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The Fate of Endangered Rock Sedge (*Carex rupestris*) in the Western Carpathians—The Future Perspective of an Arctic-Alpine Species under Climate Change

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Abstract: *Carex rupestris* is an endangered and rare arctic-alpine element of the Western Carpathian flora. Given the geographically isolated and spatially restricted peripheral ranges of arctic-alpine species, there is a good chance that many species of conservation concern irreversibly disappear from the regional flora under the ongoing climate change. In this study, we gathered all existing data on the presence of *C. rupestris* and focused on its current and future distribution in the Western Carpathians. We found that although the distribution of the species is fragmented and scarce, *C. rupestris* occurs in several mountain ranges, in four distinct plant community types, which differ considerably in altitude, geological bedrock, and other habitat characteristics. In contrast to the relatively broad range of occupied habitats, *C. rupestris* shows a narrow temperature niche (mean annual temperature range 0.4–4.0 °C). Ensembles of small models based on climatic characteristics and local topography show that regardless of the climate change scenario (rcp2.6, rcp8.5), many current occurrence sites, mainly in the peripheral zones of the range, will face the excessive loss of suitable environmental conditions. It is expected that the Tatra Mountains will be the only mountain range retaining potentially suitable habitats and providing possible refugia for this cold-adapted species in the future. Such severe shrinkage of distribution ranges and associated geographic isolation raises serious concerns for the fate of the arctic-alpine species in the Western Carpathians.

Keywords: arctic-alpine vegetation; biodiversity; climate change; conservation; ensemble of small models; refugia; Western Carpathians

1. Introduction

Arctic-alpine taxa are mainly distributed in higher latitudes. Due to their adaptation to low temperatures, these species show an extrazonal distribution occupying the highest summits of the European Alpine System (EAS) [1,2], such as the Alps, Carpathians, Sudeten, Pyrenees, Apennines, Dinarides, and Rilo–Rhodopean massifs [3–5]. Regarding the extent of their distribution outside the Arctic, there are large differences between taxa. Whereas some arctic-alpine species are common in many mountain ranges of the Northern Hemisphere, others are very rare, and in some cases, only a few fragile populations are known outside the Arctic and the directly connected mountain ranges [6,7]. Small and isolated populations of theses rare cold-adapted species are especially vulnerable to ongoing climate change [8].

Carex rupestris All. (Figure 1A; rock sedge, syn.: *Carex petraea* Wahlenb.) is an arctic-alpine species, which forms co-dominant or dominant stands in its distributional optimum. This species has a circumpolar distribution and shows an insular distribution pattern in the EAS. It has first reached Western Europe in the Pleistocene from the northern regions of the Holarctic and subsequently migrated eastwards along the chains of the Alps and the Carpathians [9].

