, *Ceratodon purpureus* and *Tortella tortuosa*, as well as typical hygrophilous species, e.g. *Cinclidotus aquaticus*, *Fontinalis antipyretica* and *Platyhypnidium riparioides*. The most common species in this transitional habitat were *Brachythecium rivulare*, *Bryum argenteum*, *Oxyrrhynchium hians*, *Barbula unguiculata*, *Ceratodon purpureus* and *Bryum caespiticium*. Dentrended correspondence analysis ordination technique identified the complex gradient of moisture and light conditions as the main environmental factor for bryophyte communities on the studied gravel bars.

Zusammenfassung: Kalníková, V., Palpurina, S., Peterka, T., Kubešová, S., Plesková, Z. & Sabovljević, M. 2017. Moose auf Fluss-Schotterbänken in den Gebirgen des Balkans: neue Funde and Erkenntnisse zu ihrer Ökologie. – Herzogia **30**: 370–386.

Fluss-Schotterbänke sind heterogene Habitate im Grenzbereich zwischen aquatischen und terrestrischen Lebensräumen, die eine hohe Diversität an Moossippen aufweisen können. Die Moosflora von Fluss-Schotterbänken war bisher nur selten der Gegenstand von Untersuchungen, so auch in Südosteuropa. Wir haben deshalb eine zweijährige Feldstudie an Fluss-Schotterbänken in ausgewählten Gebirgen und ihrem Vorland auf der Balkanhalbinsel durchgeführt, wobei alle Moose in 4 × 4 oder 3 × 5 m großen Plots untersucht wurden. Insgesamt wurden 59 Plots an 30 Bächen und Flüssen aufgenommen und dabei konnten 85 Moostaxa festgestellt werden. *Bryum klinggraeffii* konnte dabei als neu für Albanien, Montenegro und Serbien ermittelt werden; außerdem wurden fünf gefährdete Arten bzw. Arten mit ungenügender Datenlage festgestellt. Wir haben einige gegen Trockenheit unempfindliche Moosarten auf den Schotterbänken festgestellt, z. B. *Barbula convoluta*, *Ceratodon purpureus* und *Tortella tortuosa*, aber auch typische feuchtigkeitsliebende Arten, z. B. *Cinclidotus aquaticus*, *Fontinalis antipyretica* und *Platyhypnidium riparioides*. Die häufigsten Arten der Übergangsbereiche sind *Brachythecium rivulare*, *Bryum argenteum*, *Oxyrrhynchium hians*, *Barbula unguiculata*, *Ceratodon purpureus* und *Bryum caespiticium*. Eine DCA-Ordination ergab den komplexen Gradienten von Feuchtigkeits- und Lichtverhältnissen als den hauptsächlichen Umweltfaktor für die Ausbildung der Moosgesellschaften auf den untersuchten Fluss-Schotterbänken.

Key words: Mosses, liverworts, *Bryum klinggraeffii*, gravel bar vegetation, moisture gradient, streams.

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Introduction

Riverine habitats provide an environment for a diverse spectre of species, and bryophytes are important parts of these. This work focuses on one particular riverine habitat type – river gravel bars. Gravel bars in the rivers of piedmont and mountain valleys emerge in places of lower velocity where sediments from bank erosion in the upper reaches are deposited. They are usually fixed on braided rivers which are typical for shallow and broad floodplains with a shifting mosaic of various channels, pools, side bars and islands (Müller 1995, Montgomery & Buffington 1998, Lehotský & Grešková 2004).

Gravel bars are a dynamic and heterogeneous environment. Organisms living here have to cope with harsh and unstable ecological conditions such as frequent water-level fluctuations, strong flooding and the low nutrient content in the substrate surface of fresh deposits (e.g. Tockner et al. 2006, Gilvear et al. 2008). On exposed parts of gravel bars, high temperature and drought together with fluctuations in groundwater level are additional stressing factors for species. In contrast, low-laying areas and depressions, usually composed of finer sediments, are more humid with a better moisture-retaining capacity and a higher groundwater level and, at the other extreme, patches situated on the bar edges are frequently flooded (Tockner et al. 2000, Gilvear et al. 2008). As a result of disturbances and the different grain size and reaction of their substrate, gravel bars provide a variety of microhabitats and their vegetation follows a clear successional pathway. At early successional stages, there is unlimited space and resources (mainly light) allowing species with a variety of distribution abilities to colonise the gravel bar. The initial successional stages are subsequently overgrown into denser vegetation stands usually dominated by more shade-tolerant species (Vitt et al. 1986, Tockner et al. 2006).

Under the heterogeneous environmental conditions and different successional stages of the vegetation of river gravel bars we expect a wide range of bryophyte functional types, life forms and strategies as has been shown to be the case for vascular plants (Tockner et al. 2006). For bryophytes, previous studies suggest that water-level fluctuation and water flow are the two most important gradients in the riverine environment (Watson 1919, Muotka & Virtanen 1995, Vieira et al. 2012).

However, patterns of species composition and ecology of bryophyte communities on river gravel bars in the Balkan Peninsula are unknown. Moreover, the level of knowledge on bryophyte distribution differs among Balkan countries, with some regions being bryofloristically very poorly explored (Sabovljević et al. 2001, 2008, 2011, Papp et al. 2014, Hodgetts 2015). There are also only a few studies dealing with aquatic-riparian bryophyte communities and flora from several rivers in Bulgaria and Greece (see Papp et al. 1998, 2006, Papp 1999).

Given the general lack of knowledge about the distribution of bryophyte species in the Balkan Peninsula and their largely unknown species composition on river gravel bars, the aims of this study are (I) to present records of newly found species in countries within the study area, (II) to present new information about the distribution of some bryophyte species not well known within the study area, and (III) to discuss ecological preferences of bryophytes on river gravel bars and the environmental gradients that explain their species composition. The work is separated into two parts: in the first part we provide a list of all bryophyte species recorded during the field survey with a brief description of distribution and ecology for species of conservation interest and data deficient species; in the second part we describe ecological preferences of bryophytes to moisture and analyse the main environmental gradients that explain the variation in the bryophyte species composition growing on river gravel bars.

Study Area and Methods

Field sampling and data compilation

We carried out two field surveys in 14 mountains in 5 countries in the Balkan Peninsula in the summers of 2013 and 2014 (Fig. 1, Table 1). We used standardised plots to sample the vegetation on gravel bars in 30 rivers of the submountain to mountain level (310–1407 m a. s. l.; Table 1). A detailed description of the location of each plot is provided in Table S1 in the Appendix.

In the field, we recorded all bryophyte and vascular plant species within a 4×4 m plot (n = 50). If the bar was narrower than 4 m, we used a plot size of 3×5 m (n = 9). The coordinates of the plots were taken using a portable GPS device (WGS-84 system). Bryophytes were collected from ground or stones. In each plot we estimated visually the cover of each species (c) according to the extended Braun-Blanquet cover scale: r (c ≤ 5 %, 1–3 individuals), + (c ≤ 5 %, few individuals), 1 (c ≤ 5 %, abundant), 2 m (c ≤ 5 %, very abundant), 2a (5 < c ≤ 12.5 %), 2b (12.5 < c ≤ 25 %), 3 (25 < c ≤ 50 %), 4 (50 < c ≤ 75 %), 5 (> 75 %) (van der Maarel 2005). The total vegetation cover and the cover of each layer (E2 – shrub, E1 – herb, E0 – moss) were estimated on the percentage scale. We also measured the maximum and mean height of the shrub and herb layer and the height of the gravel bar (as the distance from its highest point to the actual water level) with a tape. We recorded light conditions roughly as sun-exposed or partly shaded (judging subjectively by surrounding bank vegetation or topography). Substrate structure was recorded according to the modified Wentworth scale (Bunte & Abt 2001) using three categories: stones (ø > 20 cm), gravel (ø < 20 cm) and sand (ø ≤ 2 mm). We used the plots' coordinates to extract information on substrate reaction from soil maps (Panagos et al. 2012, CEC 2004) in the program ArcGIS (ESRI Inc. 2008).

Data on vegetation structure and ecological conditions for each plot are listed in Table S2 in the Appendix and there are also some comments given in the text. All vegetation plot records are stored in the Gravel Bar Vegetation Database – ID: EU-00-025 (Kalníková &

Fig. 1. Distribution of sample plots (black dots) where bryophytes were collected (n = 59).

Kudrnovský 2017) which is included in the European Vegetation Archive (Chytrý et al. 2016). Nomenclature follows Euro+Med PlantBase (2006–2016) for vascular plants, Hill et al. (2006) for mosses, and Grolle & Long (2000) for liverworts. The conservation status of bryophyte species follows the up-to-date checklist and red list of bryophytes for Europe (Hodgetts 2015). Bryophyte specimens were deposited in the herbarium of the Moravian Museum, Brno, Czech Republic (BRNM).

Table 1. A list of the studied rivers sorted by the country in which the river is located and/or sampled. Rivers that originate from the same mountain range are grouped together. The altitude represents the altitudinal range of the plots sampled along rivers in the same mountain range. n – number of sampled plots.

