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Article

The Perspective of Arctic-Alpine Species in Southernmost Localities: *Kalmia procumbens* Example in the Pyrenees and Carpathians

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Abstract: The high-mountain and arctic plants are considered especially sensitive to the climate changes because of close adaptations to the cold environment. *Kalmia procumbens*, the typical arctic-alpine species reaches southernmost European localities in the Pyrenees and Carpathians. The aim of the study was the assessment and comparison of *K. procumbens* current potential niche areas in the Pyrenees and Carpathians and their possible reduction due to climate change, depending on the scenario. Realized niches of *K. procumbens* in the Pyrenees are compact while in the Carpathians dispersed. In both mountain chains, the species occurs in the alpine and subalpine vegetation belts, going down to elevations of about 1500-1600 m, while the most elevated localities in the Pyrenees are at ca 3000 m, about 500 m higher than in the Carpathians. The localities of *K. procumbens* in the Carpathians have a more continental climate than in the Pyrenees, with lower precipitation and temperatures but higher seasonality of temperature and of precipitation. The species covered a larger area of geographic distribution during Last Glacial, and reduced area during mid Holocene. Due to the climate warming, the strong reduction of potential area of occurrence to 2100 is expected in the Carpathians and moderate reduction in in the Pyrenees.

Keywords: biogeography; climate change; ecological niche modeling; geographic range; relict plant

1. Introduction

The origin of cold-adapted plant species and the formation of tundra in northern Europe, Asia and North America took place in turn of the Pliocene/Pleistocene [1–3] as a reaction of the plant cover to the climate cooling. The plants adapted to the low temperatures and short vegetation period in the Arctic zone and in the high mountains in southern-more regions evolved during approximately similar periods [3]. The Arctic plants reached mountains in the central Europe, Asia and North America escaping to the south before Pleistocene glaciers [1]. Inversely, the alpine plants could migrate to the North in the periglacial zone during deglaciations [4], as in the case of retreating glaciers, observed during the last centuries in the Alps [5]. During interglacial periods of Pleistocene (Holocene including), the plant species connected with the cold climate could survive only in the Arctic and in the high mountains above the timberline, sometimes also on mires at lower altitudes [6–8], being the glacial relicts [9,10].

The high-mountain and arctic plant species are considered to be especially sensitive to the climate changes because of close adaptations to the cold environment [11].The high temperatures and low humidity are expected to be the most important threats [12–19]. High risk results also from the forest line shift and expansion of trees, high shrubs and herbs, which could colonize or at least shade the sites of light-demanding tundra and alpine plant species [20–24].

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Kalmia procumbens (L.) Gift & Kron & P.F.Stevens is an arctic-alpine, circum-polar, amphi-Atlantic plant [25–27]. It is an evergreen, dwarf, prostrate shrub, frequently creeping to the ground, especially at high elevations. In northern Europe and in the mountains it prefers the rocky ridges [24,28]. In Europe, it reaches its southernmost localities in the Pyrenees, Alps, northern Dinaric Alps and Carpathians. The species is one of the typical cold-adapted, glacial relicts in the Central-European mountains [29,30]. Despite, it can survive in temperatures above 50 °C with very high diurnal amplitude of temperatures [31].

In the Pyrenees and in the Carpathians, *K. procumbens* localities are confined predominantly to the alpine and sometimes to the subalpine vegetation belts, at lower locations connected mainly with the north-facing slopes [32–34], with relatively shorter vegetation period, lower temperatures and temperature amplitudes comparing to the south expositions [35–38]. It is stress-tolerant, adapted to extreme conditions of existence, characterized by slow growth in a relatively long growing season [39]. The formation of the photosynthetic apparatus is aimed at the minimum return of energy, which contributes to the conservation of resources. The population structure is dominated by plants of mature (generative) stages [40]. It prefers rocky ridges with small snow deposition during winter [28,38]. Such characteristics indicate that the species, although resistant to external influences, recovers rather slowly when it loses its position. The sites of *K. procumbens* are susceptible to influence of the global climate change [28,38,41]. Despite that, the last observations indicated its more intense growth in the mountains of the Japan islands [42] and even expansion in the Ukrainian Carpathians resulting from the reduction of snow cover [21]. The species had a broader potential ecological niche area at the global scale during Last Glacial Maximum (LGM) than at present [41].

The study aimed to assess and compare *K. procumbens* current potential niche areas in the Pyrenees and Carpathians and their possible reduction due to climate change depending on the scenario. Additionally, the retrospection of its' local, Carpathians' and Pyrenean geographic ranges during Last Glacial Maximum (LGM) was analysed, based on the most probable high level of ecological niche conservatism in plants [43–45]. We expected the Carpathian populations would be more prone to the temperature rise and extension of the vegetation period than Pyrenean ones.

2. Results

2.1. Realized geographic niches

The distribution of *K. procumbens* in the Pyrenees and in the Carpathians is connected with the most elevated mountain massifs (Figure 1). The species has a more compact distribution of their localities in the Pyrenees than in the Carpathians. The altitudinal range in the Pyrenees is broader than in the Carpathians. The altitudinal minima in both mountain systems are similar, but the most elevated localities in the Pyrenees have reached about 400-500 m higher elevations than in the Carpathians (Figure 2). Current range of species differ from the potential range in LGM (Figure S1), when the Carpathian arc was more suitable for the species, whereas conditions in the Pyrenees were less suitable.

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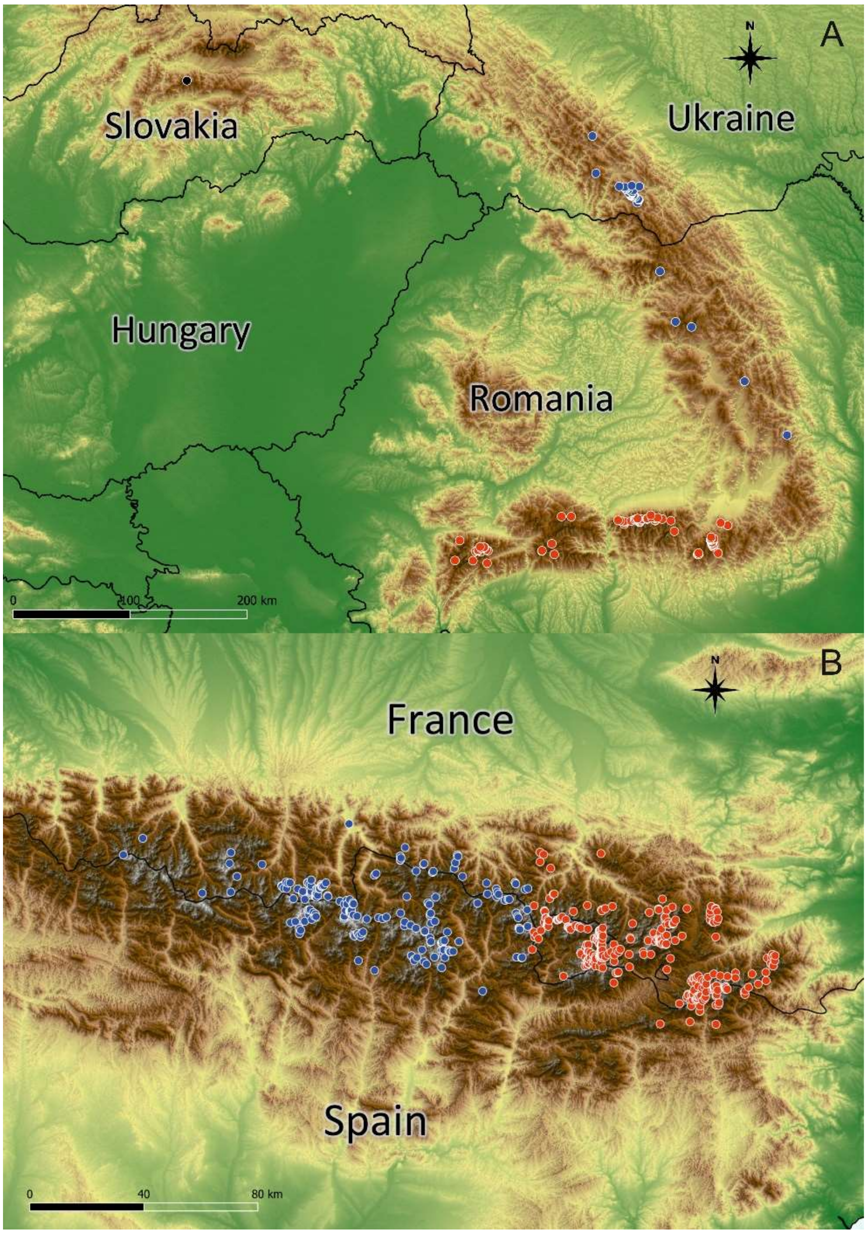