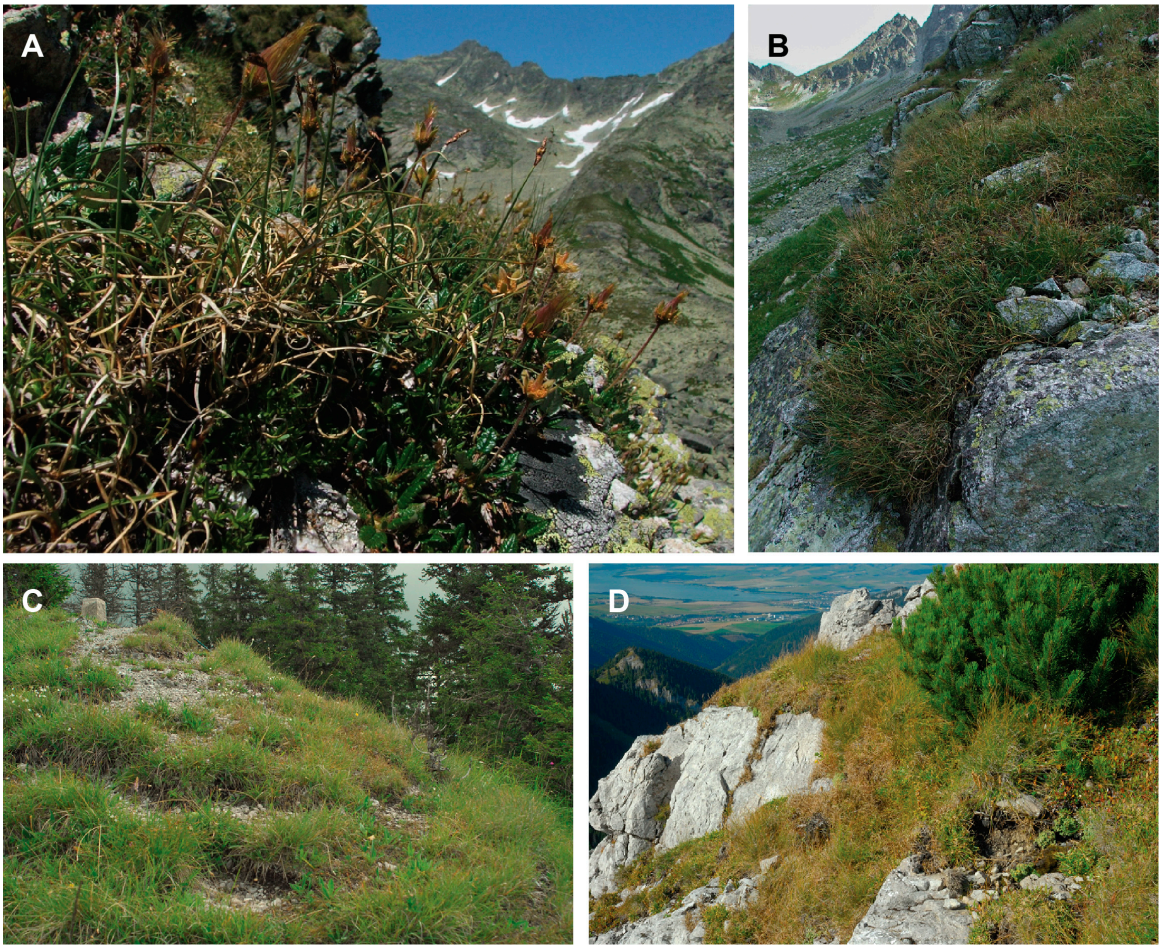

Figure 1. Detailed habitus of *Carex rupestris* in Velická dolina Valley, Vysoké Tatry Mountains (**A**); typical habitat in Hlinská dolina Valley, Vysoké Tatry Mountains (**B**); site threatened by trampling on Mt. Siná, Nízke Tatry Mountains (**C**); and overgrowing by competitively stronger dwarf pine (*Pinus mugo*) on Mt. Krakova hoľa, Nízke Tatry Mountains (**D**). Photo: J. Šibík.

C. rupestris is an extremely rare, critically endangered, and protected red-listed species in the whole Carpathian range and adjacent mountain ranges; apart from the Slovak part of the Western Carpathians, two localities are known in Sudeten (Czech Republic) [10,11], a few localities are found in the Polish part of the Eastern Beskids (Poland) [12] and in the Ukraine [13]. Rock sedge is considered to be a relic species [14] as well as an important diagnostic species of the relic arctic-alpine vegetation [3,15]. It has a very specific distribution within the Western Carpathians (Figure 2), what drew the attention of botanists for decades [16–18]. It is completely missing in the Polish (northern) part of the Tatra Mountains and its distribution in Slovakia is obviously disjunct, with the habitats differing among the highest mountain range (Vysoké Tatry Mountains) and the other, smaller mountain ranges. However, the exact environmental differentiation of presence sites has not been quantified yet.