Country	River	Mountain	Altitude (m a. s. l.)
Bulgaria	Treklyanska Reka	Milevska Planina (n = 1)	741
	Rilska Reka, Bistritza, Mesta, Cherna Mesta, Beli Iskar, Cherni Iskar	Rila (n = 10)	395–1184
	Stara Reka	Malashevska Planina (n = 1)	315
	Svinskata Reka, Beli Vit, Zavodna, Cherni Osam, Osam, Tazha	Stara Planina (n = 14)	310–734
Serbia	Đetinja	Tara (n = 1)	672
	Ribnica	Zlatibor (n = 1)	649
	Mileševka	Jadovnik (n = 2)	512–520
	Banjštica, Trebesinska reka	Besna kobila (n = 3)	456–542
	Pčinja	Široka Planina (n = 2)	524–527
Macedonia	Raḱita, Radika, tributary of Crn Kamen	Šar Planina (n = 10)	685–1407
	Ribnička reka	Korab (n = 1)	882
Albania	Drini Zi	Çermenikë (n = 1)	477
Montenegro	Tara, Drcka rijeka, Lim	Komovi (n = 9)	732–1002
	Komarnica, unknown river	Durmitor (n = 3)	982–1035

Studied vegetation types

The vegetation we sampled on gravel bars on selected rivers in the Balkan Peninsula could be divided into six general types:

(I) an open, initial vegetation on sun-exposed, overheated and dry gravel bar patches with *Epilobium dodonaei*, shrubs such as *Salix* spp. (usually in the juvenile stage), and with scattered *Myricaria germanica* in the herb or shrub layer and sparse stands of *Calamagrostis pseudophragmites*;

(II) shrubby vegetation dominated by *Myricaria germanica* – usually with many gaps, on older gravel bar sections that were dry and characterised by a high content of sandy substrate;

(III) shrubby vegetation dominated by *Salix* spp. – successionally more advanced vegetation on stabilised gravel bars, probably with a high nutrient content (for example from accumulation of leaf litter, e.g. Müller 1995); the shrub layer is usually quite dense, with a shaded and humid microclimate of its understory, while the surrounding could be more open, sun-exposed; typically with shrubs of *Salix elaeagnos*, *S. purpurea*, *S. euxina*, *S. alba*, *Alnus* spp. and *Myricaria germanica*;

(IV) *Salix* spp. sparse shrubs – more scattered, a younger successional stage of the previous one;

(V) very dense vegetation dominated by *Calamagrostis pseudophragmites*, usually situated on moist sandy depressions, may have a higher nutrient content;

(VI) vegetation dominated by *Petasites hybridus* with very humid and dark conditions underneath, could also have higher nutrient content.

A summary of environmental variables and vegetation structure for each vegetation type is presented in Table 2. Vegetation types assigned to each plot are listed in Table S2 in the Appendix.

Ordination analysis

We performed a detrended correspondence ordination analysis (DCA) using CANOCO for Windows 4.5 to show the main patterns in the bryophyte communities of the sampled vegetation plots (ter Braak & Šmilauer 1998). The ordination was based on all species data with log-transformed percentage cover values of individual species. The length of the species gradient of the first DCA axis was 4.5 SD (= standard deviation), meaning that the use of a unimodal technique such as DCA was appropriate. Taxa determined only to the genus level were excluded from the analysis, as were 3 outlier plots which distorted the results (SR 2; MN 10, 11; see Table S2 in the Appendix for explanation of the code), so the analysis was based on 56 plots in total. Vegetation structure and ecological variables were passively projected into the ordination diagram (only better explaining variables were plotted – cover total, cover of shrub, herb and moss layers, number of bryophyte species within plots, altitude and plot height above the water level).

Moisture gradient

We assigned a moisture indicator value to each bryophyte species according to the twelve-degree scale of Hill et al. (2007). We were not able to assign an indicator value to just one species – *Cinclidotus aquaticus*, occurring in one plot in our study, because the latter was missing from the list of Hill et al. (2007). Transitional moisture categories (see Hill et al. 2007) were also merged for the sake of simplicity (2 + 3; 7 + 8). We then calculated the proportion of bryophyte species falling within each moisture category per plot, and compared it between vegetation types. Similar vegetation types were merged for simplification (initial vegetation + *Myricaria germanica* dominated shrubs + sparse *Salix* spp. shrubs; *Salix* spp. shrubs; *Calamagrostis pseudophragmites* dominated vegetation + *Petasites hybridus* vegetation).

The twelve-degree scale of Hill et al. (2007) is based on the ecological preferences of bryophyte species occurring in Great Britain. Therefore, these moisture indicator values for bryophytes from Hill et al. (2007) might not be fully representative for bryophyte species from SE Europe, but there is no alternative scale for the bryophytes of the Balkan Peninsula. Another option was to use the nine-range scale of Ellenberg et al. (1991) based on occurrences of bryophytes in Germany. We compared these two scales and conducted two separate analyses, but there were no strong differences and the results using the Hill et al. (2007) scale were more representative. There is also the possibility of using the ecological classification of bryophytes by Dierssen (2001), created for Northern Europe, but there are too many overlapping categories complicating easy partition.

Table 2. A summary of environmental variables and vegetation structure for each type of gravel bar vegetation sampled in five countries in the Balkan Peninsula. n – number of plots. Values for numeric variables are given as minimum–maximum (mean ± standard deviation). Values for levels of categorical variables present number of plots.

Vegetation type	No. of bryophyte taxa	Total vegetation cover (%)	Shrub layer cover (%)	Herb layer cover (%)	Moss layer cover (%)	Shrub layer mean height (m)	Herb layer mean height (cm)	Gravel bar height (cm)	Light conditions	Substrate reaction	Prevailing substrate fraction
(I) initial vegetation (n= 12)	2–17 (6.9±4.3)	12–55 (28.4±13.8)	0–35 (6±9.8)	10–43 (22±10.4)	1–5 (1.4±2.3)	0.5–1.5 (1±0.3)	15–120 (44.5±26.8)	10–140 (68.5±45.8)	sun-exp. 9 shaded 3	acidic 5 base-rich 5 mixture 2	gravel+sand 6 stone+sand 2 gravel+stone 4
(II) shrubs with *Myricaria germanica* (n= 4)	4–9 (7.2±2)	60–98 (78.2±13.5)	48–85 (63.7±15.1)	20–40 (35±8.6)	2–8 (4.2±2.4)	1.1–2 (2.3±0.4)	20–120 (56.5±37.9)	50–80 (63.3±12.4)	sun-exp. 4	acidic 1 base-rich 3	gravel+sand 4
(III) shrubs with *Salix* spp. (n= 18)	2–18 (7.3±4.5)	50–97 (83±13.9)	40–94 (72.5±15.3)	5–90 (28.8±24.3)	1–30 (4.7±6.7)	0.8–4.5 (2.4±0.8)	15–100 (49.4±26.6)	25–160 (67.8±34.1)	sun-exp. 15 shaded 3	acidic 7 base-rich 7 mixture 4	gravel+sand 6 stone+sand 2 gravel+stone 10
(IV) *Salix* spp. sparse shrubs (n= 6)	1–9 (6.1±2.5)	35–65 (50.8±11.6)	15–34 (27±7)	2–52 (23±15.1)	1–5 (2.8±1.2)	0.4–2 (1.1±0.5)	35–100 (61.8±25.1)	35–130 (72.5±29.5)	sun-exp. 2 shaded 4	acidic 2 base-rich 3 mixture 1	stone+sand 1 gravel+stone 5
(V) *Calamagrostis pseudophragmites* vegetation (n= 18)	1–12 (6.2±3.7)	35–95 (69.4±18.9)	0–15 (6.6±9)	35–94 (62±18)	1–20 (4.1±4.7)	0.8–1.8 (1.3±0.3)	30–140 (85.8±29.1)	7–150 (54.1±39.9)	sun-exp. 13 shaded 5	acidic 8 base-rich 9 mixture 1	gravel+sand 7 stone+sand 7 gravel+stone 4
(VI) *Petasites hybridus* vegetation (n= 1)	2	95	5	93	1	1.1	110	50	partly shaded	base-rich	gravel+sand

Results and Discussion

Bryofloristic contributions

In total, we recorded 80 taxa of mosses and 5 taxa of liverworts. The most frequently recorded species were *Brachythecium rivulare*, *Bryum argenteum*, *Oxyrrhynchium hians*, *Barbula unguiculata*, *Ceratodon purpureus*, *Bryum caespiticium*, *Barbula convoluta*, *Cratoneuron filicinum* and *Platyhypnidium riparioides*. On average, there were about 7 taxa/species in the plots; the richest plot (MN10) contained 18 species. Bryophyte covers were usually not too high (the mean cover of the moss layer amounted to 3.7 %; for more details see Table S2 in the Appendix).

Of these records, one species (*Bryum klinggraeffii*) is new for Albania, Montenegro and Serbia, and five other species (*Dicranella staphylina*, *Didymodon ferrugineus*, *Hygrohypnum ochraceum*, *Plagiothecium succulentum* and *Sciuro-hypnum plumosum*) are evaluated as data-deficient or vulnerable across different countries (see Hodgetts 2015). Given below is a short comment on the distribution and ecology of each species, with special emphasis on *Bryum klinggraeffii*. The remaining species are listed only with their localities. After each taxon name we give a list of plots where it was recorded. The plot ID is a combination of the country ISO code and the plot's number during sampling (e.g. BG 11 stands for the 11th plot recorded in Bulgaria). The 2-letter ISO code for countries is as follows: BG – Bulgaria, SR – Serbia, MK – Macedonia, AL – Albania, MN – Montenegro. BRNM with ID number indicates that the taxon was deposited in the herbarium of the Moravian Museum, Brno, Czech Republic.

Notable species

Bryum klinggraeffii – BG 11; SR 8 (BRNM 795004); MK 1, 5, 9, 11; AL 1 (BRNM 794990); MN 5 (BRNM 794994)

Our study is the first to report the presence of *B. klinggraeffii* in Albania, Montenegro and Serbia. In Bulgaria, where this species has been classified as data deficient, we report a new locality in the Rila Mts (Natcheva & Ganeva 2007). *B. klinggraeffii* is still missing in some other neighbouring Balkan countries (Bosnia-Herzegovina, Croatia and Kosovo), while in other neighbouring countries it is considered endangered (Romania; Hodgetts 2015) or vulnerable (Slovenia; Martinčič 2016). *B. klinggraeffii* may be more common but frequently overlooked in the mentioned countries or particular regions because of its small size (Natcheva & Ganeva 2007, Papp et al. 2015).

B. klinggraeffii belongs to the *B. erythrocarpum* complex which is characterised by the presence of rhizoidal gemmae. It is a suboceanic species with a wide areal including N Africa, Turkey, India, China, Japan, N America, Patagonia and Europe (Kučera 2004–2016). It is a ruderal species that usually grows on bare ground, on base-rich or slightly acidic, sandy to clayey soils. Typical habitats are road sides, fields, river banks and margins of water reservoirs, from lowlands to mountain ranges (Dierssen 2001, Kučera 2004–2016, Natcheva & Ganeva 2007).

In vegetation plots in our study sites, *B. klinggraeffii* frequently grew together with other ruderal species such as *Bryum argenteum*, *B. subapiculatum*, *Barbula convoluta*, *B. unguiculata*, *Ceratodon purpureus* or *Dicranella staphylina*. It was found on gravel bars covered by sparse vegetation with open patches, usually of various types. The substrate was most frequently base-rich, sandy soils were often presented. The following vegetation plots were conducted in localities in countries where the species has not been previously reported.

