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Ecological conditions of the altitudinal substitution of *Petasites kablikianus* and *P. hybridus* in the Polish Carpathians

Aldona Katarzyna Uziębło[1]*, Barbara Fojcik[2], Dariusz Kozik[1]

[1] Department of Ecology, Faculty of Biology and Environmental Protection, University of Silesia in Katowice, Jagiellońska 28, 40-032 Katowice, Poland
[2] Department of Botany and Nature Protection, Faculty of Biology and Environmental Protection, University of Silesia in Katowice, Jagiellońska 28, 40-032 Katowice, Poland

* Corresponding author. Email: aldona.uzieblo@us.edu.pl

Abstract

Two species of the genus *Petasites*, *P. kablikianus* (occurs upstream) and *P. hybridus* (occurs downstream), form characteristic tall herb communities in two altitudinal zones of Carpathian streams and rivers. They are described as "altitudinal vicariants" due to their substitution with decreasing elevation on similar habitats along mountain streams. This would indicate that the phenomenon is conditioned by climatic factors. In this study, we investigated the factors that determine this substitution on streambanks, and whether *P. hybridus* competes with *P. kablikianus* and limits its spread from mountains to foothills. We analyzed 72 plant patches from the Western and Eastern Carpathians in terms of flora composition, and geomorphological features of the habitat. The content of organic matter, available Mg, P, K, C, total N, and pH were also analyzed for a representative group of patches. Phytocoenoses were analyzed based on the presence of one of the analyzed species or on the quantitative proportions, in the case of a co-occurrence. We found statistically significant differences in the soil structure (skeleton percentage), content of Mg, N, and C, and the values of the C:N ratio. These results revealed that *P. kablikianus* prefers skeletal soils with a lower clay content, that is rich in Mg, N, C, and organic matter. *Petasites hybridus* prefers finer soils, which are richer in pulverized and clay fractions, in a zone of decrease of soil richness and where a thick layer of humus is typical for its phytocoenoses. We found that the spread of *P. kablikianus* into lower locations is not limited by competition with *P. hybridus*, but rather by the quality and structure of the habitat. Therefore, both species should be treated as ecological rather than altitudinal vicariants.

Keywords

distribution range; ecological requirements; vicariants

Introduction

Riparian vegetation is an example of a transitional environment between stream water and surrounding areas. Along the stream valley, the vegetation forms characteristic zones according to the frequency of flooding [1]. Closest to the water current are the most frequently flooded communities of pioneer vegetation, followed by tall herbs or rushes, willow thickets, and riparian forests. The lower the location above sea level, the better formed the vegetation zones. In these zones, geomorphological, hydrological, and ecological processes interact actively, generating a highly dynamic landscape that is characterized by a heterogeneous mosaic of microhabitats [2]. Essential feedback occurs between the vegetation and fluvial processes, which have a fundamental effect on the character and dynamics of the riparian habitat mosaic [3] and plant composition. There is longitudinal connectivity between upstream and downstream riparian vegetation. Flows of water, mineral sediments, and organic matter are fundamental drivers of the

morphodynamics of these zones and their ecology, through the associated transport of organisms, plant propagules, and nutrients [1].

Numerous studies have investigated vegetation–environment relationships. Most have analyzed the impact of chosen factors on vegetation [4–13]. Among them, stream power, flood duration, various topographic variables, soil pH, content of nutrient elements or heavy metals in the soil, light intensity, soil texture, groundwater discharge, and level of the water-table are notable. Other studies have investigated vegetation as a factor influencing various environmental features [14–18]. Each of those studies analyzed some of the factors mentioned above, mostly according to vegetation type, which has been studied in relation to species richness. Most studies concerning streams and rivers analyzed elevation.

Altitudinal gradient can directly modify local climatic factors, including temperature [19–21], atmospheric pressure [22], precipitation [23], and UV irradiation [24]. An indirect modification of environmental factors according to altitudinal gradient applies to factors such as duration of snow cover [25], physical weathering and erosion [26,27], chemical composition of the soil [28,29], content of organic matter [30] and its decomposition [31], diversity of plant communities, and the frequency of disturbances [32].

Vertical vegetation diversity in mountain areas is associated with the reaction of entire plant communities to environmental changes along the altitudinal gradient. It is also accompanied by the altitudinal substitution of related species in similar habitats, which is a rarely-studied phenomenon termed altitudinal or edaphic vicariance [33]. In a biogeographic manner, this phenomenon may refer to vicariants identified as descendants of the parent taxa that have adapted as a result of speciation to habitats located at different altitudes [34,35]. Another case of vicariance applies to species that recolonized convenient habitats despite the species not arising as a result of adaptive radiation.

Two species that vicarise on the area of the Carpathians are *Petasites kablikianus* (glabrous butterbur) and *P. hybridus* (pink butterbur) [33,36]. These species form similar phytocoenoses, which are an expressive element of stream valleys landscape, and gradually replace each other on habitats located on the banks of streams and montane rivers. The climatic conditions affect the geographical distribution of both species. *Petasites kablikianus* is clearly a mountain species and *P. hybridus* is a lowland species with a much wider altitudinal range of distribution [37]. Nevertheless, we posed the following questions:

- What habitat factors determine the distribution of both species in alluvial habitats?
- Is there any interspecies competition that might be a limiting factor for the spreading of glabrous butterbur on lower areas?

The aim of this study was to determine the qualitative and quantitative characteristics underlying the substitution of both butterburs and accompanying species, in alluvial habitats and to verify the hypothesis that pink butterbur may limit the migration of glabrous butterbur on lower locations.

Material and methods

The study was conducted in the Polish Western and Eastern Carpathians in 2015–2016 on the main rivers and streams of the Żywiecki Beskid Mts, Small Beskid Mts, Gorce Mts, Western Tatra Mts, High Tatra Mts, Low Beskid Mts, and Bieszczady Mts at an elevation gradient from 352 to 1,015 m above sea level (a.s.l.) (Fig. 1, Appendix S1).