Figure 1. Geographical distribution of *Kalmia procumbens* on the basis of georeferenced data in the Carpathians (a): blue dots – East Carpathians, red dots – South Carpathians; and in the Pyrenees (b): blue dots –West Pyrenees, red dots – East Pyrenees.

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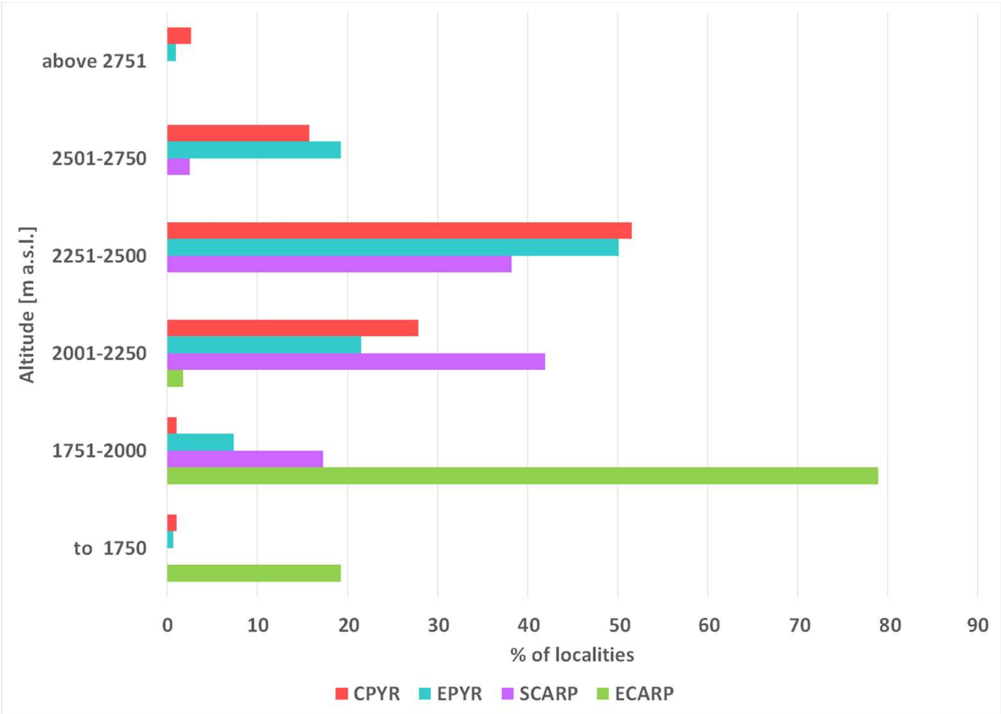

Figure 2. Vertical distribution of *Kalmia procumbens* localities in the Pyrenees: CPYR – Central and EPYR – East Pyrenees and in Carpathians SCARP – South and ECARP – East Carpathians.

Current potential niches of *K. procumbens* in the Pyrenees and Carpathians are determined first of all by elevation, which influences to the current distribution of the species attain nearly 80% in the Pyrenees and 60% in the Carpathians (Table 1). From the climatic variables, only precipitation of the driest month (bio 14) influences at a relatively high degree in both mountain chains (Table 1). Additional important bioclimatic factor, which influences the potential niche of *K. procumbens* reaching 1% or more is the temperature mean diurnal range (bio2), temperature annual range (bio7), and precipitation of the driest quarter (bio17) in the Pyrenees, and annual mean temperature (bio1), temperature seasonality (bio4) precipitation seasonality (bio15) and precipitation of warmest quarter (bio18) in the Carpathians (Table 1).

Table 1. Contribution [%] of bioclimatic variables and altitude to the realized habitats suitable for *Kalmia procumbens* in the Pyrenees (**PYR**), Central Pyrenees (CPYR), East Pyrenees (EPYR and in the Carpathians (**CARP**), East Carpatians (ECARP) and South Carpathians (SCARP); values of 1.0 and higher bolded.

	Bioclimatic factor	CPYR	EPYR	**PYR**	ECARP	SCARP	**CARP**
	AUC	0.994	0.991	0.993	0.999	0.997	0.998
Bio1	Annual Mean Temperature	0.1	0.1	0.1	**2.0**	0.3	**1.3**
Bio2	Mean Diurnal Range	**4.1**	0.9	**2.5**	0.1	0.0	0.1
Bio3	Isothermality	0.6	0.2	0.4	**1.7**	0.0	0.9
Bio4	Temperature Seasonality	0.3	0.2	0.3	**4.7**	0.0	**2.4**
Bio5	Max Temperature of Warmest Month	0.7	0.3	0.5	0.1	0.1	0.1
Bio6	Min Temperature of Coldest Month	0.3	0.0	0.2	0.2	0.2	0.2

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Bio7	Temperature Annual Range	**1.0**	**1.0**	**1.0**	0.1	0.0	0.1
Bio8	Mean Temperature of Wettest Quarter	0.4	**2.0**	**1.2**	0.2	0.2	0.2
Bio9	Mean Temperature of Driest Quarter	**3.8**	**6.0**	**4.9**	**5.5**	**8.2**	**6.9**
Bio10	Mean Temperature of Warmest Quarter	0.2	0.1	0.2	0.1	0.1	0.1
Bio11	Mean Temperature of Coldest Quarter	0.1	0.1	0.1	0.2	0.2	0.2
Bio12	Annual Precipitation	0.6	0.2	0.4	0.1	0.0	0.1
Bio13	Precipitation of Wettest Month	0.1	0.3	0.2	0.0	0.0	0.0
Bio14	Precipitation of Driest Month	**1.1**	0.4	0.8	0.0	0.1	0.1
Bio15	Precipitation Seasonality	0.3	0.1	0.2	**3.4**	**10.0**	**6.7**
Bio16	Precipitation of Wettest Quarter	0.3	**1.2**	0.8	0.0	0.0	0.0
Bio17	Precipitation of Driest Quarter	**7.8**	**6.2**	**7.0**	0.1	0.0	0.1
Bio18	Precipitation of Warmest Quarter	0.1	0.1	0.1	**31.1**	**9.9**	**20.5**
Bio19	Precipitation of Coldest Quarter	0.5	0.5	0.5	0.2	0.1	0.2
	Elevation	**77.6**	**80.2**	**78.9**	**50.1**	**70.4**	**60.3**

The average values of every bioclimatic factor differed at a statistically significant level ($p<0.05$) between localities of *K. procumbens* in the South and East Carpathians (the latter include also one locality from the West Carpathians) (Table 2). The East Carpathian region of *K. procumbens* occurrence has generally higher precipitation (bio12 – bio19) and is characterized by slightly but statistically significantly lower temperature factors (bio1, bio5, bio6, bio8 – bio 11) than South-Carpathian (Table 2). Populations from Carphatians occur most often in the North-eastern exposition, whereas in the Pyrenees in the North exposition (Figure S2).