AL 1 – sparse shrubs with *Myricaria germanica* (authors: V. Kalníková, S. Palpurina, T. Peterka & Z. Plesková). Total vegetation cover (60 %), E2 (45 %): *Myricaria germanica* 3; **E1 (20 %):** *Mentha longifolia* 2a, *Calamagrostis pseudophragmites* 1, *Salix elaeagnos* juv. 1, *Satureja hortensis* 1, *Anisantha sterilis* +, *Agrostis stolonifera* +, *Aira caryophyllea* +, *Bromus japonicus* +, *Chenopodium botrys* +, *Cirsium* sp. +, *Daucus carota* +, *Erigeron canadensis* +, *Geranium robertianum* +, *Juncus* sp. +, *Medicago lupulina* +, *Microrrhinum minus* +, *Ononis spinosa* +, *Plantago lanceolata* +, *Polygonum arenarium* +, *Polygonum lapathifolium* +, *Salix alba* juv.

+, *Salix purpurea* juv. +, *Setaria pumila* +, *Verbena officinalis* +, *Trifolium hybridum* +, *Amorpha fruticosa* juv. r, *Anagallis* sp. r, *Artemisia vulgaris* r, *Chondrilla juncea* r, *Dactylis glomerata* r, *Elytrigia repens* r, *Hypericum perforatum* r, *Leucanthemum* sp. r, *Lolium perenne* r, *Lythrum salicaria* r, *Petrorhagia prolifera* r, *Plantago major* r, *Mentha pulegium* r, *Potentilla reptans* r, *Pulicaria dysenterica* r, *Rubus fruticosus* agg. r, *Rumex conglomeratus* r, *Tamarix* sp. juv. r, *Taraxacum* sp. r, *Teucrium* sp. r, *Verbascum* sp. r, *Vulpia myuros* r; **E0 (2 %):** *Bryum argenteum* +, *Bryum klinggraeffii* +, *Oxyrrhynchium hians* +, *Bryum* sp. r.

MN 5 – species-rich sparse and open initial herbaceous vegetation with juvenile *Myricaria germanica* (authors: V. Kalníková, S. Palpurina, T. Peterka & Z. Plesková). Total vegetation cover (13 %), E1 (13 %): *Lycopus europaeus* 1, *Myricaria germanica* juv. 1, *Salix elaeagnos* juv. 1, *Agrostis stolonifera* +, *Alliaria petiolata* +, *Alnus incana* juv. +, *Anisantha sterilis* +, *Artemisia vulgaris* +, *Bromus hordeaceus* s. *hordeaceus* +, *Calamagrostis pseudophragmites* +, *Capsella bursa-pastoris* +, *Cerastium fontanum* s. *vulgare* +, *Cirsium* sp. +, *Daucus carota* +, *Epilobium adenocaulon* +, *Epilobium dodonaei* +, *Galeopsis speciosa* +, *Geranium robertianum* +, *Lactuca muralis* +, *Melilotus officinalis* +, *Mentha longifolia* +, *Microrrhinum minus* +, *Plantago lanceolata* +, *Plantago major* s. *intermedia* +, *Poa annua* +, *Polygonum aviculare* +, *Polygonum lapathifolium* +, *Prunella vulgaris* +, *Ranunculus repens* +, *Reseda phyteuma* +, *Rorippa* sp. +, *Salix alba* juv. +, *Salix euxina* juv. +, *Sanguisorba minor* +, *Saponaria officinalis* +, *Silene pusilla* +, *Silene vulgaris* +, *Stachys sylvatica* +, *Stellaria media* +, *Taraxacum* sec. *Ruderalia* +, *Trifolium hybridum* +, *Trifolium repens* +, *Veronica beccabunga* +, *Achillea millefolium* agg. r, *Alchemilla* sp. r, *Amaranthus* sp. r, *Anthemis* sp. r, *Anthriscus* sp. r, *Arabis alpina* r, *Bromus japonicus* r, *Carex* sp. r, *Chenopodium* sp. r, *Clematis vitalba* r, *Elymus caninus* r, *Epilobium hirsutum* r, *Epilobium parviflorum* r, *Epilobium roseum* r, *Equisetum arvense* r, *Galium* sp. r, *Humulus lupulus* r, *Hypericum perforatum* r, *Juncus bufonius* r, *Lactuca serriola* r, *Lamium* sp. r, *Lotus corniculatus* r, *Mentha* sp. r, *Poa compressa* r, *Polygonum aviculare* agg. r, *Rumex* sp. r, *Sagina* sp. r, *Solanum* sp. r, *Trifolium campestre* r, *Trifolium* sp. r, *Tussilago farfara* r, *Urtica dioica* r, *Verbascum* sp. r, *Veronica anagallis-aquatica* r, *Veronica persica* r, *Veronica serpyllifolia* r, *Vulpia myuros* r; **E0 (2 %):** *Barbula unguiculata* +, *Brachythecium rivulare* +, *Bryum argenteum* +, *Bryum klinggraeffii* +, *Campylium stellatum* +, *Bryum* sp. r, *Cratoneuron filicinum* r, *Platyhypnidium riparioides* r.

SR 8 – sparse shrubs with *Myricaria germanica* (authors: V. Kalníková, S. Palpurina, T. Peterka & Z. Plesková). Total vegetation cover (80 %), E2 (70 %): *Myricaria germanica* 3, *Salix purpurea* 2b, *Salix alba* +; **E1 (40 %):** *Melilotus albus* 2a, *Cota tinctoria* 1, *Echium vulgare* 1, *Holcus lanatus* 1, *Ononis spinosa* 1, *Taraxacum* sp. 1, *Achillea millefolium* ag. +, *Agrostis stolonifera* +, *Anisantha sterilis* +, *Berteroa incana* +, *Brachypodium sylvaticum* +, *Cerastium fontanum* s. *vulgare* +, *Clematis vitalba* +, *Clinopodium vulgare* +, *Crepis foetida* +, *Cynosurus echinatus* +, *Daucus carota* +, *Centaurea stoebe* +, *Erigeron annuus* +, *Erigeron canadensis* +, *Eupatorium cannabinum* +, *Euphorbia esula* s. *tommasiniana* +, *Festuca rubra* +, *Gypsophila muralis* +, *Hypericum perforatum* +, *Linaria genistifolia* +, *Medicago lupulina* +, *Medicago minima* +, *Mentha longifolia* +, *Plantago lanceolata* +, *Poa compressa* +, *Potentilla reptans* +, *Prunella vulgaris* +, *Rubus fruticosus* agg. +, *Thymus* sp. +, *Trifolium arvense* +, *Trifolium campestre* +, *Trifolium repens* +, *Scabiosa ochroleuca* +, *Tussilago farfara* +, *Vulpia myuros* +, *Aira caryophyllea* r, *Arenaria serpyllifolia* r, *Artemisia scoparia* r, *Calystegia sepium* r, *Campanula trachelium* r, *Cichorium intybus* r, *Dorycnium pentaphyllum* s. *herbaceum* r, *Fraxinus excelsior* juv. r, *Lactuca serriola* r, *Myosotis* sp. r, *Poa bulbosa* r, *Rumex* sp. r, *Sanguisorba minor* r, *Setaria pumila* r, *Trifolium striatum* r, *Verbascum* sp. r, *Vicia hirsuta* r; **E0 (2 %):** *Barbula unguiculata* +, *Bryum argenteum* +, *Bryum klinggraeffii* +, *Bryum subapiculatum* +, *Ceratodon purpureus* +, *Dicranella staphylina* +, *Barbula convoluta* r, *Brachythecium albicans* r, *Bryum* sp. r.

Dicranella staphylina – SR 8; MN 2 (BRNM 794996), 4 (BRNM 794995), 5, 8 (BRNM 794991)

D. staphylina is stated as data deficient in Montenegro (Hodgetts 2015) where it has been recently recorded (Papp & Erzberger 2010). In the Balkan Peninsula, it has also been recorded in Bulgaria, Romania and Serbia (Hodgetts 2015). *D. staphylina* grows on bare soil mainly with acidic reaction, often in agricultural fields (Kučera 2004–2016, Papp & Erzberger 2005, Papp & Erzberger 2007), grasslands or disturbed sites such as trampled habitats along trails (Dierssen 2001, Rusińska & Górski 2003). Hájková et al. (2007), however, also reported it in disturbed calcareous spring wetlands.

Didymodon ferrugineus – MN 10 (BRNM 795000), 11 (BRNM 794997)

D. ferrugineus is reported as data deficient for Montenegro, where we found two sites. It has been reported in all other countries in the Balkan Peninsula except Kosovo and Macedonia (Hodgetts 2015). The species prefers slightly shaded vegetation stands on base-rich substrates. It grows on thin soil on rocks and screes and in grasslands, calcareous sand dunes and quarries (Dierssen 2001, Kučera 2004–2016). In the localities presented here, *D. ferrugineus* grew on a limestone gravel bar in a dried river channel.

Hygrohypnum ochraceum – MN 12 (BRNM 794999)

We found *H. ochraceum* at only one site in Montenegro, where it has data deficient status. Among the Balkan countries, *H. ochraceum* also occurs in Romania and Slovenia (status: vulnerable) and in Bosnia-Herzegovina (Hodgetts 2015). *H. ochraceum* usually grows on acidic substrates, on rocks or stones that are frequently submerged and kept moist washed by water, though it can also resist occasional desiccation (Watson 1919, Dierssen 2001, Kučera 2004–2016). Contrary to its preference for acidic sites, we recorded *H. ochraceum* at a base-rich site, as suggested both by the soil maps and the substrate observed on the gravel bar.

Plagiothecium succulentum – BG 11

We recorded *P. succulentum* just at one site in Bulgaria. It has data deficient status in Bulgaria according to Hodgetts (2015), but is not included on the Bulgarian bryophyte red list (Natcheva et al. 2006) or in the Red Data Book of Bulgaria (Peev 2015). It does not seem to be rare in Bulgaria, as evidenced by several collections, e.g. Ganeva et al. (2008), Papp et al. (2011). It is also present in several other Balkan countries – Albania, Bosnia-Herzegovina, Greece, Montenegro, Romania, Serbia and Slovenia (Hodgetts 2015). *P. succulentum* can grow in a wide range of conditions – on bare soil, tree bases, directly on rock or stones, both acidic and base-rich (Smith 2004, http://www.rbge.org.uk/).