Vegetation plots were collected systematically (on average every kilometer) along four streams: the Soła River, Skawica River, Black Dunajec River, and Białka River. The rest were selected randomly to include the entire Carpathian distribution range of the species in Poland. The main selection criteria was the presence of one or both species of *Petasites* in the phytocoenosis, and localization of the patch on the streambank. Both tall herbs and riparian forest with butterburs in the herb layer were considered. A total of 72 phytosociological relevés were made, in which the percentage coverage of a species (vascular plants and mosses) was estimated based on a scale of 1%, 5%, 10%, 20%, up
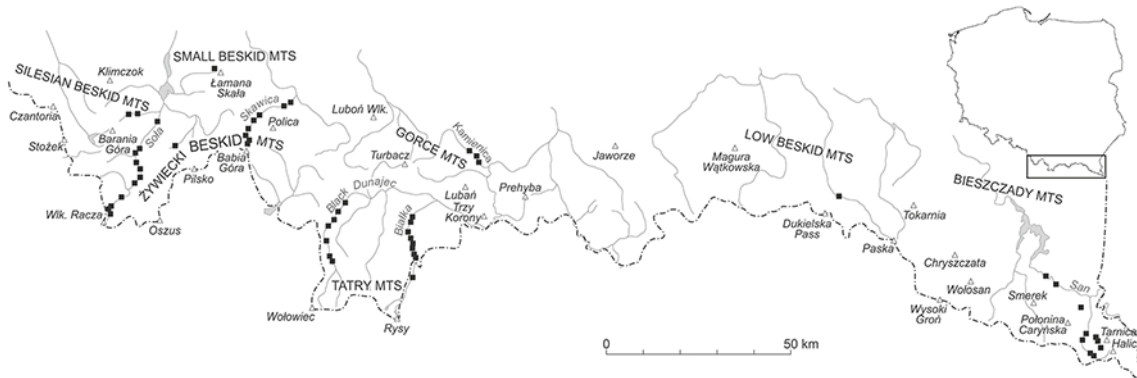
Fig. 1 Distribution of the analyzed phytocoenoses with *P. kablikianus* and *P. hybridus* in the Carpathians. Detailed locations are listed in Appendix S1.

to 100%. The area of each relevé was about 50 m². To describe the habitat conditions as fully as possible, we included both geomorphological features in the analysis reflecting the location of the patches with respect to the stream current, the frequency of flooding, texture, and chemical composition of the substrate. The following parameters and characteristics of habitat were identified on each plot:

- geographical coordinates at the central point of a plot,
- the width of a plot (m) – width,
- the elevation of the surface of the patch above the average water level (m) – height,
- the width of the flood zone – a stony part of the streambank commonly uncovered by plants because of flooding during every small rise of water level (m) – zone,
- the distance from the edge of the patch to the main current (m) – current.

Soil samples were collected and habitat parameters were estimated. Cumulative samples were collected in the rhizosphere layer (up to 40 cm depending on the share of soil skeleton) in all plots, to determine the granulometric composition (aerometric method with Prószyński's modification [38]), weight percentage of the soil skeleton (over 1 mm diameter), and acidity in distilled water. Total nitrogen content, oxidizable carbon content, available potassium, phosphorus, and magnesium content were also determined for 31 plots that represented the four groups of plots in a certified external laboratory (all according to the current ISO standards). The C:N ratio was also calculated.

To compare changes in particular factors, all plots were divided into four groups according the presence and abundance of both of the analyzed species:

- Pk – patches in which *P. kablikianus* dominated (coverage range 50–100%) without *P. hybridus* (31 relevés),
- Pk/Ph – patches in which *P. kablikianus* dominated (with 50–100% coverage) with a contribution of *P. hybridus* (with 10–50% coverage) (16 relevés),
- Ph/Pk – patches in which *P. hybridus* with *P. kablikianus* were dominant (coverage as mentioned above) (13 relevés),
- Ph – patches in which *P. hybridus* dominated, without *P. kablikianus* (12 relevés).

Variation in the numbers of research plots in particular groups was due to the limitation of the zone of *P. hybridus* occurrence on streambanks by the presence of dams and retention reservoirs, which diametrically changed the shape of the banks and the habitat conditions on them.

Qualitative differences and mutual floristic connections among groups of phytocoenoses are shown in the synoptic table (Tab. 1). The species were ordered according to the fidelity (Φ) of each group. Values in the table are multiplied by 100. For simplicity, species with a fidelity value below 15 were excluded from the table. Numbers noted as superscripts represent the percentage species frequency in each group. To eliminate the fidelity value of species with nonsignificant occurrence patterns, Fisher's exact test ($p < 0.05$) was used [39].

Nomenclature of species was based on *Flowering plants and pteridophytes of Poland – a checklist* [40], on *Census catalogue of Polish mosses* [41] and on *An annotated checklist of Polish liverworts and hornworts* [42].

Tab. 1 Synoptic table of recorded vegetation patches.