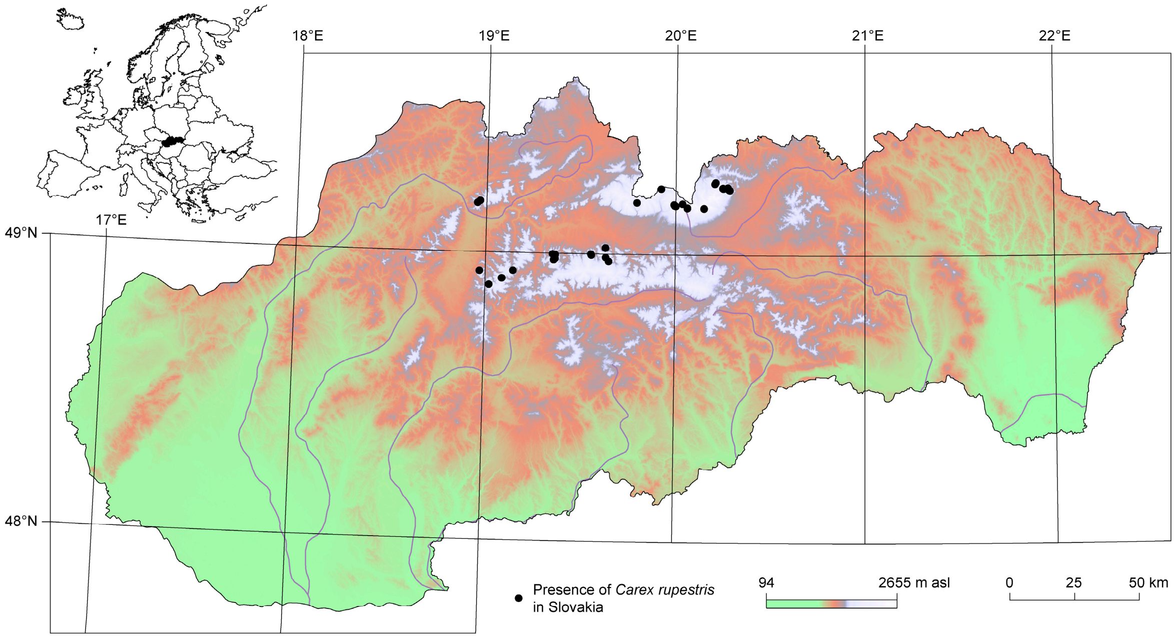

Figure 2. Map of known occurrences of *Carex rupestris* in the Western Carpathians (Slovakia).

The fact that global climate change is already having a significant impact on ecosystems is widely recognized [8,19–21]. It might alter natural disturbance regimes, such as drought frequency [22], extreme rainfall events [23], and floods [24], as well as the outbreaks of fire, insect pests, or wind storms in terms of frequency and severity, altering also the corresponding species distribution [25,26]. Arctic and alpine ecosystems are considered to be one of the most vulnerable and susceptible systems to many of the effects of climate change—e.g., increases in temperature, altered precipitation patterns, and changes of seasonal dynamics [27]. There is also an ongoing debate about species range shifts towards higher altitudes and latitudes [28–30], with the strongest shifts in species composition in the vegetation of the Tatra Mountains being found in mylonite grasslands of a small plot size [31]. Another striking effect of climate change in mountain ecosystems is the thermophilization of vegetation, where the composition of species accompanying the cold-adapted taxa changed significantly and the cold-adapted plants are recently co-occurring with species preferring warmer conditions than in the past [31,32].

In the Carpathians, long-term climatic data analyses reveal a significant rise of mean, minimum, and maximum temperature over the last decades [33]. Reflecting the geographically isolated and spatially restricted peripheral ranges of arctic-alpine species in the Western Carpathians, there is a good chance that many rare and threatened species irreversibly disappear from the regional flora under ongoing climate change. Declines of alpine species, as well as their local extinctions, have been already noted in the Eastern part of the Carpathians [30], where *C. rupestris* is listed as extinct at several localities. Almost half of the localities with the occurrence of the cold-adapted rock sedge in the Western Carpathians lie in the peripheral lower mountain ranges, where it is threatened not only by rising temperatures but also by the absence of possibly higher-elevated refugia. The high-risk distribution, as well as the biological traits of the species, such as the non-expansive way of propagation, its relic character, and eye-catching position in the spotlight of botanists over the past decades makes *C. rupestris* an ideal model system for the study. We hypothesized that under ongoing climate change, many rare plant species, especially cold-adapted arctic-alpine species, on the periphery of their distributional area are in competitive disadvantage against the more competitive, warm-tolerant species, and their life traits predestine their ability to colonize new suitable habitats, what in turn means the restriction of their overall distribution.