Table 2. Average values of bioclimatic variables in the studied regions. According to the Mann-Whitney test, all differences between the Pyrenees and the Carpathians (bolded) are significant ($p<0.05$), as are the differences between the Southern (SCARP) and Western (ECARP) Carpathians. For Eastern (EPYR) and Central (CPYR) Pyrenees, statistically significant differences ($p<0.05$) were observed for bio2, bio3, bio5, bio7, bio12, bio13, bio14, bio15, bio16, bio17, bio18 and bio19 (shaded).

Bioclimatic factor		CPYR	EPYR	**Pyrenees**	ECARP	SCARP	**Carpathians**
bio1	Annual Mean Temperature	2.37	2.40	**2.39**	1.07	-0.25	**0.30**
bio2	Mean Diurnal Range	9.27	8.67	**8.90**	6.91	7.16	**7.06**

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bio3	Isothermality	33.79	32.62	**33.07**	27.73	29.06	**28.52**
bio4	Temperature Seasonality	649.33	646.56	**647.61**	684.48	657.93	**668.81**
bio5	Max Temperature of Warmest Month	18.69	18.14	**18.35**	13.92	12.52	**13.10**
bio6	Min Temperature of Coldest Month	-8.73	-8.44	**-8.55**	-10.99	-12.08	**-11.62**
bio7	Temperature Annual Range	27.43	26.58	**26.90**	24.91	24.60	**24.73**
bio8	Mean Temperature of Wettest Quarter	-0.62	-0.30	**-0.42**	8.98	6.84	**7.73**
bio9	Mean Temperature of Driest Quarter	10.80	10.78	**10.79**	-6.81	-8.02	**-7.51**
bio10	Mean Temperature of Warmest Quarter	10.93	10.89	**10.90**	9.36	7.83	**8.46**
bio11	Mean Temperature of Coldest Quarter	-4.71	-4.60	**-4.64**	-7.19	-8.14	**-7.74**
bio12	Annual Precipitation	1434.57	1447.54	**1442.62**	1274.90	934.12	**1075.62**
bio13	Precipitation of Wettest Month	154.04	161.53	**158.69**	167.76	132.44	**147.06**
bio14	Precipitation of Driest Month	75.71	68.17	**71.03**	65.56	46.75	**54.58**
bio15	Precipitation Seasonality	20.19	23.53	**22.27**	32.36	39.56	**36.57**
bio16	Precipitation of Wettest Quarter	430.82	457.02	**447.08**	462.96	363.02	**404.52**
bio17	Precipitation of Driest Quarter	263.48	251.75	**256.20**	221.51	149.49	**179.33**
bio18	Precipitation of Warmest Quarter	263.57	251.91	**256.33**	462.67	358.05	**401.49**
bio19	Precipitation of Coldest Quarter	388.06	399.96	**395.45**	228.93	149.75	**182.63**

Principal Component Analysis (PCA) of the bioclimatic factors for *K. procumbens* realized niches indicated separate grouping of Carpathian and Pyrenean localities. The East Carpathian localities are well separated from the South Carpathian ones, while Central Pyrenean localities in the great part intermixed East Pyrenean ones (Figure 3). The potential ecological niches estimated on the basis of the species localities in Central and East Pyrenees recognized the realized niches in both Pyrenean regions (Figure 4). Inversely, the potential niche of *K. procumbens* estimated on the East Carpathian localities recognized realized niche in the East Carpathians, but not in the South Carpathians. Additionally, this combination indicated also highly suitable conditions in the Tatra Mts. in the West Carpathians, where only one natural locality of the species currently exists. The potential ecological niche of *K. procumbens* estimated on the South Carpathian localities did not detect suitable environmental conditions for the species occurrence neither in the East, nor in the West Carpathians (Figure 4).

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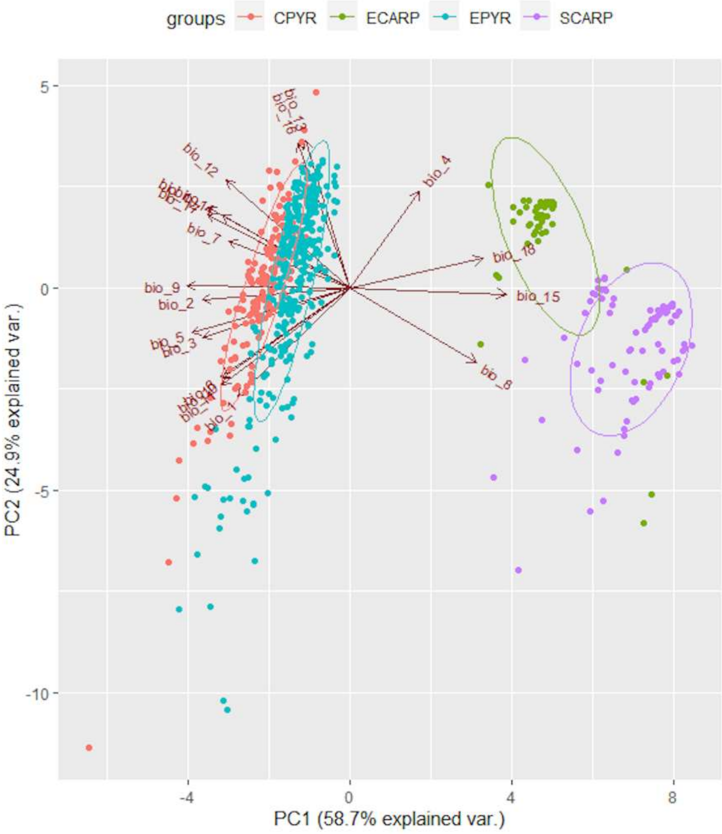

Figure 3. Position of localities of *Kalmia procumbens* from Central Pyrenees (CPYR), East Pyrenees (EPYR), East Carpathians (ECARP) and South Carpatians (SCARP) in PCA on the basis of bioclimatic variables (acronyms as in Table 1); ellipses indicate the 95% confidence intervals.