Species	Layer	Group of plots			
		Pk	Pk/Ph	Ph/Pk	Ph
		No. of relevés			
		31	16	13	11
Thalictrum aquilegifolium	c	45.5 [26]	-	-	-
Fragaria vesca	c	42.4 [23]	-	-	-
Veronica montana	c	39.1 [19]	-	-	-
Salix eleagnos	b	24.7 [23]	-	- [8]	- [9]
Poa annua	c	20.3 [23]	- [6]	- [8]	- [9]
Chrysosplenium alternifolium	c	19.8 [32]	9.1 [25]	-	- [18]
Calamagrostis arundinacea	c	16.6 [16]	-	- [8]	1.8 [9]
Impatiens noli-tangere	c	- [23]	25.0 [44]	- [15]	- [18]
Senecio hercynicus	c	2.7 [13]	24.7 [25]	- [8]	-
Geranium robertianum	c	6.9 [16]	22.6 [25]	- [8]	-
Salix triandra	b	-	21.8 [6]	-	-
Salix caprea	b	- [6]	21.0 [19]	-	1.1 [9]
Cirsium oleraceum	c	- [16]	20.0 [31]	- [15]	- [9]
Carduus personata	c	- [26]	17.9 [44]	1.4 [31]	- [27]
Stellaria nemorum	c	- [39]	16.6 [56]	4.7 [46]	- [18]
Primula elatior	c	7.2 [19]	16.3 [25]	- [15]	-
Carex sylvatica	c	- [13]	5.0 [19]	24.1 [31]	-
Cardamine pratensis	c	- [19]	2.8 [25]	21.3 [38]	- [9]
Brachythecium rutabulum	d	- [23]	- [38]	20.3 [62]	12.2 [55]
Trifolium repens	c	- [16]	- [19]	17.9 [31]	- [9]
Anthoxanthum odoratum	c	- [6]	- [12]	17.8 [23]	- [9]
Geum rivale	c	- [19]	- [25]	17.6 [38]	- [18]
Lamium maculatum	c	- [26]	6.9 [38]	17.6 [46]	- [18]
Silene vulgaris	c	8.3 [39]	- [25]	17.5 [46]	- [18]
Oxyrrhynchium speciosum	d	- [6]	- [12]	16.9 [31]	11.8 [27]
Rumex sanguineus	c	-	- [6]	16.7 [15]	3.1 [9]
Filipendula ulmaria	c	- [13]	8.1 [25]	16.5 [31]	- [9]
Heracleum sphondylium	c	- [23]	- [19]	15.3 [38]	- [27]
Rumex obtusifolius	c	- [16]	6.8 [25]	15.1 [31]	- [9]
Impatiens glandulifera	c	- [10]	- [6]	-	30.6 [27]
Rubus idaeus	c	- [29]	- [25]	- [15]	29.4 [55]
Galium aparine	c	- [16]	- [38]	- [38]	29.3 [64]
Geum urbanum	c	- [6]	- [6]	- [8]	27.4 [27]
Glechoma hederacea	c	- [26]	- [25]	- [31]	25.0 [55]
Phalaris arundinacea	c	7.4 [26]	- [12]	- [8]	22.5 [36]
Salix alba	c	- [6]	-	- [8]	21.4 [18]
Urtica dioica	c	- [55]	12.7 [75]	- [46]	20.9 [82]
Veronica chamaedrys	c	7.4 [26]	- [12]	- [15]	20.5 [36]
Poa pratensis	c	- [16]	- [12]	- [8]	18.0 [27]
Dactylis glomerata	c	- [26]	1.9 [50]	6.4 [54]	17.7 [64]
Aegopodium podagraria	c	- [48]	- [44]	12.5 [69]	16.6 [73]
Plagiomnium undulatum	d	- [19]	- [19]	- [23]	16.1 [36]

Tab. 1 Continued

		Group of plots			
		Pk	Pk/Ph	Ph/Pk	Ph
		No. of relevés			
Species	Layer	31	16	13	11
Salix alba	a	-	7.3 [6]	-	15.8 [9]
Agrostis stolonifera	c	3.5 [19]	– [6]	– [15]	15.7 [27]
Alnus incana	a	– [10]	4.6 [12]	-	15.5 [18]
Festuca gigantea	c	– [16]	– [31]	6.9 [38]	15.5 [45]
Petasites kablikianus	c	33.3 [100]	33.3 [100]	33.3 [100]	-
Petasites hybridus	c	– [3]	32.6 [100]	32.6 [100]	32.6 [100]

Relevés were divided into four groups: with *P. kablikianus* as the only dominant (Pk), mixed plots with a dominance of *P. kablikianus* (Pk/Ph), mixed plots with a dominance of *P. hybridus* (Ph/Pk) and with *P. hybridus* as the only dominant (Ph). The species were ordered according to their fidelity (Φ) of each group. Values in the table are multiplied by 100. The species with Φ value <15 were excluded. Superscripts express percentage values of species frequency in each group. To eliminate the fidelity value of species with nonsignificant occurrence patterns, Fisher's exact test ($p < 0.05$) was used. Layers: a – tree layer; b – shrubs; c – herb layer; d – bryophytes. Shaded cells denote distinctive species.

Sporadic species, with a single individual present, were only included in the analysis of floristic richness, and were excluded from the other analyses.

Statistical analyses were performed using cluster analysis [similarity coefficient of Manhattan and the UPGMA method of agglomeration (unweighted pair group method with arithmetic mean); Fig. 3], correlation analysis (Pearson's *r*), and principal component analysis (PCA). Due to gradual changes in the contribution of individual factors or their occurrence in pairs of groups (with a particular dominant species), we tested the significance of intergroup differences in two variants for all four groups (significant differences most frequently concerned only in extreme groups Pk and Ph, or were insignificant because of gradual changes) and in two groups (Pk + Pk/Ph and Ph + Ph/Pk) using the nonparametric Kruskal–Wallis test. The results of the second variant of tests are listed below the box and whiskers plots (Fig. 4–Fig. 6). All analyses were performed using the Statistica package version 13.1.
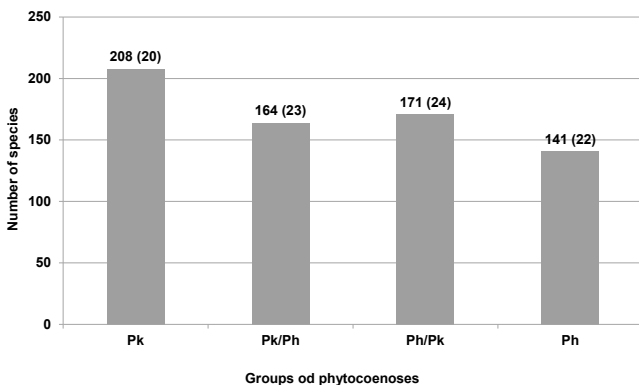

Fig. 2 Floristical richness of particular groups of relevés with both *Petasites* sp. as the dominants. The numbers in brackets represent the average number of species per relevé.

Results

Analysis of phytosociological data revealed that phytocoenoses with butterburs became gradually impoverished from 208 species in the Pk group, 164 in the Pk/Ph group, 171 in the Ph/Pk group, to 141 species in the Ph group. However, the average numbers of species (including mosses) in a relevé in these groups were 20–24 (Fig. 2).