The purpose of this paper is: (a) to examine habitat preferences of *C. rupestris* in the Western Carpathians; (b) to record the current distributional pattern of the species, and (c) to predict potential shifts in the distribution under climate change scenarios.

2. Materials and Methods

2.1. Vegetation Data

The field research was conducted in the Western Carpathians (Slovakia) within the years 2005–2009. We have resurveyed all the known localities with the occurrence of *C. rupestris* in order to confirm the current presence of the species. All 65 phytosociological relevés from 23 localities were gained following the same standard procedures of the Zürich-Montpellier School [34,35] using the modified 9-degree Braun-Blanquet's sampling scale [36] and stored in the Slovak Vegetation Database—EU-SK-001 (SVD) [37] or in the private databases of the authors using the TURBOVEG program [38].

The nomenclature of the taxa generally follows the Checklist by Marhold and Hindák [39], taxa not used in this work are quoted with the author citation. The names of syntaxa follow the outline of Kliment et al. [40,41] and Jarolímek and Šibík [42].

2.2. Environmental Data

To examine environmental differences among habitats with *C. rupestris* occurrence, several environmental variables were recorded or calculated for 62 vegetation plots with the presence of *C. rupestris* and their known geographic position (Table 1). Data on the elevation, slope, aspect, temperature, precipitations, and solar energy were derived from fine-resolution GIS layers (10 m resolution). A regular grid-based digital terrain model (DTM) was generated from contour lines and height points vectorized from 1:10,000 raster maps in GRASS GIS v6.4 [43]. Aspect values were linearized and rescaled to range from 0 (south), through 2 (east, west) to 4 (north). Solar energy income was calculated according to Hofierka and Šúri [44] using solar geometry [45,46]. Solar energy characteristics included the monthly and yearly sum of insolation time of direct solar radiation, monthly and yearly sum of the direct, diffuse, and reflected solar radiation. Variables were calculated using our r.sunangle Python script created in the GRASS GIS environment with 10-min increments [47]. Air temperature and vertical atmospheric precipitation were calculated from rasters of mean annual precipitations for the years between 1961–1990. The source data were provided by the Slovak Hydrometeorological Institute. Information on geological settings in 1:50,000 scale were acquired from State Geological Institute of Dionýz Štúr and the geological bedrock of sites was classified into three groups: mylonite (includes mylonite and granitic mylonite), marl (includes shale, hornstone, and marl), and lime (includes limestone and dolomite).

A soil sample was collected from 44 plots and they were bulked, homogenized, purified, and air-dried. Subsequently they were analyzed in a certified laboratory (Institute of Botany, Czech Academy of Sciences, Průhonice) following the standard international protocols (N, C, pH); the determination of individual elements was performed using the methods of atomic emission spectroscopy (K), atomic absorption spectroscopy (Mg, Ca); the available phosphorus in soils was determined by photometric method [48].

For the assessment of distribution shifts under climate scenarios, 19 bioclimatic variables with a resolution of ~1km were obtained from the WorldClim database [49]. Current values of the variables (average for 1960–1990) were supplemented with estimates for the years 2050 (average for 2041–2060) and 2070 (average for 2061–2080) based on two possible greenhouse gas scenarios: minimal rcp2.6 [50] and maximal rcp8.5 [51].

2.3. Data Analysis

Phytosociological relevés were processed in JUICE 7.0 [52] and numerical classification was performed using the program SYNTAX 2000 [53] using the ordinal method with Goodman–Kruskal's coefficient. The resulting vegetation groups were displayed in ordination space using a constrained analysis of principal coordinates (CAP) based on the distance matrix of Goodman–Kruskal's coefficients [54]. The indicator species analysis [55] was performed to identify taxa with the highest indicator value (IndVal > 0.65), i.e., species with the highest specificity and fidelity to a particular group derived in vegetation classification. Scores of indicator species were displayed in CAP as weighted averages.