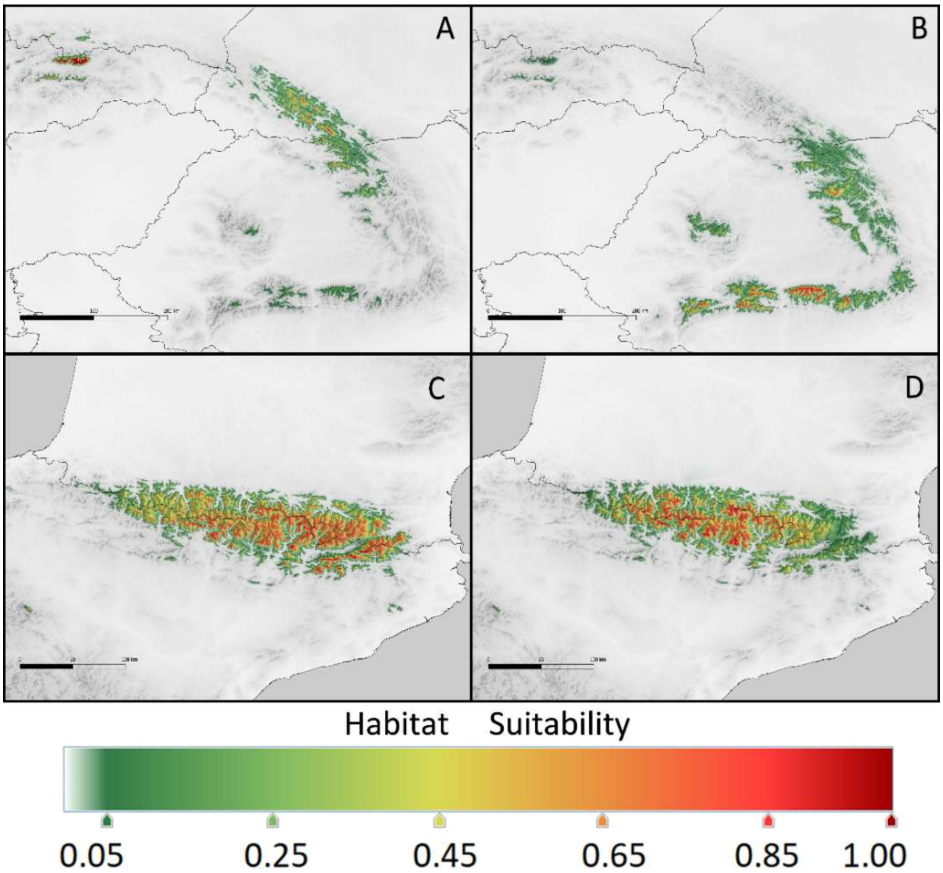

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Figure 4. Current potential range of *Kalmia procumbens* in the Carpathians (a and b) estimated using: a – environmental conditions from the East Carpathians, b – from the South Carpathians; in the Pyrenees (c and d) using: c – conditions from the East Pyrenees, d – from the Central Pyrenees.

2.2. Future geographic niches

The potential niches highly suitable for *K. procumbens* in the Carpathians completely disappear in 2100, independently of the scenario of climate warming. Only not many South Carpathian populations could persist, mainly in the Fagarash, while the East Carpathian ones would not find suitable conditions (Figure 5). The potential niches in 2100 in the Carpathians would be determined in ca. 50% by elevation in the East, and in ca. 70% in the South Carpathians. The next restrictive factor in the East Carpathians would be precipitation of the warmest quarter (bio18), attaining 30% and more (Table 3). The other bioclimate factors influencing the potential niches in 2100 are the same as current (compare Tables 1 and 3), but values are slightly smaller.

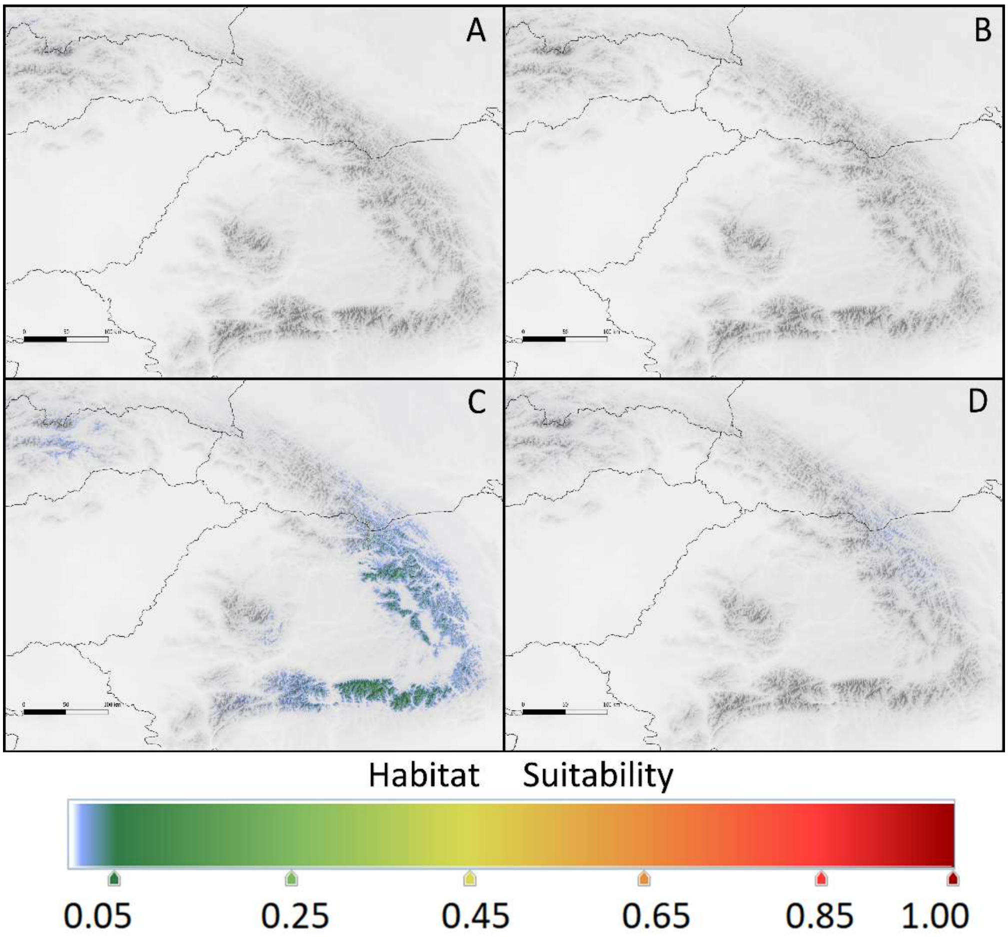

Figure 5. Provided potential range of *Kalmia procumbens* in the Carpathians at 2100 estimated using current environmental conditions from East Carpathians: a – scenario RCP 2.6, b – scenario RCP 8.5, and from South Carpathians: c – scenario RCP 2.6, d – scenario RCP 8.5.

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Table 3. Contribution [%] of bioclimatic variables and altitude to models of future potential range of *Kalmia procumbens* in the Central Pyrenees (CPYR), East Pyrenees (EPYR), East Carpatians (ECARP) and South Carpathians (SCARP); values of 1.0% and higher **bolded**.

	Bioclimatic factor	CPYR		EPYR		ECARP		SCARP	
		RCP 2.6	RCP 8.5	RCP 2.6	RCP 8.5	RCP 2.6	RCP 8.5	RCP 2.6	RCP 8.5
	AUC	0.994	0.994	0.991	0.991	0.999	0.999	0.997	0.997
Bio 1	Annual Mean Temperature	0.0	0.1	0.0	0.0	**1.5**	**1.1**	0.6	0.4
Bio 2	Mean Diurnal Range	**3.9**	**3.1**	0.9	0.9	0.1	0.1	0.0	0.0
Bio 3	Isothermality	0.8	**1.1**	**1.7**	0.1	**2.1**	**2.7**	0.0	0.0
Bio 4	Temperature Seasonality	0.3	0.7	0.2	0.2	**4.2**	**4.9**	0.0	0.1
Bio 5	Max Temperature of Warmest Month	0.8	0.3	0.2	0.5	0.1	0.1	0.1	0.1
Bio 6	Min Temperature of Coldest Month	0.4	0.1	0.1	0.9	0.1	0.1	0.1	0.2
Bio 7	Temperature Annual Range	0.9	0.5	0.4	**1.0**	0.1	0.1	0.0	0.0
Bio 8	Mean Temperature of Wettest Quarter	**1.2**	0.7	0.4	**4.0**	0.0	0.1	0.1	0.2
Bio 9	Mean Temperature of Driest Quarter	**4.3**	**5.5**	**6.4**	**4.0**	**9.5**	**3.8**	**6.6**	**5.9**
Bio 10	Mean Temperature of Warmest Quarter	0.2	0.1	0.1	0.2	0.1	0.0	0.1	0.1
Bio 11	Mean Temperature of Coldest Quarter	0.1	0.0	0.1	0.1	0.3	0.3	0.3	0.2
Bio 12	Annual Precipitation	0.8	0.7	0.4	0.4	0.0	0.1	0.0	0.0
Bio 13	Precipitation of Wettest Month	0.3	0.2	0.1	**1.1**	0.0	0.0	0.1	0.0
Bio 14	Precipitation of Driest Month	**1.0**	**1.0**	0.4	0.5	0.0	0.1	0.0	0.1
Bio 15	Precipitation Seasonality	0.3	0.3	0.0	0.1	**2.0**	**5.4**	**12.1**	**9.8**
Bio 16	Precipitation of Wettest Quarter	0.5	0.3	0.2	0.3	0.0	0.0	0.0	0.0