In groups of patches where *P. kablikianus* was dominant, 16 species were clearly related, seven distinguished the Pk group and nine distinguished the Pk+Ph group (Tab. 1). Among them, *Thalictrum aquilegifolium*, *Fragaria vesca*, *Veronica montana*, *Salix eleagnos*, *Impatiens noli-tangere*, *Senecio hercynicus*, *Geranium robertianum*, *Salix triandra*, and *Salix caprea* were notable. Thirty species, including *Carex sylvatica*, *Cardamine pratensis*, *Impatiens glandulifera*, *Rubus idaeus*, *Galium aparine*, *Geum urbanum*, *Glechoma hederacea*,

Phalaris arundinacea, and *Salix alba* presented more significant relationships to plots with *P. hybridus*. Thirteen of these were more characteristic to the Ph/Pk mixed group and 13 to the group in which *P. hybridus* was dominant (Tab. 1).

Thirty-eight species of bryophytes were observed. Among them, only *Brachythecium rutabulum* and *Oxyrrhynchium hians* revealed distinct relationships with the Ph/Pk group of patches, whereas *Plagiomnium undulatum* was related to patches in which *P. hybridus* was dominant (Tab. 1). In the group of hydro- and hygrophilic bryophyte species that was found in the tall herbs with both *Petasites* species, the following were observed: *Brachythecium rivulare*, *Bryum pseudotriquetrum*, *Cratoneuron filicinum*, *Oxyrrhynchium speciosum*, *Plagiomnium elatum*, and *P. undulatum*. Moreover, species that prefer bare mineral soil (e.g., *Barbula unguiculata*, *Dicranella schreberiana*, and *O. hians*) occurred, while species that grow on protruding boulders (*Sciuro-hypnum populeum*) and terrestrial habitats, spread from neighboring forest communities (e.g., *Hypnum cupressiforme*, *Polytrichastrum formosum*, *Plagiomnium affine*, and *Sanionia uncinata*). However, most did not present high fidelity in particular groups of plots.

Analysis of the floristic similarities between phytocoenoses showed the relative separation of the phytocoenoses with the domination of *P. hybridus* and 18 plots with domination of *P. kablikianus* (Fig. 3). Within particular clusters, the patches with both butterburs (mixed ones) coexist with patches with one dominant. No geographic clustering of the plots was observed.

The altitudinal range of particular phytocoenose groups varied from 418 to 1,015 m a.s.l. (Pk group), from 414 to 970 m a.s.l. (Pk/Ph group), from 392 to 848 m a.s.l. (Ph/Pk group), and from 352 to 785 m a.s.l. (Ph group) (Fig. 4).
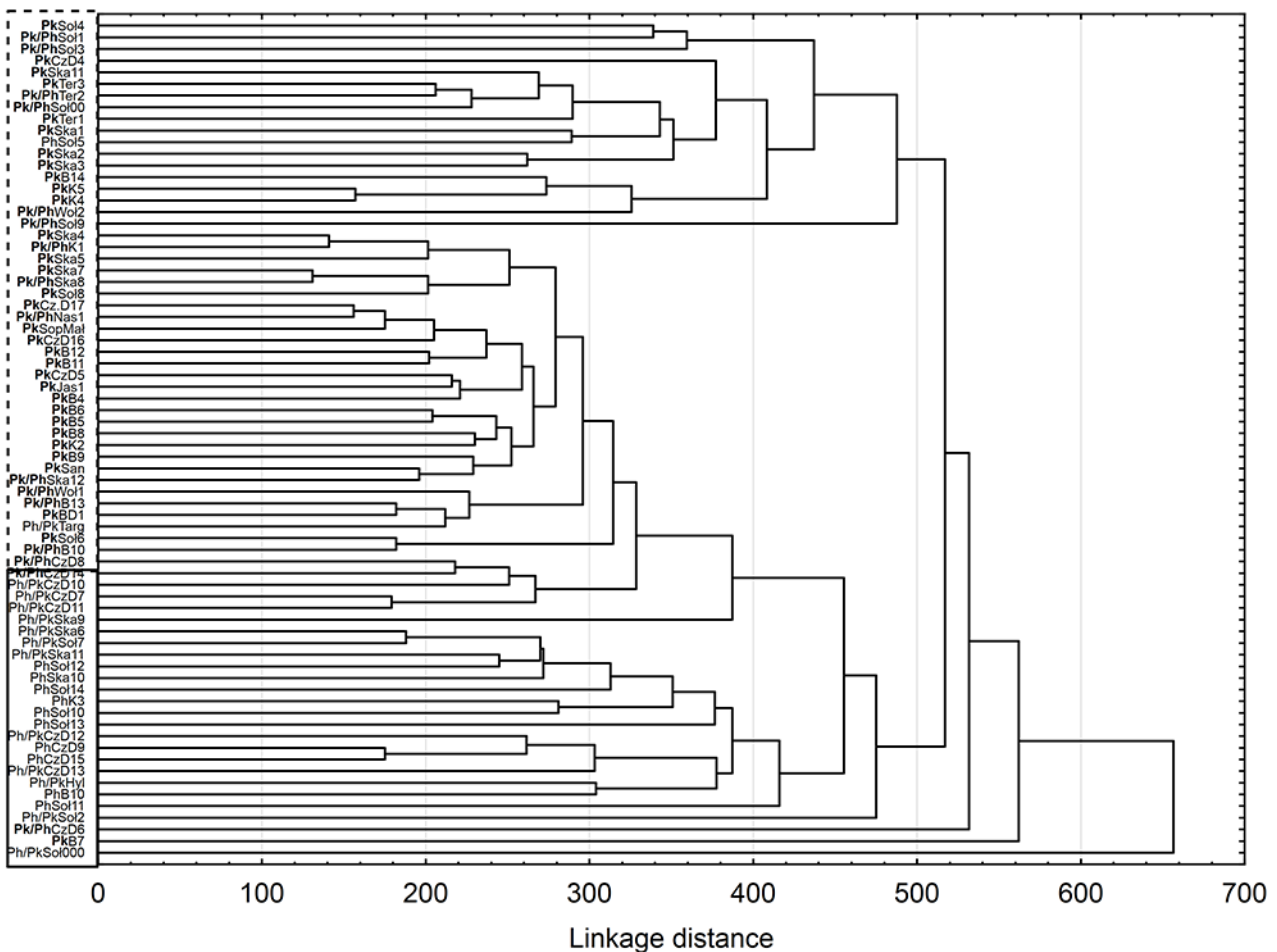