We fit a series of simple models to identify environmental differences among vegetation groups. For quantitative environmental variables, a one-way ANOVA followed by a Tukey HSD test were employed. The same approach was used to test for differences in species richness among groups. For qualitative data (geological bedrock), a multinomial model was fitted via neural networks [56] and pairwise post-hoc tests were performed using the same method with Bonferroni adjusted significance levels. Normality, homoscedasticity, and independence of residuals were assessed using diagnostic plots and spatial correlograms. If needed, variables were power- or log-transformed to meet the assumptions of normality and homoscedasticity. In the case of significant autocorrelation patters in the residuals, generalized least square models with a Gaussian spatial correlation structure were employed [57].

Subsequently, we built classification tree models [58] to identify a subset of the environmental variables most strongly associated with a vegetation classification scheme. Trees were fitted using a conditional inference approach with multiple statistical tests to prevent over-fitting [59]. A five-percent significance level was employed for variable selection and as a stopping criterion for growing the trees. The predictive performance of the trees was assessed using cross-validated (leave-one-out) classification accuracy. Separate trees were built for the environmental data from 62 plots and soil data from 44 plots. Since classification trees may be susceptible to collinearity of predictors, we screened the data prior to analysis and removed highly correlated variables—temperature and precipitations (both strongly correlated with altitude), global, direct, diffused, and reflected radiation (all correlated with the duration of solar radiation), pH_{H2O} (strongly correlated with pH_{KCl}), C and Ca content (both strongly correlated with N and P content). Residuals of the trees were checked for autocorrelation using spatial correlograms; no significant spatial autocorrelation pattern was observed.

We built habitat suitability models (HSMs) to estimate the current extent of favorable habitat conditions for the species and to predict the extent of suitable habitats in the year 2050 and 2070 under the two climate change scenarios (see above). Nineteen bioclimatic variables [49] were used as habitat characteristics for HSMs. Since the local topography may create refugia that may not be recognized in purely climate-based models [60], the slope and aspect were therefore included into the modeling. Due to the relatively steep geographic gradient in Slovakia, there was a high degree of collinearity among the habitat characteristics. Therefore, prior to analysis, we removed strongly correlated variables (Pearson $|r| > 0.7$) in a stepwise manner to diminish redundant information in the dataset. Mean annual temperature, isothermality, precipitation seasonality, slope, and aspect were retained as informative predictors in the HSMs. The data on the presence of *C. rupestris* were supplemented with true absences obtained from the SVD [37]. Twenty-three sites with known presences of species contrasted sharply with 8697 absences recorded after the year 2000 in the SVD. Due to greatly unbalanced dataset, we used ensembles of small models (ESMs) to calibrate HSMs. This novel approach is especially suitable for the distribution modeling of rare species, as it tends to outperform standard HSMs when a dataset consists of a few occurrences only [61,62]. Briefly, ESMs are built by fitting many small models (typically with 1–3 predictors) and then averaging them into an ensemble model, where the small models are weighted by their cross-validated predictive performance. Here, we used all possible bivariate combinations of the predictor variables and fit ESMs with four frequently used species distribution modeling techniques: artificial neural networks [63], boosted regression trees [64], generalized additive models [65], and random forests [66], yielding 40 bivariate models in total. We followed Breiner et al. [67] and varied the model parameters and complexity separately for each bivariate model and evaluated their predictive performance using a 10-fold cross-validation. The area under the receiver operating characteristic curve (AUC) was used as a quantitative measure of predictive power [68]. For each bivariate model, the parameter setting with the highest cross-validated AUC score was retained as the final optimized bivariate model. These tuned bivariate models were then averaged, weighted by their mean cross-validated AUC scores, to form tuned ESMs. The predictive performance of the ESMs was evaluated using 10-times repeated leave-groups-out cross-validation with 70% of the data used to train the models while 30% was left for validation [68]. Spatial predictions of the ESMs were used to plot habitat suitability maps in QGIS v. 3.6 [69].

The analyses were performed in R [70] using packages ecospat [71], nlme [72] nnet [56], party [59], and vegan [73].

3. Results

3.1. Vegetation Classification of Plots with *Carex rupestris*

The cluster analysis of all 65 relevés with the occurrence of *C. rupestris* in the Western Carpathians resulted in classification with four groups of floristically well-differentiated vegetation units, clearly interpretable on the level of higher syntaxa or association level (Figure 3).