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Bio 17	Precipitation of Driest Quarter	**7.5**	**8.7**	**7.3**	**5.5**	0.0	0.0	0.0	0.0
Bio 18	Precipitation of Warmest Quarter	0.1	0.1	0.2	0.2	**32.0**	**30.3**	**9.6**	**10.2**
Bio 19	Precipitation of Coldest Quarter	0.4	0.2	0.3	0.2	0.2	0.2	0.2	0.2
	Elevation	**76.1**	**76.4**	**80.5**	**79.9**	**47.5**	**50.5**	**70.0**	**72.4**

In the Pyrenees, the situation of *K. procumbens* populations in 2100 would not be so drastically worse than at present (Figure 6). The environmental conditions in the East Pyrenees allow persist the species populations and even attain broader area of potential niches distribution in the more optimistic scenario (Table 4). In the Central Pyrenees, the potential niche area suitable for *K. procumbens* in the high and very high level would be restricted (Table 4). As currently, the most influential would be the elevation, reaching about 76 and 80% in the Central and East Pyrenees, respectively (Table 3). The remaining bioclimate factors are the same, as determining current ecological niches of the species in the Pyrenees (see Tables 1 and 3).

Table 4. Area of potential range according to the tested model and four sets of stands: CPYR – Central Pyrenees, EPYR – Eastern Pyrenees, ECARP – Eastern Carpathians, SCARP – Southern Carpathians.

Region	Model	Area in the probability levels [hectares]				Total
		Low (0.1-0.25)	Medium (0.25-0.50)	High (0.5-0.75)	Very High (>0.75)	
CPYR	Current	6 099.48	6 545.66	**4 920.93**	**1 288.34**	18 854.41
	RCP 2.6	6 344.43	10 857.13	**420.55**	**16.35**	17 638.46
	RCP 8.5	6 698.12	711.52	**4.67**	**0.00**	7 414.31
EPYR	Current	4 825.15	7 280.36	**8 192.59**	**1 338.57**	21 636.67
	RCP 2.6	5 756.46	5 986.58	**6 773.90**	**5 156.05**	23 672.99
	RCP 8.5	4 482.04	4 812.61	**4 664.27**	**4 470.36**	18 429.28
ECARP	Current	7 406.57	2 796.66	**1 059.53**	**686.48**	11 949.24
	RCP 2.6	0.00	0.00	**0.00**	**0.00**	0.00
	RCP 8.5	0.00	0.00	**0.00**	**0.00**	0.00
SCARP	Current	9 808.72	4 446.85	**2 123.17**	**708.15**	17 086.89
	RCP 2.6	771.79	0.00	**0.00**	**0.00**	771.79
	RCP 8.5	0.00	0.00	**0.00**	**0.00**	0.00

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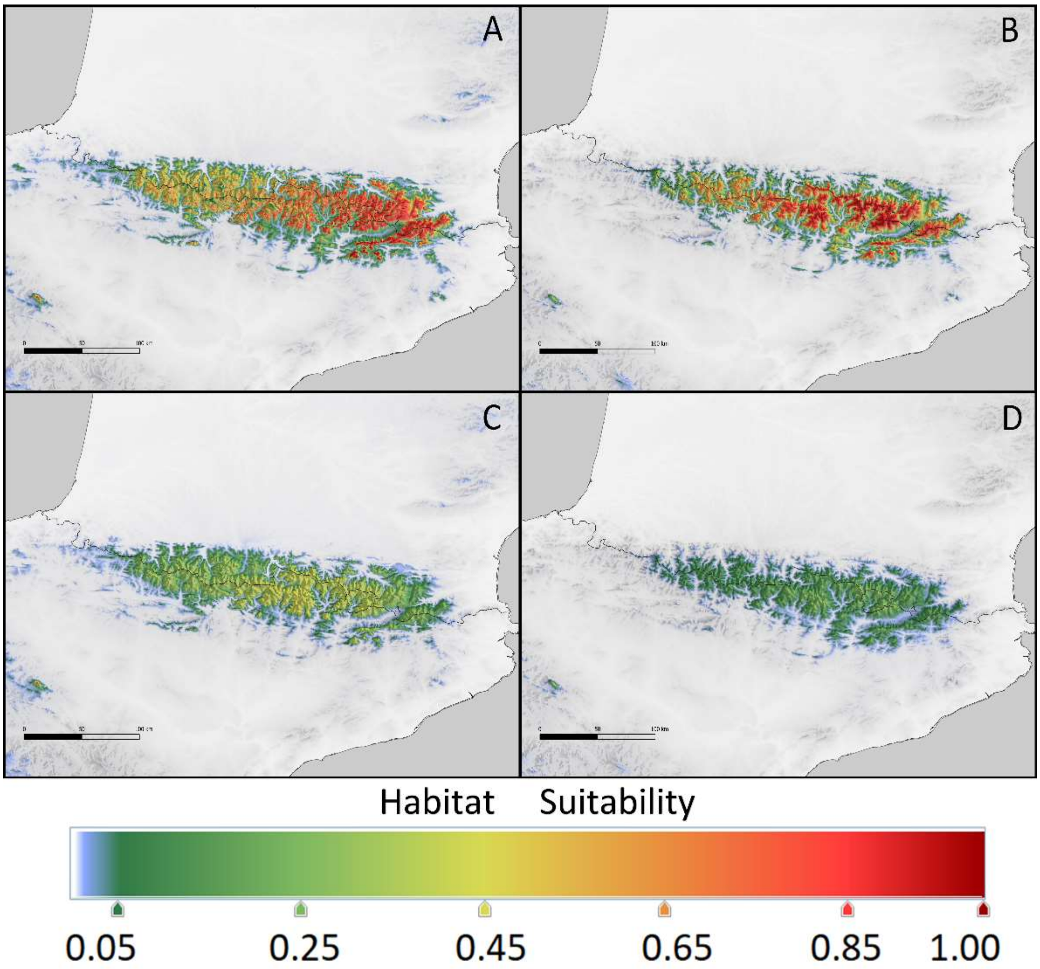

Figure 6. Provided potential range of *Kalmia procumbens* in the Pyrenees at 2100 estimated using current environmental conditions from the East Pyrenees: a – scenario RCP 2.6, b – scenario RCP 8.5 and from the Central Pyrenees: c – scenario RCP 2.6, d – scenario RCP 8.5.

The phytoindication method revealed potential threat to *K. procumbens* occurrence in the East Carpathians in Ukraine. It results mainly from the changes of hydrological regime of the specias sites. The growth of average yearly temperature by 2 °C (pessimistic scenario) put K. procumbens at moderate, while by 3 °C at catastrophic risk of extinction (Figure 7).