Fig. 3 Floristic similarity of the analyzed plots (data: coverage of species; Manhattan distance, UPGMA method). Ph – plots with *P. hybridus*; Ph/Pk – mixed plots with *P. hybridus* as the dominant; Pk – plots with *P. kablikianus*; Pk/Ph – mixed plots with *P. kablikianus* as the dominant; letters indicate the location (see Appendix S1); bold letters and a dotted line represent the Pk and Pk/Ph groups; a continuous line represents the Ph and Ph/Pk groups.
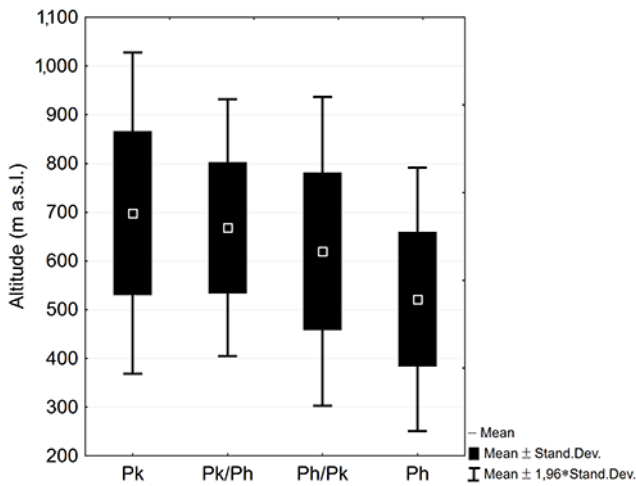
Fig. 4 Altitudinal ranges of the analyzed groups of plots with *P. kablikianus* as the only dominant (Pk), mixed plots with a dominance of *P. kablikianus* (Pk/Ph), mixed plots with a dominance of *P. hybridus* (Ph/Pk), and with *P. hybridus* as the only dominant (Ph); differences between two groups with a particular dominant (Pk + Pk/Ph) and (Ph + Ph/Pk) are statistically significant $p < 0.05$.

Analysis of the correlation between the coverage of both butterburs and altitude a.s.l. revealed that the two species were significantly and negatively correlated with each other ($r = -0.8$), and were significantly correlated with altitude, although the correlation coefficient was much lower: $r = 0.3$ for *P. kablikianus* and $r = -0.3$ for *P. hybridus* (Tab. 2). Therefore, this suggests that factors other than climate impact the substitution of both butterburs in alluvial habitats.

Coverage of *P. kablikianus* was also significantly correlated with the percentage of skeleton in soil substratum, available magnesium and total nitrogen content, humification coefficient (C:N), oxidizable carbon, and organic matter. Coverage of *P. hybridus* was significantly correlated with all aforementioned variables, with the exception of the latter two (Tab. 2, Tab. 3).

Among the analyzed features and factors of habitat structure, only patch width, percentage of skeleton, and the fraction of clay in soil significantly differentiated both types of phytocoenoses (Fig. 5A–C).

In turn, among the features that illustrate the soil properties of the analyzed plots, only the content of magnesium, nitrogen, and humus expressed in the humification coefficient (C:N) changed gradually or in pairs of patch groups. The differences between both types of plots (dominated by each of the analyzed species) and in extreme groups were statistically significant (Fig. 6A–C).

The other factors analyzed were not statistically significant in both variants of the analysis, although some intergroup differences were observed.

The results of the PCA with respect to the geomorphological characteristics of the habitat (Fig. 7A) and the soil contents (Fig. 8A) showed that most of the analyzed factors determine the occurrence of *P. kablikianus* more clearly than *P. hybridus*. In the former, the phytocoenoses with *P. hybridus* were distinguished by a greater content of dust and clay particles in the soil, and the cover of this species was negatively correlated with skeleton content and, to a lesser degree, with elevation of patch surface above the average water level and width of plot. While the other features were more clearly related to the presence of *P. kablikianus*, the first two factors described only 52% of the total variation (Fig. 7A).

Tab. 2 Correlation matrix of following variables: coverage of both *Petasites* sp., altitude a.s.l., width of patches (width), elevation above the average water level (height), width of flooded zone (zone), distance from the main current of water (current) and elements of the soil structure.

	P. hybridus	P. kablikianus	Altitude	Width	Height	Zone	Current	% skeleton	Sand	Clay	Dust
P. hybridus	1.00										
P. kablikianus	−0.85*	1.00									
Altitude	−0.80*	0.30*	1.00								
Width	−0.21	0.22	0.25*	1.00							
Height	−0.10	0.08	0.10	0.06	1.00						
Zone	−0.15	0.11	−0.15	−0.14	−0.06	1.00					
Current	−0.09	−0.02	−0.05	−0.15	−0.06	0.74*	1.00				
% skeleton	−0.47*	0.41*	0.05	−0.02	0.23*	0.12	0.05	1.00			
Sand	−0.13	0.09	−0.06	0.23	−0.04	0.13	0.18	−0.105	1.00		
Clay	0.23	−0.18	−0.19	−0.16	−0.04	−0.08	−0.18	0.065	−0.88*	1.00	
Dust	0.01	0.01	0.29*	−0.25*	0.11	−0.15	−0.13	0.11	−0.88*	0.55*	1.00

Significant correlations are marked by asterisks.

Tab. 3   Correlation matrix of coverage of both *Petasites* sp. and parameters of chemical structure of the soil.