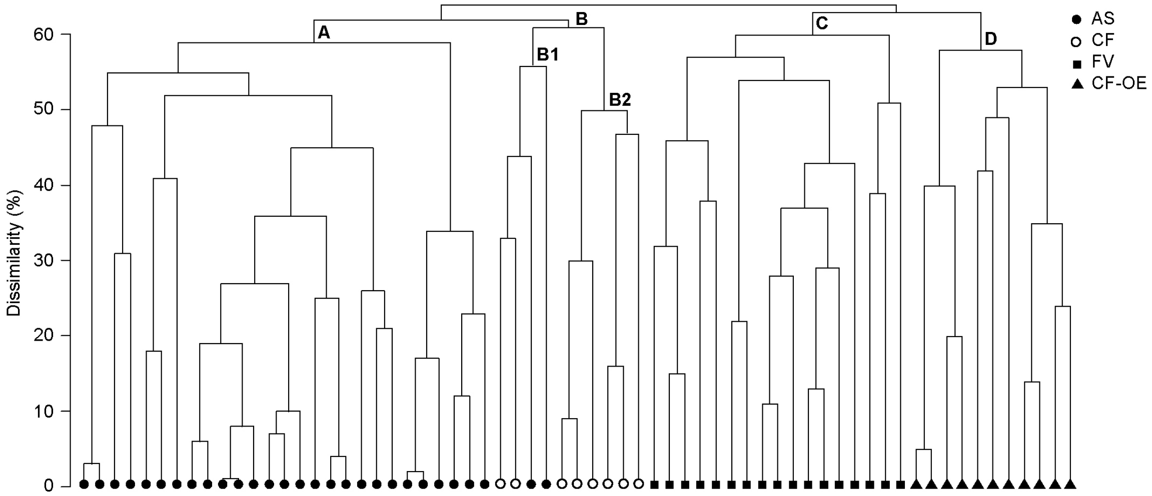

Figure 3. Dendrogram of the numerical classification of relevés with the occurrence of *Carex rupestris* in the Western Carpathians based on the ordinal method and Goodman–Kruskal's coefficient. Abbreviations: AS—*Astero-Seslerion* (cluster A), CF—*Caricion firmae* (cluster B; the two sub-clusters reflect geographical differentiation, whereas cluster B2 includes typical relevés of the alliance from Belianske Tatry Mountains, and cluster B1 includes relevés from different parts of the Western Carpathians), FV—*Festucion versicoloris* (cluster C); CF-OE—transitional relevés between *Caricion firmae* and *Oxytropido-Elynion* (cluster D).

Cluster A represents the group of relevés from the alliance *Astero-Seslerion* (class *Elyno-Seslerietea*) and encompasses relevés from lower altitudes (Nízke Tatry Mountains, Veľká Fatra Mountains, and Krivánska Malá Fatra Mountains). This group of relevés is typical for presence of (ordered by decreasing indicator value) *Minuartia langii, Gentiana clusii, Jovibarba globifera, Sesleria alba, Kernera saxatilis, Thymus pulcherrimus, Primula auricula, Trisetum alpestre, Campanula cochlearifolia*, and *Festuca tatrae* (Figure 4).

Cluster B represents relevés from the alliance *Caricion firmae* (class *Elyno-Seslerietea*). It is divided into two sub-clusters, whereas the second one (cluster B2) includes typical relevés of the alliance from the Belianske Tatry Mountains, and the first one (cluster B1) includes relevés from different parts of the Western Carpathians. We did not find any indicator species that would strongly (IndVal > 0.65) distinguish cluster B from the other clusters.

Cluster C comprises clearly differentiated relevés from the alliance *Festucion versicoloris* (class *Carici rupestris-Kobresietea*) from high altitudes of the Vysoké Tatry Mountains and one relevé from Západné Tatry Mountains (all of them are from mylonite bedrock). The cluster was typical for presence of *Hupersia selago, Festuca supina, Juncus trifidus, Salix reticulata, Saxifraga retusa, Carex fuliginosa, Silene acaulis, Lloydia serotina, Campanula alpina,* and *Bartsia alpina*.