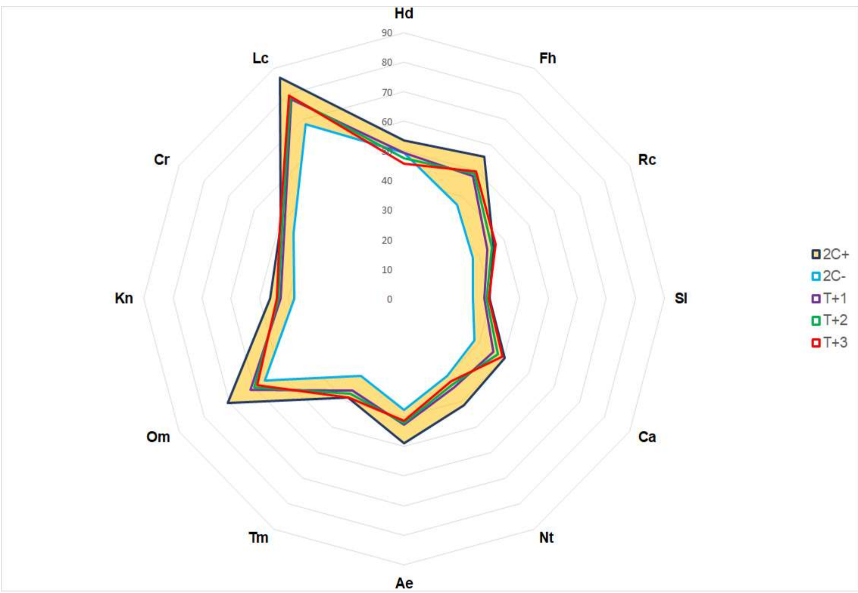

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Figure 7. Percentage values of econiche factors of *Kalmia procumbens* characterisation in the East Carpathians in Ukraine and potential changes depending on temperature changes: +1 °C (T+1), +2 °C (T+2) and +3 °C (T+3); Hd – soil moisture, Fh – variability of soil moisture, Rc – soil acidity, Sl – soil salinity, Ca – soil carbonate, Nt – content of mineral nitrogen available for assimilation, Ae – soil aeration, Tm – thermal regime, Om - ombro regime, Kn - continental climate, Cr - cryo regime, Lc – illumination; indicator values 2C+ - X+2σ, 2C- X-2σ; the range of indicators x±2σ marked in orange.

3. Discussion

3.1. Realized potential niches in the Carpathians and Pyrenees

During LGM, the potential range of *K. procumbens* was broader in the Carpathians, and for East Carpathians populations the model predict suitable areas also at the lower elevation, closer to the ice sheet. In the Pyrenees during LGM, potential range was located in lower elevations, and conditions for Central Pyrenees populations were almost unsuitable. In current conditions, the species attain in the Pyrenees their southern-most, and in the Carpathians close to southern-most localities in Europe [24,27]. *Kalmia procumbens* survived in both mountain chains in the subalpine and alpine vegetation belts due to high-mountain climate with low temperatures and relatively high precipitations, mostly in the places with restricted snow cover during winters [21,22,28,38].

The low altitudinal border of *K. procumbens* occurrence in the Carpathians and in the Pyrenees are at similar elevations, as a rule in the habits orographically or edaphically inaccessible for the shrubs, tall herbs, and grasses. The specific site conditions are mostly on the slopes exposed to the North, in the rocky places with very thin layers of soil or on the rocks completely without soil, and in the places open to the winds. Sometimes such conditions can be anthropogenic, for example, could effect from over-pasturing. This kind of pressure stopped last decades and could be one of the reasons for the disappearance of the lowest localities of *K. procumbens* in the East Carpathians, reported from 1455 m in the Chornokhora [46], not found later [22,33]. The reduction of pastoralism in the Pyrenees during the last decades could also cause the disappearance of the species' lowest localities due to the expansion of the tall herbs and shrubs.

The maximal altitudes of occurrence of *K. procumbens* in the Pyrenees are more elevated than in the Carpathians. Such a rule was also observed in other subalpine and alpine plants, common for the Pyrenees and Carpathians, as for example *Juniperus communis* L. var. *saxatilis* Pall., *Salix reticulata* L., *Salix herbacea* L., *Salix hastata* L., *Dryas octopetala* L., *Vaccinium gaultherioides* Bigelow (*V. uliginosum* L.) (Table S1). The differences in the altitudinal maxima of the subalpine and alpine plants between the Carpathians and Pyrenees surely result from the higher elevations of the latter. The Carpathians arc is composed predominantly of medium-sized mountain ridges, with only three or four massifs revealing sufficiently well, and several other with only fragmentary developed alpine vegetation belt [47,48]. Inversely, in the Pyrenees, this type of vegetation is more frequent and cover a broader area [28,49–51].

Kalmia procumbens is well adapted to micro-habitats with continental climatic conditions, to the extremely high diary amplitude of temperatures during vegetation season [52,53] and early snowmelt [54], but the species could suffer from the frost during the beginning of the vegetation season, when development of the generative structures starts [55]. On the other hand, the late frost disturbances and high temperatures in the exposed places of *K. procumbens* occurrence are reducing quite all other plant species, promoting *Kalmia* successful regeneration [55]. In relation to the surrounding grass plant communities, for which the Index of Continentality is 19.7 or 16.5, after Gorchynsky and Rivas-Martinez, respectively, in *Loiseleurio-Cetrarietum* of the East Carpathians it attains 21.6 and/or 17.5 [40]. Additionally, the average annual temperatures on the elevation of 1000 m in grass plant communities reach 2.6 °C, but in the rock coenoses dominated by *K. procumbens* attains 3.6 °C [19]. Nevertheless, *K. procumbens* does not reach its potential altitudinal maximum in most of the Carpathian ridges, as it was concluded for some other alpine shrubby plants in the East Carpathians [48].

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3.2. Environmental conditions of K. procumbens realized niches

Kalmia procumbens is a calcifuge species occurring in the mountains composed of metamorphic siliceous rocks pH [28,56–58]. The plant communities with dominance of this species are classified as association *Cetrario nivalis-Loiseleurietum procumbentis* Br.-Bl. in Br.-Bl. et Jenny 1926 [59], from alliance *Rhododendro-Vaccinion* Br.-Bl. 1926). In the Pyrenees, the plant community *Cetrario nivalis-Loiseleurietum* is developed on the North-exposed, acid sites where the winds blow-out snow reducing snow cover [49,50,57,58,60]. Similar plant community is formed in the South Carpathians [61,62], and fragmentary in the East Carpathians [38,56]. In the latter mountains and in the South Carpathians, *K. procumbens* occurs in the grassland communities on the siliceous rocks [56,63,64].

The climate in the regions of *K. procumbens* occurrence in the mountains of the Central Europe is of oceanic to sub-continental type, cryo-oro-temperate termotype and sub-humid to hyper-humid ombrotype [65,66]. Despite this, the average bioclimatic data retrieved from World Clim for *K. procumbens* localities in the Pyrenees revealed slightly milder conditions, than in the Carpathians (Table 2). The climate of the Carpathian localities of. *K. procumbens* appeared more continental with lower factors of temperature and precipitation and higher temperature seasonality. The continental climate of the steppes easterly and southerly from the Carpathians and closer distance to the continental climate of the central Euro-Asiatic continent could play some role in lowering positions of *K. procumbens* there, and alpine and sub-alpine vegetation belt, comparing to the Pyrenees.