	P. hybridus	*P. kablikinus*	pH	P_2O_5	MgO	K_2O	Org. mat.	C	N	C/N
P. hybridus	1.00									
P. kablikianus	−0.85*	1.00								
pH	0.33	−0.35	1.00							
P_2O_5	−0.09	0.17	0.10	1.00						
MgO	−0.48*	0.47*	0.12	0.36*	1.00					
K_2O	−0.34	0.33	−0.42*	−0.01	0.54*	1.00				
Org. mat.	−0.34	0.57*	−0.40*	−0.03	0.11	0.20	1.00			
C	−0.32	0.55*	−0.40*	−0.07	0.095	0.20	0.99*	1.00		
N	−0.37*	0.53*	−0.34	−0.03	−0.025	0.11	0.87*	0.87*	1.00	
C/N	0.46*	−0.54*	0.29	0.05	−0.19	−0.10	−0.41*	−0.41*	−0.46*	1.00

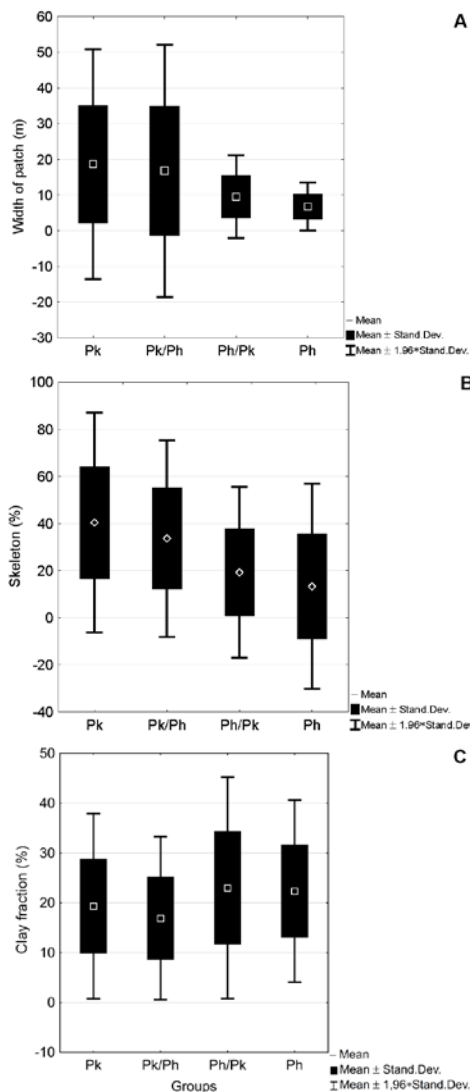Significant correlations are marked by asterisks. Org. mat. – organic matter.

Fig. 5   Differentiation of habitat factors in groups of analyzed plots with *P. kablikianus* as the only dominant (Pk), mixed plots with a dominance of *P. kablikianus* (Pk/Ph), mixed plots with a dominance of *P. hybridus* (Ph/Pk), and with *P. hybridus* as the only dominant (Ph). Differences between the groups (Pk + Pk/Ph) and (Ph/Pk + Ph) are statistically significant: (**A**) $p < 0.05$; (**B**) $p < 0.001$; (**C**) $p = 0.05$.
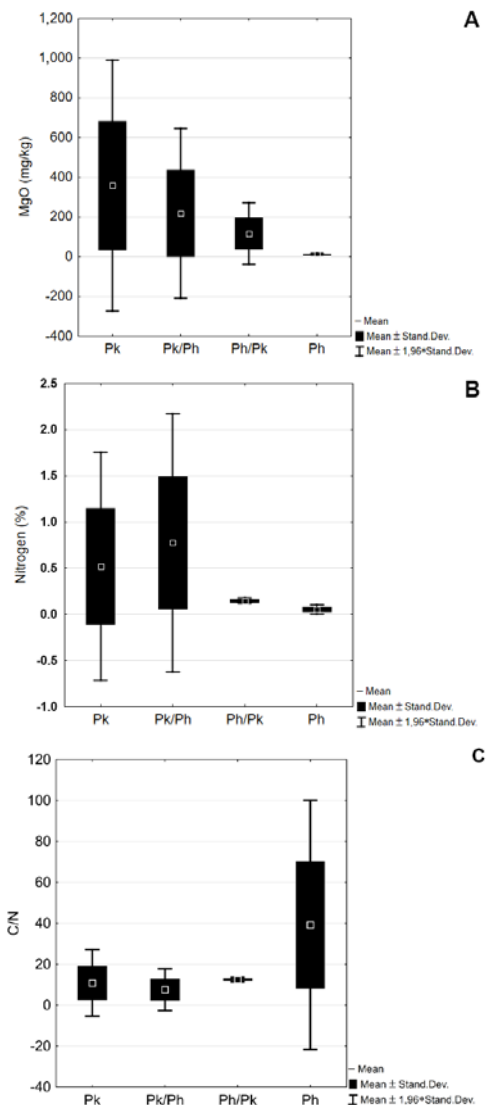