Within cluster D, there are the relevés from the alliance *Caricion firmae*, which have a very strong relationship to the plant communities of the alliance *Oxytropido-Elynion* (class *Carici rupestris-Kobresietea*) that creates a mosaic of both vegetation types, therefore, the species pool for both communities is the same. *Arenaria tenella* was the only species with sufficient indicator power to distinguish relevés of the cluster D from the other clusters.

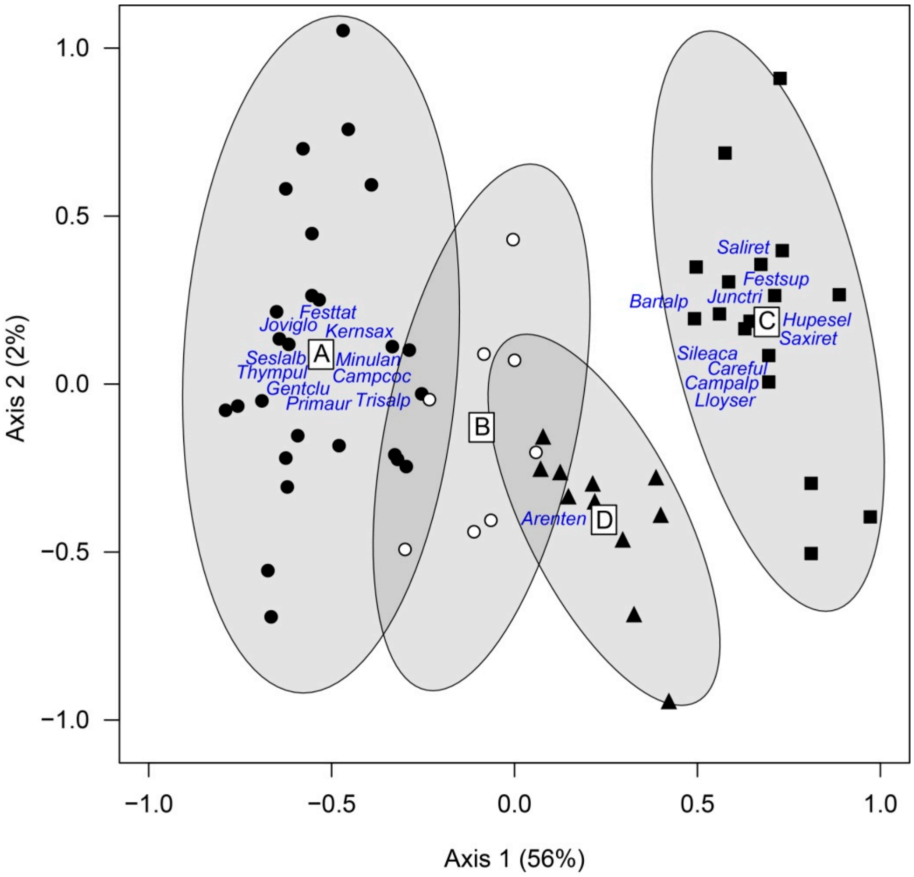

Figure 4. CAP ordination plot based on distance matrix of Goodman–Kruskal's coefficients showing differences in species composition among four clusters of relevés (A–B) with the occurrence of *C. rupestris* in the Western Carpathians. Scores of indicator species (IndVal > 0.65) are overlaid onto the ordination. Confidence ellipses (95%) are displayed to depict expected overlap of the clusters. Abbreviations of species names are as follows: Festtat *Festuca tatrae*; Joviglo *Jovibarba globifera*; Kernsax *Kernera saxatilis*; Seslalb *Sesleria albicans*; Minulan *Minuartia langii*; Thympul *Thymus pulcherrimus*; Campcoc *Campanula cochleariifolia*; Gentclu *Gentiana clusii*; Primaur *Primula auricula*; Trisalp *Trisetum alpestre*; Arenten *Arenaria tenella*; Saliret *Salix reticulata*; Festsup *Festuca supina*; Junctri *Juncus trifidus*; Bartalp *Bartia alpina*; Hupesel *Huperzia selago*, Saxiret *Saxifraga retusa*; Sileaca *Silene acaulis*; Careful *Carex fuliginosa*; Campalp *Campanula alpina*; Lloyser *Lloydia serotina*. For explanation of symbols see Figure 3.