Sciuro-hypnum plumosum – BG 17, 22, 25, 32, 39; SR 1; MK 1

We recorded *S. plumosum* in five sites in Bulgaria where the species is classified as vulnerable (Natcheva et al. 2006, Hodgetts 2015), but it is not included in the Red Data Book of Bulgaria published in 2015 (Peev 2015). It is quite common and abundant on the upstream sections of the Iskur River in the Rila Mts (Papp et al. 2006). Among Balkan countries, it is missing only in Kosovo and Albania (Hodgetts 2015). It typically grows on rocks and stones regularly flooded or flushed by water along swiftly flowing rivers and streams (Watson 1919, Dierssen 2001, Kučera 2004–2016). It prefers acidic substrates, though we also found it on more base-rich stands.

Other species

Abietinella abietina – SR 4; MN 10, 11, 12

Amblystegium serpens – BG 4

Anomodon viticulosus – MN 11

Atrichum undulatum – BG 21, 22

Barbula convoluta – SR 7, 8, 9; MK 2, 10; MN 6, 7, 9, 10, 11

Barbula unguiculata – BG 4, 24, 40; SR 7, 8, 9, 10; MK 4, 7, 10, 11; MN 1, 5, 8, 10, 12

Brachytheciastrum velutinum – BG 4

Brachythecium albicans – BG 21, 31; SR 6, 8

Brachythecium rivulare – BG 4, 9, 11, 13, 14, 18, 19, 20, 21, 22, 24, 25, 31, 34, 38, 39, 40, 41; SR 1; MK 1, 3, 4, 5, 6, 7, 8, 9, 10, 11; MN 1, 4, 5, 10, 12

Bryum argenteum – BG 1, 17, 18, 23, 24, 31, 39; SR 4, 6, 7, 8, 9, 10; MK 5, 6, 7, 9, 10; AL 1; MN 1, 2, 3, 5, 6, 7, 8, 10

Bryum caespiticium – BG 18, 20, 23, 24; SR 7; MK 2, 7, 10; MN 6, 7, 12

Bryum capillare – BG 32; MK 10; MN 11

Bryum pseudotriquetrum – BG 4, 20, 22, 39; MK 1, 6, 11

Bryum subapiculatum – SR 8

Calliergonella cuspidata – BG 23; SR 6; MN 6

Campylium stellatum – BG 20, 21; MK 11, 5; MN 5, 11

Ceratodon purpureus – BG 11, 17, 18, 23, 24; SR 4, 6, 8, 9; MK 6, 7; MN 7

Chiloscyphus polyanthos – BG 4 (*C. p.* var. *pallescens*), BG 22 (*C. p.* var. *polyanthos*)

Cinclidotus aquaticus – BG 39

Cinclidotus fontinalioides – MK 3

Cirriphyllum piliferum – BG 18, 21; MN 10

Climacium dendroides – BG 25; MK 7
Cratoneuron filicinum – BG 4, 39; SR 3; MK 3, 6, 10, 11; MN 5, 11, 12
Ctenidium molluscum – MN 10
Dichodontium pellucidum – BG 31
Dicranella varia – MN 7, 8 (BRNM 794992)
Dicranum scoparium – BG 20, 21
Didymodon fallax – BG 33; MN 8 (BRNM 794993)
Didymodon rigidulus – BG 33
Ditrichum flexicaule – MN 10, 11
Drepanocladus aduncus – BG 19
Encalypta streptocarpa – SR 2; MK 7; MN 1
Fissidens dubius – BG 22
Fontinalis antipyretica – BG 22
Funaria hygrometrica – SR 3, 4, 7; MK 1, 7; MN 8
Grimmia alpestris – SR 3, 4, 7; MK 1, 7; MN 8
Grimmia montana – MK 6
Grimmia pulvinata – SR 2
Homalothecium lutescens – BG 38; SE 4, 6, 7; MN 4, 10, 11
Hygroamblystegium tenax – BG 4, 18, 25, 32, 33, 35; MK 9; MN 6
Hygroamblystegium varium – BG 11; SR 2, 6
Hygrohypnum luridum – BG 21, 39; MK 3, 4; MN 11
Hylocomium splendens – BG 22; MN 1, 9
Hypnum cupressiforme – BG 9, 11; SR 2, 6; MK 2; MN 9, 10, 11
Marchantia polymorpha – BG 4, 18, 22, 32; MK 11
Mnium marginatum – MK 9
Orthotrichum affine – MK 9 (BRNM 794998)
Oxyrrhynchium hians – BG 5, 9, 14, 22, 23, 24, 32, 37, 41; SR 4, 6, 9; MK 1, 11; AL 1; MN 3, 6, 9, 11
Palustriella commutata – MK 1
Pellia neesiana – MK 11 (BRNM 795003)
Philonotis caespitosa – MK 1
Philonotis fontana – MK 1
Plagiomnium affine – BG 23, 35, 39; SR 3; MK 3, 9, 10, 11
Plagiomnium cuspidatum – BG 31
Plagiomnium ellipticum – SR 2, 6
Plagiomnium rostratum – MN 10
Plagiomnium undulatum – BG 22, 23, 25, 31; SR 6; MK 7; MN 6, 9
Platyhypnidium riparioides – BG 11, 22, 29, 32, 33, 35, 37; MK 1, 11; MN 5
Pohlia nutans – MK 5
Polytrichum juniperinum – SR 6, 9
Pseudoleskeella catenulata – MN 10
Racomitrium aciculare – BG 34
Racomitrium canescens – SR 7, 9, 10; MK 2, 7; MN 3, 10
Racomitrium elongatum – SR 6
Rhizomnium punctatum – BG 9, 20, 22
Rhytidiadelphus triquetrus – MN 9, 10
Rhytidium rugosum – SR 4

Scapania undulata – BG 21, 22
Schistidium elegantulum – MN 10 (BRNM 795002), MN 12 (cf. BRNM 795001)
Schistidium rivulare – MK 6 (BRNM 794989)
Sciuro-hypnum populeum – MK 7; MN 12
Syntrichia ruralis – SR 4, 9; MK 6, 11; MN 10, 11, 12
Thuidium assimile – MN 7
Thuidium recognitum – MN 6
Tortella inclinata – MN 11
Tortella tortuosa – SR 2; MN 9, 10, 11
Tortula muralis – MK 6

Main ecological patterns of gravel bar bryoflora

We used the DCA ordination method with environmental and vegetation factors passively projected into the ordination space to analyse and visualise the ecological preferences of bryophytes. The main pattern along the first ordination axis might be interpreted as a complex gradient of moisture, light conditions and canopy openness, stretching from initial successional stages with sparse and more open vegetation on drier sites to communities that were denser, closer and therefore wetter and shadier inside (Fig. 2A, B).

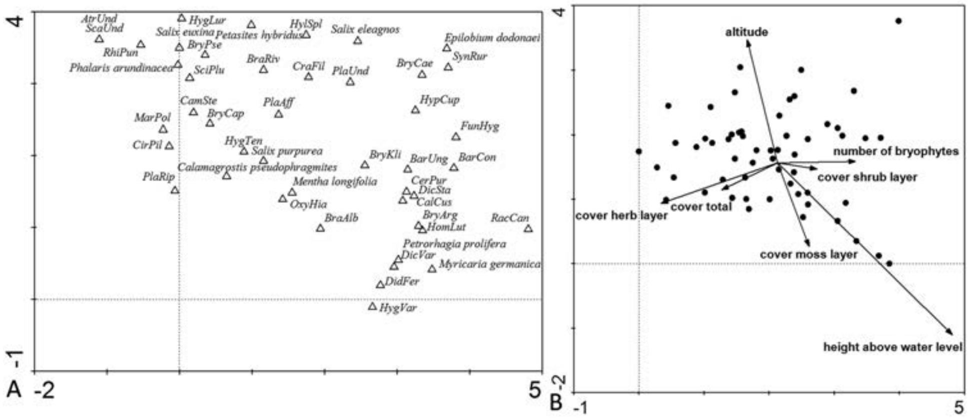

Fig. 2. DCA ordination diagram of the vegetation data from river gravel bars in several Balkan countries. The position of the species along the first two ordination axes is shown. The eigenvalues of the axes: 1st (DCA1) 0.465, 2nd (DCA2) 0.39, total inertia 10.403; length of gradient: SD = 4.5. Only the most frequent bryophytes and vascular plants diagnostic for particular vegetation types are visualised in species scatter plot A. Diagram B represents passively projected variables (altitude, number of bryophytes, cover total, cover shrub, herb and moss layer and height above water level). In (A) vascular plant names are not abbreviated; *Myricaria germanica* and *Salix* spp. were in the shrub layer and the remaining vascular plants were in the herb layer. Bryophyte names are abbreviated as follows: *AtrUnd*: *Atrichum undulatum*, *BarCon*: *Barbula convoluta*, *BarUng*: *Barbula unguiculata*, *BraAlb*: *Brachythecium albicans*, *BraRiv*: *Brachythecium rivulare*, *BryArg*: *Bryum argenteum*, *BryCae*: *Bryum caespiticium*, *BryCap*: *Bryum capillare*, *BryKli*: *Bryum klinggraeffii*, *BryPse*: *Bryum pseudotriquetrum*, *CalCus*: *Calliergonella cuspidata*, *CamSte*: *Campylium stellatum*, *CerPur*: *Ceratodon purpureus*, *CirPil*: *Cirriphyllum piliferum*, *CraFil*: *Cratoneuron filicinum*, *DicSta*: *Dicranella staphylina*, *DicVar*: *Dicranella varia*, *DidFer*: *Didymodon ferrugineus*, *FunHyg*: *Funaria hygrometrica*, *HomLut*: *Homalothecium lutescens*, *HygLur*: *Hygrohypnum luridum*, *HygTen*: *Hygroamblystegium tenax*, *HygVar*: *Hygroamblystegium varium*, *HylSp*: *Hylocomium splendens*, *HypCup*: *Hypnum cupressiforme*, *MarPol*: *Marchantia polymorpha*, *OxyHia*: *Oxyrrhynchium hians*, *PlaAff*: *Plagiomnium affine*, *PlaRip*: *Platyhypnidium riparioides*, *PlaUnd*: *Plagiomnium undulatum*, *RacCan*: *Racomitrium canescens*, *RhiPun*: *Rhizomnium punctatum*, *ScaUnd*: *Scapania undulata*, *SciPlu*: *Sciuro-hypnum plumosum* and *SynRur*: *Syntrichia ruralis*.