Fig. 6   Differentiation of the chemical soil parameters in groups of analyzed plots with *P. kablikianus* as the only dominant (Pk), mixed plots with a dominance of *P. kablikianus* (Pk/Ph), mixed plots with a dominance of *P. hybridus* (Ph/Pk), and with *P. hybridus* as the only dominant (Ph). Differences between groups are statistically significant: (**A**) $p < 0.01$; (**B**) $p < 0.01$; (**C**) $p < 0.01$.
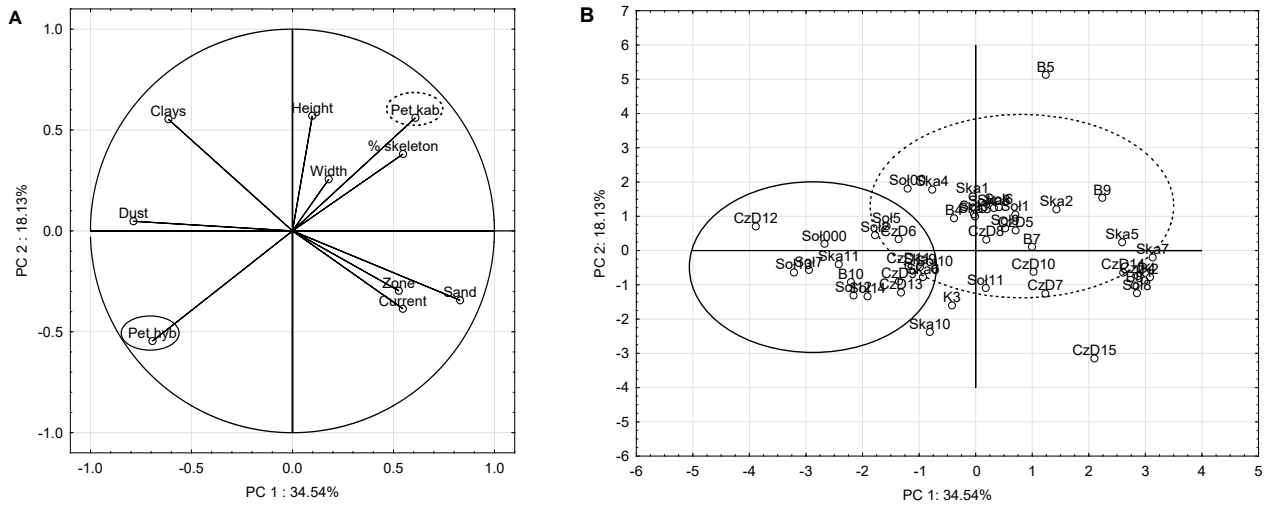
Fig. 7 Principal component analysis (PCA) ordination diagram of habitat factors of *Petasites* plots based on (**A**) cover of both of the analyzed species and factors of the habitat structure and (**B**) particular analyzed plots along the first two PCs. Continuous line – group Ph + Ph/Pk; dotted line – group Pk + Pk/Ph. Plot B5 is classified in the Pk group and CzD15 in the Ph group.
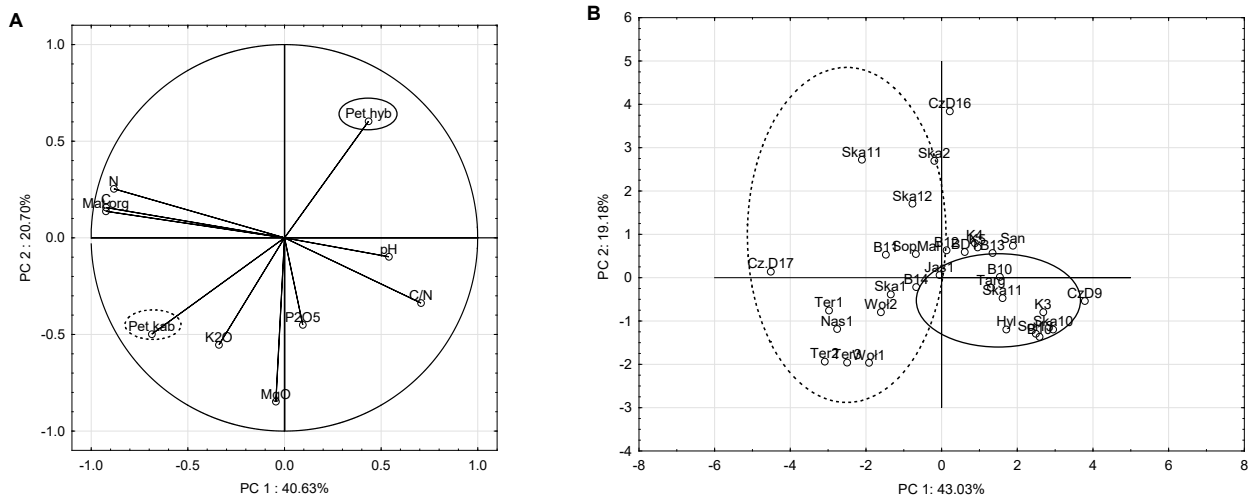

Fig. 8 PCA ordination diagram of chemical soil parameters of *Petasites* plots based on (**A**) the cover of both of the analyzed species and factors of the chemical soil composition and (**B**) particular analyzed plots along the first two PCs. Continuous line – group Ph + Ph/Pk; dotted line – group Pk + Pk/Ph.

The PCA for the chemical content of the soil showed a similar set of features. In this case, only the humus content, which was expressed by the humification factor (C:N), distinguished the phytocoenoses with *P. hybridus*. The remaining features determined the presence of *P. kablikianus*, whereas the first two factors described 61% of the total variability (Fig. 8A). Moreover, in both variants of the PCA, all plots analyzed were grouped into two types of phytocoenoses, both dominated by one of the *Petasites* sp. (Fig. 7B, Fig. 8B).

In summary, both analyzed species exhibited clearly different habitat preferences, which were related to select habitat features including the granulometric composition of the soil substratum, the content of available magnesium and nitrogen, as well as the associated amount of humus.

Discussion

Each of four groups of phytocoenoses with *Petasites* sp. were clearly distinguished by their own groups of plants. However, they should not be treated as diagnostic species,

because both Pk, Pk+Ph and Ph, Ph+Pk groups were ecological groups of species rather than phytosociological units. They included tall herb communities as well as forests with *Petasites* sp. in the herb layer. The ecological diversity of the noted species was due to the habitats of both butterbur communities being characterized by large mosaics of microhabitats. They also reflected the altitudinal range of particular groups and adjacent vegetation. In the groups with *P. kablikianus*, typical mountain species occurred, and in the groups with *P. hybridus*, the species characteristic to meadows, riparian forests, or even alien and synanthropic species were more frequent. Such floristic composition confirmed recent findings that emphasized the role of both deterministic responses to environmental gradients and stochastic processes [43]. The conditions observed in each phytosociological relevé were the result of habitat heterogeneity on this small scale. The nature of differential species responses to climate and other habitat factors is complex [44]. Most species reveal a wide ecological spectrum and adaptive potential, and may therefore present different but similar plant associations. In this case, species common in distinguished groups in other mountain regions occurred in communities in which another butterbur was dominant, e.g., *Chrysosplenium alternifolium* or *I. noli-tangere*, in our study were mostly associated with the Pk and Pk+Ph groups of phytocoenoses, but in the mountains of Slovakia, the Czech Republik, or Romania were strongly associated with *P. hybridi* [45–48]. Nevertheless, many species presented the same altitudinal distribution as stated by Kalniková et al. in the Czech Carpathians [49].