The average bioclimatic factors of *K. procumbens* localities presented a low level of differences between the Central and Eastern Pyrenees, revealed mostly in the lower values of factors connected with precipitation in the central, more continental parts of this mountain chain (Figure 3). Nevertheless, the more humid climatic conditions in the Eastern Pyrenees can be a reason of more dispersed and not so abundant localities of the species due to prolonged snow cover [28]. Similarly, the more Atlantic climate conditions in the Northern than in the Southern Pyrenees [65,66] can explain a lower abundance and frequency of occurrence of *K. procumbens* on the southern macro-slopes [28]. On the other hand, the higher and longer lasting of snow observed in the Eastern Pyrenees could reduce the potential habitats accessible for *K. procumbens*, as the species occurrence is connected mostly with the places with thin snow deposits [21,22,28,38,54]. *Kalmia procumbens* occurs mostly on specific microhabitats, mainly the rocky ridges and rocks, where the snow is being blown away and temperatures reveal high diurnal amplitudes.

The bioclimatic differences between localities of *K. procumbens* in the East versus South Carpathians appeared a higher than between East and Central Pyrenees (Figure 3). This finding could result from the higher elevations of the South Carpathians mountain massifs than those in the East Carpathians, and consequently, the greater number of *K. procumbens* populations reported from the higher elevations, which are characterized with lower temperatures and higher mean diurnal amplitude and isotermality.

The snow-free period appeared important for micro-sites inhabited by small ericaceous shrubs in the high mountains and in the arctic zone [67]. The longer snow-free period positively influenced the wood-ring increment in the *Empetrum hermaphroditum* Hagerup [68], the species frequently occurring with *K. procumbens*. At the same time, less snowfall and shorter duration of snow cover observed during the last decade were a reason for more abundant *K. procumbens* growth [21,69].

The differences of climatic conditions of *K. procumbens* current localities in the Pyrenees and Carpathians could result from (1) adaptation to different climates during the Holocene (2), origin of the Pyrenean and Carpathian populations from two different regions of the Arctic, the Atlantic in the Pyrenees and more continental in the Carpathians, or simultaneous action of both processes.

3.3. Possible influence of climate differences

It shall be expected, that detected differences between average climatic conditions of *K. procumbens* localities in the Carpathians and Pyrenees influenced genetic structure of the species. The isolation of *K. procumbens* populations between Pyrenees, Alps and Carpathians lasting at least during Holocene [4,70,71], should be a reason of genetic and morphological differences. The gene exchange in Ericaceae is limited due to the low rate of seed dispersal [72] and restricted pollen

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transport, especially between populations from distant mountain chains [73]. These limitations could be a reasons for genetic and morphological differences, as described for other subalpine/alpine plant species, *Salix herbacea* L. [74], *Ranunculus glacialis* L. [75], *Saxifraga oppositifolia* L. [76], *Soldanella alpina* L. [77] or *Rhododendron ferrugineum* L. [78,79], and even a reason of speciacion, as in case of *Rhododendron ferrugineum* and *R. myrtifolim* Schott & Kotschy [80].

The world-wide genetic structure of *K. procumbens* detected using sequences of multiple nuclear loci revealed that southernmost European and East-Asiatic populations are genetically similar but different from the Arctic ones [81,82]. The southern populations of *K. procumbens* in the mountains diverged from the Arctic during the LG [82,83]. This is in contrast with the results of the amplified fragment length polymorphism (AFLP) analyses, which indicated the isolation of Central-European mountain clade [84]. The number of verified populations and individuals used in these papers [82,84] was sufficient for description of *K. procumbens* general pattern of geographic differentiation but was rather too small to its genetic differentiation in the Central-European mountains. It could be expected, the species reveal differences between Pyrenean, Alpine and Carpathian localities, this hypothesis, however, should be verified in a specific study.

3.4. Future ecological niches in the Carpathians and Pyrenees

The climate change caused reduction of the potential niches of *K. procumbens* at their southern limit of realized ecological niches in the mountains of Central Europe could be predicted and even expected, similarly as in case of other subalpine and alpine plants [10,28,29,38,41,48]. In that context, the drastic reduction of potential niches in the Carpathians in general and quite complete disappearance of suitable niches in the East Carpathians is not surprising. The process of reduction of the geographic ranges of cold adapted, high-mountain plants and their shifts to the higher elevations first of all is restricted by mountain highest elevations. The extinction could also results from rather slow uppermost colonization by the plants [85]. The East Carpathians have not the massifs crossing an elevation of 2500 m, which are the main centres of occurrence of alpine and subalpine plants [47,86]. It shall be stressed, that process of disappearance of area of potential niches detected in case of *K. procumbens*, in fact concerns more or less the entire alpine and subalpine flora in the East Carpathians [24,48].

In the Pyrenees, the reduction of potential niches area suitable for *K. procumbens* is less drastic than in the Carpathians. It results from the more 'alpine' character of the Pyrenees and the higher elevations of their highest peaks, which form the conditions for the occurrence of alpine flora [28,50]. The more intense reduction of potential niches suitable for *K. procumbens* in the Central than in the East Pyrenees could be explained by more continental climate of the Central Pyrenees, influenced by the close distance to the very dry and warm central part of the Ebro Basin from the South. This could reduce the influence of the Atlantic climate [58,66] (66-Rivas-Martínez et al. 2017; 58-Ninot et al. 2017). In fact, the westernmost localities of the species were detected on the northern macroslopes of the Pyrenees, with the more prominent impact of the Atlantic climate (Figure 1). This could also corroborate the amphi-Atlantic biogeographic character of *K. procumbens* proposed by Hultén [25] (1973).

The influence of the reduction of the area of potential niches to the currently realized niches of *K. procumbens* could be diminished by presence of the microrefugia suitable for the species within the area of its occurrence [87] (87-Hülber et al. 2016). The species in fact settled in this kind of microsites at their lowermost localities. The current localities of *K. procumbens* in the East Carpathians (Figure 1), however, exist in the area of very low level of the potential niches, especially at low elevations, which are quite exclusively on the North-facing slopes. It could be expected, that *K. procumbens* can exist for a long time outside the optimal environmental conditions on the northern slopes, which make the extinction following the climate change more prolonged, especially for the plants moderately sensitive to the lack of humidity [88] (88-Maclean et al., 2015) and to heat [31] (31-Buchner et al., 2013). Thus, the persistence of *K. procumbens* in the environments at a very low level of suitability could result from the specific site conditions of the particular localities eliminating competition of the other plants, but it also could be caused by mykorrhiza. The symbiosis of *K.*

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procumbens with fungi [89,90] (89-Treu et al., 1996; 90-Koizumi & Nara, 2017) could mitigate the extinction rate, as the plants with the fungal symbiosis are less prone to the harsh environmental conditions [91,92] (91-Haselwandter, 1979; 92-Cripps & Eddington, 2005).

The extinction rate of *K. procumbens* due to the climate change could also be restricted by the shrub longevity, found as more than 100 years [93] (93-Schweingruber & Poschlod 2005). The longevity with tolerance to the harsh environment, in particular relatively high temperatures, the high diurnal temperature amplitudes, winter frosts [24,52,53,94–96] (52-53-Larcher & Wagner, 2009, 2011; 94-Scherrer & Körner, 2011; 95-Zeidler & Banaš, 2013; 96-García et al. 2020; 24-Löffler & Pape, 2020), episodic summer frosts [97] (97-Kuprian et al. 2014), allow moderate the climate change influence. The *K. procumbens* plants covered with shallow snow stratum are less vulnerable to the spring frosts [98] (98-Palacio et al., 2015). From the other hand, the speed of shifting of *K. procumbens* in the mountains after glacier regression could be rather moderate. In the Alps, it exists together with other ericaceous shrubs, in the areas with relatively stabilized plant cover, and colonize new terrain about a century after the glacier regression [5] (5-Fischer et al. 2019). Our results suggest that cooler slopes may act as microrefugia, buffering the effects on plant communities of increases in temperature by delaying the extinctions of species with low temperature requirements [88] (88-Maclean et al., 2015).