Open initial stages, whose stands are supposed to be drier and less shaded, are situated on the right-hand side of Diagram A. They are represented by vegetation dominated by initial vegetation with *Epilobium dodonaei* (I) and *Myricaria germanica* shrubs (II).

Compared to the other sampled vegetation types, these two vegetation types occupy sites where the gravel bars were highest (as indicated by the measured distance from the highest point of the gravel bar to the actual water level; Fig. 2B) and where the gravel and sand fraction frequently prevailed in the substrate. The most typical vegetation – shrubby vegetation dominated by *Myricaria germanica*, however, inhabited only places not higher than 80 cm above the actual water level (see Table 2). *Myricaria germanica* usually needs fine and fresh sediment for its regeneration from seeds (Jeník 1955) which is in contrast to the dry conditions in our records. However, stands with *Myricaria germanica* shrubs on the sampled gravel bars were at a mature stage which no longer requires the optimal conditions typical for the time of its germination, e.g. more wet season period, higher water levels, differently structured gravel bars. The groundwater level could be high enough for mature plants of *Myricaria germanica*, though the surface of such gravel bars can still become very dry during the summer (Müller 1995) which explains the presence of many drought-tolerant bryophytes. The bryophyte layer of plots with *Myricaria* is characterised by many small, light-demanding, early-successional bryophyte colonists (Dierssen 2001) and drought-tolerant ruderal bryophytes (Hill et al. 2007) – e.g. *Barbula convoluta*, *B. unguiculata*, *Bryum argenteum*, *Ceratodon purpureus* and *Racomitrium canescens*. Another distinct type of initial vegetation of open and drier habitats (top-right corner in Fig. 2A) represents stands typically with *Epilobium dodonaei* in the herb layer and with *Bryum caespiticium* and *Syntrichia ruralis* in the moss layer. These two bryophytes are short-living colonists (Dierssen 2001) capable of growing in drier places (Hill et al. 2007). In general, plots in the “drier” part of the gradient, represented by more open vegetation, had a higher number of bryophyte species than plots in the “wetter” part (Fig. 2B).

The left part of the gradient (Fig. 2A) is represented by denser and mesophilous vegetation dominated by *Calamagrostis pseudophragmites* (V) and by stands with *Salix euxina* (III) or *Petasites hybridus* (VI). These communities represent the “wetter” part of the main gradient. The substrate, especially of patches with *Calamagrostis pseudophragmites*, was also usually finer, dominated by the sandy fraction, though the vegetation stands were situated in depressions in the gravel bar or closer to the waterline (Table 2). According to the literature, gravel bars with *Calamagrostis pseudophragmites* are usually inundated several times a year or are, at least, rather moist (Müller 1995). In our study, gravel bar vegetation associated with the “wetter” part of the gradient was also denser and thus more shady and wetter inside and the moss layer was composed of mesophilous and hygrophilous bryophytes such as *Atrichum undulatum*, *Brachythecium rivulare*, *Bryum pseudotriquetrum*, *Cirriphyllum piliferum*, *Hygroamblystegium tenax*, *Scapania undulata* or *Platyhypnidium riparioides* (Hill et al. 2007). This is consistent with previous studies that suggest that bryophyte communities on gravel bars with vegetation of the above-mentioned types are dominated by long-living perennial, even competitive, species (Muotka & Virtanen 1995, Dierssen 2001).

The second axis suggests a shift in species composition driven by altitudinal range and separates plots with the occurrence of *Petasites hybridus* and hygrophilous bryophytes (e.g. *Hygrohypnum luridum*, *Bryum pseudotriquetrum*) on the “wetter” part of the first gradient and open initial stands with *Epilobium dodonei* and *Salix eleagnos* on the opposite, i.e. “drier”, end of the moisture gradient.

The key role of moisture in the species composition gradient fits well with the results from the supplementary analysis based on the moisture habitat indicator value (Hill et al. 2007) which was conducted to obtain a deeper view into the patterns of bryophyte distribution on gravel bars (Fig. 3). This analysis revealed that a higher proportion of drought-tolerant bryophytes, i.e. those capable of growing under dry and well-drained conditions, occurred on drier, more sandy patches, with open initial vegetation or sparse *Salix* spp. and *Myricaria germanica* dominated shrubs, whereas the more hygrophilous bryophytes, typical of moist to waterlogged sites, occurred on places dominated by denser *Calamagrostis pseudophragmites* or *Petasites hybridus* vegetation. Although individual vegetation types were generally characterised by species with different moisture requirements, our results also suggest that drought-tolerant and water-demanding bryophytes can co-occur together on gravel bars (see the next section for a more-detailed discussion).

The effect of substrate acidity, frequently found as an important factor for bryophyte communities across habitats (e.g. Glime & Vitt 1987), has not been apparent in our study. Although several sites could have been characterised as alkaline (base-rich) or acidic (Table S2 in the Appendix), gravel bars generally accumulate grains of different geological origin and hence different chemistry.

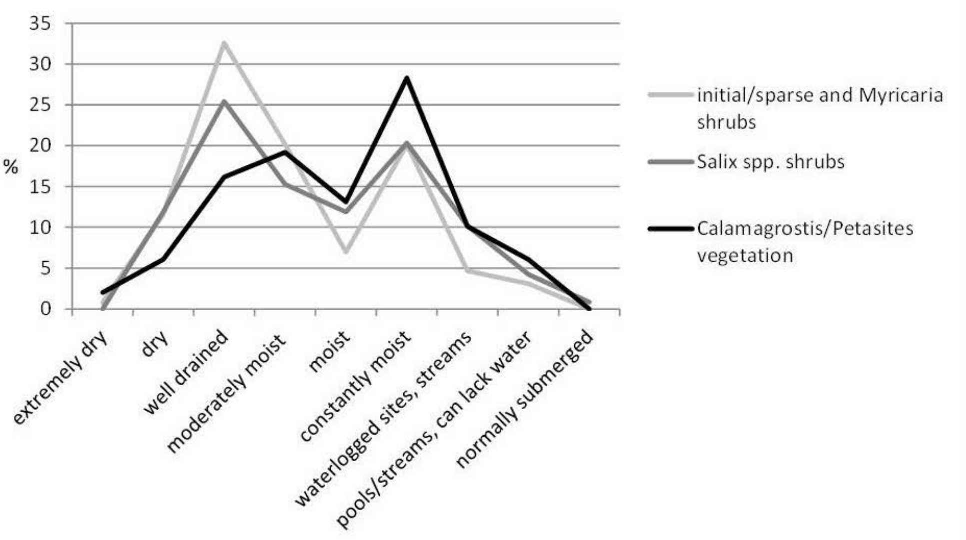

Fig. 3. Percentage representation of bryophytes with different moisture requirements recorded in the three distinct vegetation types (initial/sparse and *Myricaria germanica* shrubs, n = 22; *Salix* spp. shrubs, n = 18; *Calamagrostis pseudophragmites* and *Petasites hybridus* vegetation, n = 19). Bryophyte moisture requirements were taken from the 12-grade scale of Hill et al. (2007).

Ecological spectrum of gravel bar bryoflora

Our study revealed that gravel bar habitats could host a high diversity of bryophyte species in terms of requirements for moisture. Analogous results for Balkan riverine habitats were also obtained by Papp et al. (2006). One of the reasons for the variety of ecological requirements in bryophytes on gravel bars could be the patch dynamics and heterogeneous environmental conditions on gravel bars. Species could be occasionally submerged, exposed to wet by splashes or spray, or affected by dry conditions at the top. Natural disturbance caused by flood and high water flow are important factors in maintaining high bryophyte diversity on gravel bars by opening up space for less-competitive species (Vitt et al. 1986, Muotka & Virtanen 1995), whereas stable conditions allow strong competitors to monopolise suitable habitats (Muotka & Virtanen 1995). In our case, both the competitive and the more hygrophilous species (e.g. *Brachythecium rivulare*, *Hygroamblystegium tenax*, *Oxyrrhynchium hians* and *Platyhypnidium riparioides*) became abundant in the successionally advanced vegetation on gravel bars with a denser herb or shrub layer.

The open and exposed surfaces of the initial gravel bars would seem to provide an adequate habitat for short-living colonist species adapted to drier and lighter conditions (e.g. *Barbula convoluta*, *Bryum argenteum*, *B. klinggraeffii*, *Ceratodon purpureus*, *Dicranella varia* and *Syntrichia ruralis*). Ruderal short-living species may also avoid flooding disturbance by completing their life cycles before the next flood event. Other species must tolerate a period of submergence and water disturbances (Muotka & Virtanen 1995). *Racomitrium canescens* is a typical example of a pioneer bryophyte species on gravel bars that is able to resist water-level fluctuations (Odland et al. 1991, Vetaas 1994).

Finally, we also found many bryophytes typical of streams and running water that have special adaptations to survive the strain of flowing water on gravel bars in our study (Watson 1919, Vitt & Glime 1984). Such adaptations include smaller cells, firmer or thicker walls, strong rhizoids and protections against mechanical injury by water and drifting particles, such as leaves that are keeled (*Fontinalis antipyretica*), curved falcate (*Palustriella commutata*) or concave (*Hygrohypnum luridum, Sciuro-hypnum plumosum*), or have a thick border (*Cinclidotus fontinaloides*), recurved margin (*Bryum pseudotriquetrum*), strong nerve and thick cell walls (*Cratoneuron filicinum*, *Hygroamblystegium tenax*) or papillae (*Dichodontium pellucidum*). What is interesting is that most of these adaptations are also mentioned as common xerophylic adaptations (Watson 1914, Watson 1919, Vitt & Glime 1984) and could, therefore, be an advantage when growing on a rocky shoreline or higher parts of gravel bars which may dry out in summer.