Both of the analyzed species revealed some tolerance to certain habitat factors that enabled them to coexist in the same patches of vegetation on the stream banks. Yet, both exhibited a distinct habitat antagonism, at least in relation to the skeleton content in the soil (the factor determining substratum texture) and the content of Mg and N. The skeleton content in the soil and the variability of granulometric structure is closely related to the dynamics of floods and the geomorphological activity of the streams. With rapid floods in the river valley, coarse (skeletal) material is deposited in the initial run of the river. With a decrease in height a.s.l., the floodwaters lose strength, thus transporting much finer material that settles on the alluvia [1,50]. Therefore, *P. kablikianus* prefers stronger skeletal soils with a higher sand content, which are also typical for its subalpine localities. Conversely, *P. hybridus* prefers finer soils, which are richer in pulverized and clay fractions.

The same relationship is associated with the width of plant patches. In higher locations, vegetation plots are wider than in lower plots. In many cases, they overgrow entire stony islands in the streambed. In the *P. hybridus* distribution zone, its communities form narrow vegetation bands along river banks. This is mainly associated with human pressure, including the development of valleys, exploitation of gravel, and the regulation of streambanks.

Regarding magnesium and nitrogen, river basins are usually rich in both elements [50], but their content may decrease in the topsoil due to denudation processes and rinsing. By nature, in properly functioning river valleys, periodic floods enrich the soil with nutrients, including the nutrients contained in the water. During strong anthropopressure, which results in deeper river beds and regulated banks, the alluvia are reduced [1]. Therefore, the vegetation patches become narrower; thus, the reduced occurrence of floods may have led to a decrease in the nutrient content in the middle and lower reaches of the rivers. Moreover, the middle and lower parts of riverbanks are the most affected by flood control (*P. hybridus* area) [51].

As shown by the data, *P. kablikianus* occurred separately on soils that are rich in magnesium and nitrogen, and in carbon and organic matter. *Petasites hybridus* occurred in lower parts of river valleys, on alluvial soils in a zone with decreased soil richness, but with a thick layer of humus (especially in forest plots), which was less developed in patches dominated by *P. kablikianus*. In higher locations, this species was associated with initial alluvial soils.

Phytocoenoses with *P. hybridus* were characterized by unusually high C:N ratios, ranging from 14 to 92 (median 29.7), whereas for phytocoenoses with *P. kablikianus*, the ratio was in the range of 1.9 to 33 (median 9.65). A ratio higher than 24 is thought to result in the immobilization of nitrogen and thus, in a significant deficit for plants. The rates of denitrification are high on the surface of riparian soils when organic matter and nitrates are high [50]. The contrasting situation results in an increase in the availability of nitrogen (faster mineralization), and may also be related to the higher

share of nitrophilous species, which with low fidelity accompany *P. kablikianus*, and along with it subside from the habitats with the decreasing nitrogen content. This significant deficit in nitrogen content in the substrate on which the *P. hybridus* patches were present, may be bound to the limitation of floods and the limited input of the organic compounds into the habitats. However, Šoltés and Ciriaková [52] described this butterbur as a nitrophilous species in Slovakia, which was significantly correlated with the content of NO_3 in the soil.

The greater floristic richness, with the almost constant number of species in the patch in all four groups, in phytocoenoses dominated by *P. kablikianus*, as it was mentioned above, was probably more related to the greater variety of adjacent habitats, which are the source of propagules than to N content in the soil. In lower locations, within the distribution range of *P. hybridus*, greater anthropopressure, smaller biological diversity of communities occurring in the valley, may affect the greater similarity of floristic composition of phytocoenoses with general impoverishment of the species pool.

When analyzing the occurrence of both species in Poland and Europe, the differences in the coverage and number of locations [37] may suggest that *P. hybridus* has a wider ecological spectrum than *P. kablikianus*. This leads to the conclusion that *P. kablikianus* is a species of alpine origin that uses alluvial habitats as natural but secondary habitats. Additionally, for *P. hybridus*, the riparian habitats are only one type of habitat it occupies in mountain regions. Both butterburs share the area based on a specific pattern in order to colonize areas with the appropriate habitat conditions. Therefore, recognizing the theory that *P. kablikianus* is an alpine species that presently has been spreading on lower areas [36], we should assume that the presence and competition from *P. hybridus* are not limiting factors for the spread of glabrous butterbur. *Petasites kablikianus* has more specific habitat requirements and is distributed in the river valleys; it is mainly limited by the habitat quality that results from the geomorphological activity of the watercourse.

Although it is not unreasonable to qualify the two analyzed species as "altitudinal vicariants" [33,36], the term "ecological vicariants" appears to be more appropriate, because the habitat characteristics that are associated with the geomorphological activity of the stream are more important for determining their distribution on alluvial sites than the climatic conditions related to altitude a.s.l. The structure and chemical properties of the substrate represent the key factors.

Limited distribution range on the mountain areas, significant human interference in the shape of the streambanks that decreases the number of natural floods, and the spontaneous creation of habitats on which *P. kablikianus* is a typical pioneer [36] and can colonize them, means that this species is clearly threatened by human activity and is worth monitoring and even protecting.

Conclusions

- The species analyzed were not typical altitudinal vicariants but rather ecological vicariants and, in terms of some factors, habitat antagonists.
- Both species, which have a much broader ecological spectrum than only riverside habitats, inhabit them on given altitude zones due to favorable habitat characteristics.
- Lowering the range of *P. kablikianus* in river habitats is inhibited by several habitat factors that are gradually changing, and are the result of human activity rather than competition from *P. hybridus*.

Supplementary material

The following supplementary material for this article is available at http://pbsociety.org.pl/journals/index.php/asbp/rt/suppFiles/asbp.3590/0:

Appendix S1   Geographical and geomorphological characteristics of the studied plots.

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