The precipitation of the driest month (bio 14) and precipitation of the warmest quarter (bio 18) are the most influential to the present realized niche of *K. procumbens* in the East Carpathians in Ukraine. These bioclimatic factors acts as limitation by lack of water in the vegetation period, which determine position of *K. procumbens* out of the zone of acceptable risk when the average annual temperature rises by 2 °C, and deep into the zone of catastrophic risk when temperature rises by 3 °C. The role of other ecofactors is much lower and concerns only the acidity and salinity of soils, which are stable in the rocks on the localities of *K. procumbens*.

4. Materials and Methods

4.1. Study areas

The Pyrenees and Carpathians have been elevated during alpine orogenesis and currently conserve the alpine floras with an abundance of endemic species [4,48,86,99,100]. The Pyrenees includes several massifs reaching elevation of more than 3000 m, with subalpine and alpine vegetation belts harbouring several arctic-alpine plants [28,50,51]. *Kalmia procumbens* occupies elevated parts of the eastern and central Pyrenees [28,34].

In comparison to the Pyrenees, the Carpathians cover a broader area, are more fragmented and divided into several mountain chains, but only a few of them sufficiently high the subalpine and alpine vegetation zones could be developed [47,48,86,101,102]. Localities of *K. procumbens* are occupying the most elevated sites in the South and East Carpathians [33,103], with only one natural locality in the West Carpathians [104–106].

4.2. Data sampling and geographic analyses

Data on the natural localities of the species were extracted from Global Biodiversity Information Facility (GBIF) database, the literature, herbaria, and authors' field notes. The geographic coordinates of localities were determined using Google Earth when not reported in the original data. Totally, we gathered more than 2000 data but after verification and exclusion of duplicates we analysed 641 georeferenced data, 140 for the Carpathians and 501 for the Pyrenees. Maps of the distribution of *K. procumbens* in the Pyrenees and Carpathians were prepared using QGIS 3.16.4 "Hannover" [107]. Altitudinal ranges of the species in both mountains system were presented on the graphs.

4.3. Environmental variables

The temperature, precipitation and elevation determined at the highest degree current (realized) ecological niches of species [108]. In spite of that, we used nineteen bioclimatic variables [109] and altitude (Table 1) to find factors, which determine current potential niche of *K. procumbens*. Usage of

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all these data could shed new light on the adaptation of the species to specific climatic data, retrieved from WorldClim (WC) database (http://worldclim.org/) [110]. For LGM (21 ka BP) we used PaleoClim (PC) data (http://www.paleoclim.org/), which is based on the CHELSA algorithm on PMIP3 data [111,112]. The spatial resolution of 30 arc-seconds (~1 km) of climate variables was applied. For the current climate (average for the years 1970-2000), we used WorldClim 2.1 database [110] bioclimatic data. For the future climate, we based on the Community Climate System Model (CCSM) [113] and used two representative concentration pathways (RCPs), RCP 2.6 and RCP 8.5 [114]. The RCP 2.6 provided increase of radiation forcing by 2.6 W/m^2 and an increase of temperature by 1 °C before 2070 (average for 2061-2080), the RCP 8.5 by 8.5 W/m^2 and 2 °C during the same period. Both are climate projections from GCMs, that were downscaled and calibrated using WorldClim 1.4 as baseline climate.

The PC used climate data of CAPE project [115] and of Community Climate System Model (CCSM) [113] for delineation of potential niches during Eemian Interglacial (LIG, 120-140 ka BP). These climatic data are based on geomorphological and geographical characteristics and do not take into account edaphic features and the structure of the substrate, which somewhat changes the microclimatic conditions.

For retrospective analyses of climate of EM (LGM, 21 ka BP), the CHELSA algorithm on PMIP3 data were used. For Mid-Holocene (MH) climate (ca 6 ka BP) the CCSM4 were used. For the current climate (average for the years 1970-2000), we used WorldClim 2.1 database [110] bioclimatic data. The previsions of the future climate changes were utilized scenarios of two representative concentration pathways (RCPs), RCP 2.6 and RCP 8.5 [114]. The RCP 2.6 provided increase of radiation forcing by 2.6 W/m^2 and increase of temperature by 1 °C before 2070 (average for 2061-2080), the RCP 8.5 by 8.5 W/m^2 and 2 °C during the same period. Both are climate projections from GCMs, that were downscaled and calibrated using WorldClim 1.4 as baseline climate.

The average values of bioclimatic variables were compared between the Carpathians and Pyrenees, as well as between regions within these mountain ranges. The Mann-Whitney U test conducted in the R environment was used for this purpose [116]. The influence of particular climatic variables on the current potential niches of *K. procumbens* in the Carpathians and in the Pyrenees was verified by Principal component analysis (PCA). In PCA, the data for localities in the North Carpathians and South Carpathians, as well as for Central and East Pyrenees were treated as separate groups.

4.4. Niche modeling

For the prediction of the potential range of *K. procumbens*, bioclimatic data related to their localities were used. The MaxEnt 3.4.1. [117–119] was applied in analyses with maximum entropy modelling for the estimation of a probable distribution of the species outside their realized niche. The model with ENMeval R software [120] for the current climate was evaluated at first. The procedure of evaluation follows those described by Salva-Catarineu et al. [121]. For evaluation of the results of modelling, the Receiver Operating Characteristic (ROC) curves were used [122,123], assessing the values of Area Under the Curve (AUC) below 0.6 as nearly random.

The QGIS 3.16.4 “Hannover” [107] was applied for mapping the current and predicted potential niches on the climate variables. The potential distribution of *K. procumbens* species was calculated for the different classes of suitability [45,121].

The phytoindication method was used for the assessment of econiches, indicators of the leading climatic and edaphic ecofactors, forecasting their changes depending on the climate for the Eastern Carpathians [40,124]. Modeling of econiche change and assessment of habitat loss threats for populations of the Eastern Carpathians was performed on the basis of phytoindication data. For this purpose, the point values of the amplitude ($x \pm 2\sigma$) were calculated for the leading ecofactors, and their changes were evaluated depending on the increase in average annual temperatures by 1, 2, and 3 °C. The acceptable risk zone is, when the average values of the obtained data are intside the confidence intervals of the $\pm 2\sigma$, and a catastrophic risk zone when the amplitudes did not overlap, which means the complete disappearance of the species from this place [40].

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5. Conclusions

Kalmia procumbens occurs in the alpine and subalpine vegetation belts, going down to the elevations of about 1500-1600 m, while the most elevated localities in the Pyrenees are at ca 3000 m, about 500 m higher than in the Carpathians. The localities of *K. procumbens* in the Carpathians have the more continental climate than in the Pyrenees, with lower precipitation and temperatures but higher seasonality of temperature and precipitation. Due to climate warming, the strong reduction of potential area of occurrence to 2100 is expected in the Carpathians and moderate reduction in in the Pyrenees.

Supplementary Materials: The following supporting information can be downloaded at the website of this paper posted on Preprints.org. **Figure S1**: Provided potential range of *Kalmia procumbens* during Last Glacial Maximum in the Carpathians (a and b) estimated using: a – environmental conditions from the East Carpathians, b – from the South Carpathians; in the Pyrenees (c and d) using: c – conditions from the East Pyrenees, d – from the Central Pyrenees; **Figure S2:** Occurene of populations of *Kalmia procumbens* in different exposition in the Carpathians (a and b): a – East Carpathians, b –South Carpathians; and in the Pyrenees (c and d): c –East Pyrenees, d –Central Pyrenees; Table S1: Altitudinal maxima of subalpine and alpine species in the Carpathians [48,103,104] and Pyrenees [28]; CEUR – Central European mountain, ARALP – Arctic-Alpine; EUROS – Euro-Siberian mountain.

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