In conclusion, the temporal variability in ecological conditions on gravel bars enables the coexistence of species of different ecological groups at their niche margins and, together with irregular natural disturbances, seems to be responsible for the high bryophyte diversity of the habitat.

Acknowledgements

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Supplementary documents online:

Supplementary Table S1: Description of the location of each plot.

Supplementary Table S2: Data on vegetation structure and ecological conditions for each plot.

Supplementary Figures S3: Figures of bryophytes and habitats.

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Electronic supplementary materials (paper 5)

Table S1 Vegetation-plot data.

Table S2 Data on vegetation structure and ecological conditions for each plot.

Fig S3 Pictures of bryophytes and habitats.

Paper 6

Kalníková, V., Chytrý, K., Novák, P. and Kubešová, S. (2018) *Bryum klinggraeffii*, a moss new to Georgia – first record for the Greater Caucasus. *Herzogia*, 31, 982–987.

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Bryum klinggraeffii, a moss new to Georgia – first record for the Greater Caucasus

Veronika Kalníková*, Kryštof Chytrý, Pavel Novák & Svatava Kubešová

Abstract: Kalníková, V., Chytrý, K., Novák, P. & Kubešová, S. 2018. *Bryum klinggraeffii*, a moss new to Georgia and a first record for the Greater Caucasus. – Herzogia **31**: 982–987.

Bryum klinggraeffii is a widespread small ruderal moss. It inhabits a wide altitudinal gradient, and typically grows on the bare ground of frequently disturbed open habitats. Here we report its first finds for Georgia and simultaneously, we bring new evidence of the species for the Greater Caucasus. The moss was discovered in Racha-Lechkhumi and Kvemo Svaneti Regions in the Greater Caucasus and in Samtskhe-Javakheti Region in the Lesser Caucasus. *B. klinggraeffii* was found on river gravel bars in various kinds of vegetation successional stages.

Zusammenfassung: Kalníková, V., Chytrý, K., Novák, P. & Kubešová, S. 2018. *Bryum klinggraeffii*, ein neues Moos für Georgien – ein Erstfund für den Großen Kaukasus. – Herzogia **31**: 982–987.

Bryum klinggraeffii ist ein weit verbreitetes, kleines Moos ruderaler Standorte. Seine Verbreitung beinhaltet einen ausgedehnten Höhengradienten und es siedelt typischerweise auf nackten Böden gestörter Standorte. Für Georgien wird es hiermit erstmals nachgewiesen. Gleichzeitig ergeben sich neue Hinweise für den Großen Kaukasus. Die Art wurde in der Racha-Lechkhumi und Kvemo Svaneti Region des Großen Kaukasus und in der Samtskhe-Javakheti Region des Kleinen Kaukasus entdeckt. *B. klinggraeffii* wurde hier in verschiedenen Sukzessionsstadien der Flussschotterfluren nachgewiesen.

Key words: Bryophyte, *Bryum*, Caucasus, river gravel bars, vegetation.

Introduction

Bryum klinggraeffii is a small, 2–5 mm tall, moss belonging to the *B. erythrocarpum* complex, which is characteristic by presence of rhizoidal gemmae (Fig. 1). It creates tufts or is scattered among other bryophytes. The species has a wide area of distribution including North Africa, Turkey, India, China, Japan, North America, Patagonia and Europe (Kučera 2004–2017, Smith 2004). As a ruderal moss, it typically grows on a bare ground, on highly base-rich to slightly acidic, sandy to clayey soils. *B. klinggraeffii* occurs on frequently disturbed open habitats such as roadsides, fields, river banks, margins of water reservoirs or river gravel bars. Its distribution ranges from lowlands to mountain zone (e.g. Dierssen 2001, Kučera 2004–2017, Natcheva & Ganeva 2007, Shirzadian et al. 2014, Kalníková et al. 2017).

Probably due to its small size and occurrence in disturbed habitats, *B. klinggraeffii* is overlooked and its first finds e.g. in several Balkan countries (Bulgaria; Natcheva & Ganeva 2007; Albania, Montenegro and Serbia; Kalníková et al. 2017) or west-central Asia (Iran; Shirzadian et al. 2014) were done recently. In some south-eastern European countries, its

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evidence is still missing. In others, the species is considered as a data deficient or is included in national red list. However, this may also point only to its data deficiency, especially in bryofloristically less explored regions of south-eastern Europe (Natcheva & Ganeva 2007, Hodgetts 2015, Papp et al. 2015).

The knowledge on the bryoflora of Georgia, and the whole Caucasus region in general, is also insufficient, probably because of large area and often barely accessible locations which have not yet been observed by any bryologist. The regional checklist (Chikovani & Svanidze 2004) and several publications and additions concerning the Georgian bryoflora were published in the last years (e.g. Townsend 2005, Kürschner et al. 2013). However, there is no evidence of *B. klinggraeffii* for the country (Chikovani and Svanidze 2004) and it is even unknown in the Greater Caucasus (Ignatov et al. 2006). In Russia, it is known only within the Moscow and Pskov regions (Zolotov 2018). Nevertheless, *B. klinggraeffii* is reported from Turkey including locations on the Turkish side of the Lesser Caucasus (Uyar & Çetin 2004, Kürschner & Erdağ 2005, Kürschner 2008, Batan et al. 2017). There is no evidence about the species occurrence in Armenia (Manakyan 1995).

During the field research of river gravel bar vegetation across Georgia in the summer 2017, *Bryum klinggraeffii* was discovered on three localities, one in the Greater, two in the Lesser Caucasus. The aim of this short note is to present details about these records and characterize the new localities.

Methods

The new records were made during phytosociological sampling (16 m^2) following the Braun-Blanquet's approach (van der Maarel 1979). Additionally, we measured the elevation of the gravel bar to the actual water level and substrate structure using three categories stones (ø > 20 cm), gravel (ø < 20 cm) and sand (ø ≤ 2 mm; Bunte & Abt 2001).

Nomenclature follows EURO+MED PlantBase (2006–2018) and Hill et al. (2006) for vascular plants and bryophytes, respectively. Bryophyte specimens were deposited in the herbarium of the Moravian Museum, Brno, Czech Republic (BRNM).

Results and Discussion

All newly discovered localities of *Bryum klinggraeffii* are situated on the mountain river gravel bars. The first is located close to the Shovi village on the Chanchakhi River in the Greater Caucasus. The other two localities belong to the Lesser Caucasus; one near the Zarzma village on the Kvabliani River (Fig. 2) and the second near the Arali village on the Postkhovi River. The bedrock of all localities is rather base-rich. Around the Chanchakhi River, Cretaceous carbonate turbidites prevail and the bedrock of the Lesser Caucasian localities is composed mainly of Eocene volcanic rocks (Adamia 2010). All sites are flat and sandy with unknown flood regime, compounded by other different substrate fractions.

The following vegetation plots were obtained:

Shovi (distr. Oni, region Racha-Lechkhumi and Kvemo Svaneti): island gravel bar close to the left bank of the Chanchakhi River, 1420 m a.s.l., 42°42'22"N, 43°39'30"E; height of high herb layer: 60 cm, average height of herb layer: 25 cm, elevation above actual water level: 60 cm, stones+gravel+sand; July 5, 2017; P. Novák; BRNM 795131 (Fig. 1).

Fig. 1. *Bryum klinggraeffii* with detail of its rhizoids and rhizoid gemmae, the Chanchakhi River locality. Photo: Svatava Kubešová.

E_{total} (10 %), E_1 (10 %): *Calamagrostis pseudophragmites* 1, *Salix* sp. juv. 1, *Agrostis* sp. +, *Alnus incana* juv. +, *Hedysarum caucasicum* +, *Heracleum* sp. +, *Leucanthemum vulgare* +, *Picea orientalis* juv. +, *Pinus sylvestris* juv. r, *Poa* sp. +, *Prunella vulgaris* +, *Scrophularia* sp. +, *Taraxacum* sect. *Taraxacum* +, *Astragalus* sp. r, *Fragaria vesca* r

E_0 (1 %): *Barbula unguiculata* +, *Bryum argenteum* +, *Bryum klinggraeffii* +, *Didymodon* sp. r, *Funaria hygrometrica* r.

Zarzma (distr. Adigeni, region Samtskhe-Javakheti): gravel bar on the left bank of the Kvabliani River, 1175 m a.s.l., 41°40'47"N, 42°39'44"E; height of high herb layer: 60 cm, average height of herb layer: 10 cm, elevation above actual water level: 20 cm, sand+gravel; July 14, 2017; K. Chytrý; BRNM 795132.

E_{total} (22 %), E_1 (21 %): *Herniaria glabra* 1, *Silene compacta* 1, *Tanacetum parthenium* 1, *Alyssum alyssoides* +, *Anisantha tectorum* +, *Arenaria serpyllifolia* +, *Astragalus* sp. +, *Bromus japonicus* +, *Echium vulgare* +, *Epilobium tetragonum* +, *Filago arvensis* +, *Helianthemum* sp.+, *Lappula squarrosa* +, *Lotus corniculatus* +, *Paracynoglossum glochidiatum* +, *Plantago lanceolata* +, *Rumex acetosella* +, *Salix purpurea* juv. +, *Sedum spurium* +, *Setaria viridis* +, *Stachys annua* +, *Taraxacum* sect. *Taraxacum* +, *Teucrium polium* +, *Trifolium repens* +, *Verbascum* sp. +, *Viola kitaibeliana* +, *Agrostis stolonifera* r, *Erigeron canadensis* r, *Humulus lupulus* r, *Salix alba* juv. r, *Scrophularia* sp. r

E_0 (1 %): *Bryum klinggraeffii* +, *Bryum* sp. r.

Arali (distr. Adigeni, region Samtskhe-Javakheti): gravel bar on the right bank of the Postkhovi River, 1024 m a.s.l., 41°38'48"N, 42°51'37"E; height of high herb layer: 130 cm, average height of herb layer: 70 cm, elevation above actual water level: 50 cm, sand+gravel; July 15, 2017; V. Kalníková; BRNM 795133.

E_{total} (90 %), E_1 (90 %): *Calamagrostis pseudophragmites* 4, *Phalaroides arundinacea* 2a, *Agrostis gigantea* 1, *Juncus articulatus* 1, *Mentha longifolia* 1, *Persicaria lapathifolia* 1, *Ranunculus repens* 1, *Salix* sp. juv. 1, *Scirpus sylvaticus* 1, *Dysphania botrys* +, *Equisetum arvense* +, *Equisetum ramosissimum* +, *Juncus effusus* +, *Lotus corniculatus* +, *Medicago lupulina* +, *Phleum pratense* +, *Plantago major* +, *Rorippa* sp. +, *Rumex crispus* +, *Salix purpurea* juv. +, *Xanthium* sp. +, *Bidens frondosus* r, *Vicia* sp. r

E_0 (5 %): *Cratoneuron filicinum* 1, *Brachythecium rivulare* +, *Bryum klinggraeffii* +, *Bryum* sp. +, *Plagiomnium cuspidatum* +.

Fig. 2. Site of the gravel bar on the left bank of the Kvabliani River. Photo: Kryštof Chytrý.

Gravel bars are developed at sites with a specific combination of floodplain morphology, water discharge pattern, and sediment transport regime (Montgomery & Buffington 1998). They are dynamic and frequently disturbed and therefore offer a wide scale of heterogeneous environments. *B. klinggraeffii* is a ruderal light-demanding species connected to open habitats (e.g. Dierssen 2001) and gravel bars fit its ecological requirements. Moreover as a short-living colonist species may on such habitat also avoid flooding disturbance by completing their life cycles before the next floods (Muotka & Virtanen 1995).

It usually grows on gravel bars which are covered by sparse vegetation including open patches (Kalníková et al. 2017). The vegetation of the sampled gravel bar sites could be classified as a montane gravel bar herbaceous vegetation of the order *Epilobietalia fleischeri* and class *Thlaspietea rotundifolii* (Mucina et al. 2016). Two of the mentioned sites were covered by open initial scattered vegetation with rather low cover of both herb (typical species e.g. *Arenaria serpyllifolia*, *Herniaria glabra*, *Silene compacta* and scattered growth of *Calamagrostis pseudophragmites*) and moss layer (maximum 22 % in total). *B. klinggraeffii* occurred there together with other ruderal mosses such as *Bryum argenteum*, *Barbula unguiculata* or *Funaria hygrometrica*. Considering its ecological requirements reported from south-eastern Europe, one of the localities, the gravel bar of Postkovi River, is less typical. *B. klinggraeffii* was found there in a dense vegetation dominated by tall grasses *Calamagrostis* *pseudophragmites* and *Phalaroides arundinacea* (with vegetation cover 90 % of bryophytes and vascular plants). Other accompanying bryophytes on the site were relatively moisture demanding and shade-tolerant species – *Brachythecium rivulare* or *Plagiomnium cuspidatum*. Possible explanation considers microscale patches in the vegetation as the moss was collected on more open patch within the sampled plot or it could be a remnant of the former sparser successional vegetation stage.

It seems likely that *B. klinggraeffii* is relatively common species in Georgia and also in neighbouring countries. Its highly unexplored status is probably caused by the limited local research and also research on bryoflora of river gravel bars, which is generally understudied field. Concerning the endangered status (Janssen et al. 2016) of this dwindling habitat, its understudied status is striking and calling for attention.

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Curriculum Vitae

Personal details

Veronika Kalníková, born on 2nd April 1987, Frýdek-Místek, Czech Republic

Education

2012–currently – Masaryk University, Faculty of Science, Doctoral degree programme: Botany
2009–2012 – Masaryk University, Faculty of Science, Master's degree programme: Systematic Biology and Ecology with specialization in Botany and Master's degree in Upper Secondary School Teacher Training in Biology; thesis: *Distribution of invasive neophytes and succession on gravel sediments along streams of the Moravskoslezské Beskydy Mts and their foothills* (in Czech)
2006–2012 – Masaryk University, Faculty of Science, Bachelor's degree in programme: Systematic Biology and Ecology with specialization in Botany; thesis: *Distribution of invasive neophytes along the Ostravice and Morávka rivers* (in Czech)
2002–2006 – T. G. Masaryk Grammar school in Frýdlant nad Ostravicí

Professional work experience

2018–currently – botanist in Nature Conservation Agency of the Czech Republic, PLA Administration Beskydy
2019–2020 – participation on the project "Stream drying and biodiversity of running waters: the impact of natural conditions and anthropogenic alterations" (TAČR Beta 2; 2018–2021)
2017–2019 – participation the project "Photobionts of the lichens growing on the river gravel bars – symbiosis on the border of wet/dry habitats" (funded by GA UK 230416)
2012–2019 – part time job at the Department of Botany and Zoology, Faculty of Science, Masaryk University in Brno; participation on projects "Centre of Plant Diversity Analysis and Synthesis" (PLADIAS; Czech Science Foundation 14-36079G) and "Urban plant communities: a model of emerging communities of the future" (Czech Science Foundation 14-10723S)
2017 – leading of the project "Comparison of the vegetation of the river bars on the Labe River with other rivers across the Czech Republic" (funded by the Ministry of the Environment of the Czech Republic)
2009–currently – participation and leading of projects in ČSOP a Ekocentrum Koniklec, Prague; cooperation on several projects dealing with rainwater management and water retention (http://www.pocitamesvodou.cz/); 2009 – leader of project "Mapping of invasive neophytes along the streams in Beskydy Mountains" (funded by ČSOP Biodiversity protection projects 110907), 2014–2015 – leader of project "Monitoring of selected invasive plants in the Prague" (funded by Municipality of Prague DOT/85/03/002267/2014)
2011–2012 – participation in the projects "Monitoring of succession in localities selected for water management of gravel bars on the Ostravice River" and "Mapping and monitoring of *Calamagrostis pseudophragmites* on the Ostravice River" in the Silva Tarouca Research Institute for Landscape and Ornamental Gardening in Brno (funded by the Ministry of the Environment of the Czech Republic)

International experience and conferences

Selected participating workshops and conferences

Conference and workshop Towards Understanding the Impact of Global Climate Change on the Biodiversity of Tropical Rainforests, Brunei Darussalam; 3.–14. January 2010

Natural Disturbance Conference, Bavarian Forest National Park, Neuschönau, Germany; 29. April–3. May 2013

14. International Alpine Workshop – Durance 2016 & 4th Workshop of the European *Typha minima* Group, Sigoyer, France; 18.–25. May 2016

Conferences with oral presentation

Kalníková V., Chytrý M. & Data contributors. An overview of the European gravel bar vegetation. 25th Meeting of the European vegetation survey, Rome, Italy; 6.–9. April 2016

Kalníková V., Chytrý M. & Data contributors. Formalized classification of the mountain and alpine European gravel bar vegetation. 27th Congress of the European Vegetation Survey, Wrocław, Poland; 23.–26. May 2018

Invited oral presentations

Kalníková V. & Eremiášová R. Jak je výskyt *Calamagrostis pseudophragmites* závislý na dynamice štěrkových náplavů? Konference 40 let CHKO Beskydy – Zachováme pestrost Beskyd? Frýdek-Místek, Czech Republic; 27. March 2013

Kalníková V. Dřevojan P., Večeřa M. & Novák P. Srovnání bahnitých říčních náplavů řeky Labe s řekami v napříč Českou republikou. Seminář k sledování stavu biotopů a druhů, AOPK, Sněžné, Czech Republic; 1.–2. March 2018

Conferences with poster

Kalníková V. Rostlinné invaze podél vodních toků v Moravskoslezských Beskydech a jejich podhůří. Konference Význam liniové zeleně v krajině, Ústí nad Labem, Czech Republic; 16. September 2010

Kalníková V., Eremiášová R. & Skokanová H. Monitoring of vegetation succession at sites selected for gravel bar management. European Vegetation Survey 21st Workshop Vienna, Austria; 24.–27. May 2012

Kalníková V. & Chytrý M. Vegetation succession on river gravel bars after an extreme flood. 56th IAVS Symposium in Tartu, Estonia; 26.–30. June 2013

Kalníková V. & Chytrý M. Vegetation succession on river gravel bars after an extreme flood. Konference České společnosti pro ekologii, Brno, Czech Republic; 18.–23. October 2013

Kalníková V., Chytrý M. & Data Contributors. Vegetation of gravel bars across Europe. 13th meeting on vegetation databases: Vegetation Databases and Ecological Restoration, Koblenz, Germany; 24.–26. February 2014

Kalníková V., Palpurina S. & Chytrý M. New Bulgarian plant communities described from gravel bars. European Vegetation Survey 23rd Workshop Ljubljana, Slovenia; 8.–12. May 2014

Kalníková V., Chytrý M. & Data Contributors. European gravel bar vegetation survey. European Vegetation Survey 24th Workshop Rennes, France; 4.–8. May 2015

Kalníková V. & Chytrý M. Succession rate on gravel bars of small streams. 58th IAVS Symposium in Brno, Czech Republic; 19.–24. July 2015

Oral presentations given at Ph.D. student meetings

Kalníková V. European gravel bar vegetation survey. Sixth Meeting of PhD students in Plant Ecology and Botany, Karpacz, Poland; 10–12 October 2014

Kalníková V. Diverzita a ekologie vegetace štěrkových říčních náplavů. Ledeč nad Sázavou, Czech Republic; 30. November–2. December 2012

Main own field research

Bulgaria 2013; Serbia, North Macedonia and Montenegro 2014; Sweden and Norway 2014; Poland 2015; Georgia 2015–2017; Switzerland 2017

Publications in international peer-reviewed journals (in English)

Kalníková, V. and Palpurina, S. (2015) *Epilobium adenocaulon* and *Oenothera glazioviana* (Onagraceae): new alien species for the Bulgarian flora. *Phytologia Balcanica*, 21, 21–27.

Chytrý, M., Dražil, T., Hájek, M., **Kalníková, V.**, Preislerová, Z., Šibík, J., Ujházy, K., Axmanová, I., Bernátová, D., Blanár, D., Dančák, M., Dřevojan, P., Fajmon, K., Galvánek D., Hájková, P., Herben, T., Hrivnák, R., Janeček, Š., Janišová, M., Jiráská, Š., Kliment, J., Kochjarová, J., Lepš, J., Leskovjanská, A., Merunková, K., Mládek, J., Slezák, M., Šeffer, J., Šefferová, V., Škodová, I., Uhlířová, J., Ujházyová, M. and Vymazalová, M. (2015) The most species-rich plant communities in the Czech Republic and Slovakia (with new world records). *Preslia*, 87, 217–278.

Peterka, T., Plesková, Z., Palpurina, S., **Kalníková, V.**, Lazarević, P.M. and Hájek M. (2016) *Meesia triquetra*, new relict moss for the Republic of Macedonia. *Herzogia*, 29, 66–71.

Vassilev, K., Pedashenko, H., Alexandrova, A., Tashev, A., Ganeva, A., Gavrilova, A., Gradevska, A., Assenov, A., Vitkova, A., Grigorov, B., Gussev, Ch., Filipova, E., Aneva, I., Knolova, I., Nikolov, I., Georgiev, G., Gogushev, G., Tinchev, G., Pachedzieva, K., Koev, K., Lubenova, M., Dimitrov, M., Apostolova-Stoyanova, N., Velev, N., Zhelev, P., Glogov, P., Natcheva, R., Tzonev, R., Boch, S., Hennekens, S., Georgiev, S., Stoyanov, S., Karakiev, T., **Kalníková, V.**, Shivarov, V., Russakova, V. and Vulchev, V. (2016) Balkan vegetation database: historical background, current status and future perspectives. *Phytocenologia*, 46, 89–95.

Kalníková, V. and Kudrnovsky, H. (2017) Gravel Bar Vegetation Database. *Phytocoenologia*, 47, 109–110.

Kalníková, V., Palpurina, S., Peterka, T., Kubešová, S., Plesková, Z. and Sabovljević, M. (2017) Bryophytes on river gravel bars in the Balkan Mountains: New records and insights into ecology. *Herzogia*, 30, 370–386.

Peterka, T., **Kalníková, V.** and Plesková, Z. (2017) *Pseudocalliergon lycopodioides*, a New Bryophyte Species for Montenegro. *Herzogia*, 30, 496–500.

Lososová, Z., Tichý, L., Divíšek, J., Čeplová, N., Chytrý, M., Danihelka, J., Dřevojan, P., Fajmon, K., **Kalníková, V.**, Kalusová, V., Novák, P., Řehořek, V. and Wirth, T. (2018) Predicting potential shifts in urban plant communities under climate change. Future shifts in structure of urban plant communities. *Diversity and Distributions*, 24, 765–775.

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Kalníková, V., Chytrý, K., Novák, P. and Kubešová, S. (2018) *Bryum klinggraeffii*, a moss new to Georgia – first record for the Greater Caucasus. *Herzogia*, 31, 982–987.

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Kalusová, V., Čeplová, N., Chytrý, M., Danihelka, J., Dřevojan, P., Fajmon, K., **Kalníková, V.**, Novák, P., Hájek, O., Řehořek, V., Tichý, L., Wirth, T. and Lososová, Z. (2019) The response of European urban floras to climate: no difference between native and alien species. *Journal of Biogeography*, 46, 1406–1418.
Chytrý, K., Novák, P., **Kalníková, V.**, Prokešová, H., Večeřa, M., Chytrý, M. and Dřevojan, P. (2019) Dry grassland vegetation in the Transcarpathian Lowland (western Ukraine). *Tuxenia*, 39, 335–355.

Unpublished manuscripts (in English)

Kalníková, V., Chytrý, K., Novák, P., Zukal, D. and Chytrý, M. (accepted) Vegetation of river gravel bars in the Caucasus Mountains, Georgia. *Folia Geobotanica*.
Chytrý, M., Tichý, L., Hennekens, S.M., Knollová, I., Janssen, J.A.M., Rodwell, J.S., Peterka, T., Marcenò, C., Landucci, F., Danihelka, J., Hájek, M., Dengler, J., Novák, P., Zukal, D., Jiménez-Alfaro, B., Mucina, L., Abdulhak, S., Aćić, S., Agrillo, E., Attorre, F., Bergmeier, E., Biurrun, I., Boch, S., Bölöni, J., Bonari, G., Braslavskaya, T., Bruelheide, H., Campos, J.A., Casella, L., Ćuk, M., Ćušterevska, R., Čarni, A., De Bie, E., Demina, O., Didukh, Y., Dítě, D., Dziuba, T., Ewald, J., Gavilán, R.G., Gégout, J.-C., Giusso del Galdo, G.P., Golub, V., Goral, F., Graf, U., Indreica, A., Isermann, M., Jand, U., Jansen, F., Jansen, J., Jašková, A., Jiroušek, M., Kącki, Z., **Kalníková, V.**, Kavgacı, A., Khanina, L., Korolyuk, A.Y., Kozhevnikova, M., Kuzemko, A., Küzmič, F., Laiviņš, M., Lavrinenko, I., Lavrinenko, O., Lebedeva, M., Lysenko, T., Maciejewski, L., Mardari, C., Onyshchenko, V., Pérez-Haase, A., Pielech, R., Prokhorov, V., Rašomavičius, V., Rodríguez Rojo, M.P., Rūsiņa, S., Schrautzer, J., Stančić, Z., Stanisci, A., Šibík, J., Šilc, U., Škvorc, Ž., Tikhonova, E., Tonteri, T., Uogintas, D., Valachovič, M., Vassilev, K., Willner, W., Yamalov, S., Evans, D., Lund, M.P., Spyropoulou, R., Tryfon, E. and Schaminée, J.H.J. (submitted) EUNIS Habitat Classification: expert system, characteristic species combinations and distribution maps of European habitats. *Applied Vegetation Science*.
Vančurová, L., **Kalníková, V.**, Peksa, O., Škvorová, Z., Malíček, J., Moya, P., Chytrý, K., Černajová, I. and Škaloud, P. (submitted) Diversity of lichen phycobionts along successional gradient of river gravel bars. *Symbiosis*.
Kalníková, V., Chytrý, M., Chytrý, K., Biţa-Nicolae, C., Bracco, F., Font, X., Iakushenko, D., Kącki, Z., Kudrnovsky, H., Landucci, F., Lustyk, P., Milanović, D., Šibík, J., Šilc, U., Uziębło A.K. and Villani, M. (manuscript) Vegetation of the European mountain river gravel bars: a formalized classification.

Publications in Czech peer-reviewed journals (in Czech)

Kalníková, V. (2012) Rozšíření invazních neofytů podél toků severovýchodní Moravy a Slezska. *Zprávy České botanické společnosti*, 47, 297–318.
Kalníková, V. and Eremiášová, R. (2013) Rozšíření třtiny pobřežní (*Calamagrostis pseudophragmites* /Haller f./Koeler) na řece Ostravici. *Acta Carpathica Occidentalis*, 4, 3–14.

Kalníková, V., Dřevojan, P., Večeřa, M. and Novák, P. (2019) Srovnání vegetace říčních náplavů Labe s řekami napříč Českou republikou. *Příroda*, 39, 167–187.

Unpublished manuscripts (in Czech)

Bachan, R. and **Kalníková, V.** (manuscript) Mapování vodních makrofyt v řekách s využitím bezipoltního letadla. *Příroda*.

Chosen popularization publications (in Czech)

Kalníková, V. (2012) Co je mezi povodněmi a suchem? *Ekolist* (http://ekolist.cz/cz/zpravodajstvi/zpravy/co-je-mezi-povodnemi-a-suchem).

Kalníková, V. (2014) Hospodařením s dešťovou vodou proti extrémům počasí? *Ekolist* (http://ekolist.cz/cz/publicistika/nazory-a-komentare/veronika-kalnikova-hospodarenim-s-destovou-vodou-proti-extremum-pocasi).

Kalníková, V. (2015) Invazní rostliny. Jak se šíří, co můžeme sami udělat pro prevenci jejich dalšího šíření a jak může být nápomocen nový zákon o bioodpadech? *Nika*, 10, 16–17.

Kalníková, V. (2015) Jak se pátrá po invazních rostlinách, aneb jejich mapování v praxi. *Nika*, 10, 18–19.

Kalníková, V. (2016) Exkurze řekou Morávkou. *Zprávy Moravskoslezské pobočky ČBS*, 5, 37–42.

Kalníková, V. (2016) Jak mohou sjezdovky ovlivnit vodní režim krajiny? *Vodní hospodářství*, 3, 42.

Novák, P., **Kalníková, V.**, Chytrý, K. and Prokešová, H. (2017) Za botanickými krásami jižní Kolchidy I. *Živa*, 1/2017, 21–24.

Kalníková, V., Novák, P., Chytrý, K. and Prokešová, H. (2017) Za botanickými krásami jižní Kolchidy II. *Živa*, 2/2017, 67–69.

Kalníková, V. and Tkáčiková, J. (2019) Údolím řeky Mohelnice – floristicko-bryologická exkurze. *Zprávy Moravskoslezské pobočky ČBS*, 8, 34–39.

Kalníková, V. and Popelářová, M. (2020) Exkurze po zajímavých bezlesých enklávách aneb Z bláta do louže kolem Smradlavé. *Zprávy Moravskoslezské pobočky ČBS*, 9, 29–33.

Chytrý, K., Prokešová, H., **Kalníková, V.** and Novák, P. (2020) Teplomilné rostlinstvo Podkarpatské Rusi. *Živa*, 1/2020, 23–26.

Other activities

2008–2012 – technical work on Department of Botany and Zoology, Faculty of Science, Masaryk University (data digitalization mainly)

2010–2014 – external lector of Environmental Education in Lipka – school facility for environmental education, Rozmarýnek, Brno

2013–2015 – participation on organization of student competition "KEKS – Korespondenční ekologický seminář pro středoškoláky" (http://keks.math.muni.cz/)

2013–2018 – participation on organization of popularization event Night of Scientists, Masaryk University, Faculty of Science

2015, 2017 – introduction to vegetation science survey course – field work Košetice for Recetox students (Research Centre for Toxic Compounds in the Environment, Faculty of Science, Masaryk University)

2014–2016 – participation on organization of regional round of Biological Olympiad in Brno

2016–2017 – participation on organization of regional round of Ecological Olympiad in Frýdek-Místek
2016 – participation on ecological competition Quarry Life Award with project “Experiment in biodiversity management of quarry Mokrá: Innovative approaches in ecological restoration”
2010–currently – co-author of web pages (database) and author of photographs on the Botanical photo-gallery
2014–currently – editorial board of regional botanical journal “Zprávy Moravskoslezské pobočky České botanické společnosti”