Table 1. The overview of vegetation and environmental data of 65 *C. rupestris* plots with known coordinates. The table shows the range of values (min–max), results of simple models testing for differences among clusters of vegetation plots (test statistics—F, or χ^2 and associated probabilities—P), average values, and 95% confidence intervals (lower–upper limit) for each cluster. Results of post-hoc tests are displayed by the uppercase letters (clusters with the same letters are not significantly different).

Variable	Unit	Range	F/χ^2	P	Cluster A	Cluster B	Cluster C	Cluster D
Vegetation data								
Nr. of relevés					27	10	17	11
Species richness		14–50	10.43	<0.0001	23.5 (21.3–25.8) ^{a}	27.1 (19.1–35.2) ^{a}	36.1 (32.3–39.8) ^{b}	29.6 (26.6–32.7) ^{ab}
Topology								
Altitude	m	1297–2012	89.24	<0.0001	1455 (1425–1485) ^{a}	1652 (1597–1708) ^{b}	1862 (1805–1919) ^{c}	1930 (1862–1997) ^{c}
Slope	°	10–80	14.13	<0.0001	47 (43–51) ^{a}	43 (34–51) ^{a}	54 (48–60) ^{a}	25 (18–33) ^{b}
Aspect		0.04–3.47	0.15	0.9319	1.99 (1.77–2.22)	1.39 (0.38–2.40)	2.09 (1.66–2.52)	1.22 (0.43–2.01)
Geological bedrock	% lime/marl/mylonite	–	85.63	<0.0001	100/0/0 ^{a}	62/38/0 ^{b}	0/6/94 ^{c}	45/55/0 ^{b}
Climate								
Temperature	°C	0.35–4.07	111.6	<0.0001	3.0 (2.8–3.2) ^{a}	2.1 (1.7–2.5) ^{b}	0.5 (0.4–0.7) ^{c}	1.3 (1.2–1.4) ^{d}
Precipitation	mm	1283–2123	124.4	<0.0001	1431 (1403–1458) ^{a}	1463 (1351–1574) ^{a}	1938 (1899–1977) ^{b}	1809 (1755–1863) ^{c}
Solar radiation								
Duration	$h \cdot m^{-2} \cdot y^{-1}$	10–140	5.59	0.0019	120 (114–125) ^{a}	96 (84–109) ^{ab}	100 (79–121) ^{ab}	83 (74–92) ^{b}
Global radiation	$MWh \cdot m^{-2} \cdot y^{-1}$	16–76	4.68	0.0054	67 (62–71) ^{a}	57 (45–69) ^{ab}	50 (40–60) ^{b}	53 (46–61) ^{ab}
Direct radiation	$MWh \cdot m^{-2} \cdot y^{-1}$	0.2–55	3.75	0.0156	48 (44–52) ^{a}	40 (30–50) ^{ab}	35 (26–43) ^{b}	36 (30–43) ^{ab}
Diffused radiation	$MWh \cdot m^{-2} \cdot y^{-1}$	0.01–19.5	16.85	<0.0001	18.3 (17.7–18.9) ^{a}	16.0 (14.6–17.5) ^{b}	13.8 (11.7–15.8) ^{b}	15.8 (14.8–16.7) ^{b}
Reflected radiation	$MWh \cdot m^{-2} \cdot y^{-1}$	0.03–16.93	3.33	0.0256	0.98 (0.80–1.16) ^{ab}	1.37 (0.85–1.89) ^{ab}	1.55 (0.36–3.45) ^{a}	1.34 (1.11–1.58) ^{b}
Soil characteristics								
pH_{H20}	–	4.30–7.75	41.64	<0.0001	7.39 (7.26–7.53) ^{a}	7.11 (6.77–7.44) ^{ac}	5.54 (5.21–5.86) ^{b}	6.53 (5.95–7.11) ^{c}
pH_{KCl}	–	4.03–7.69	39.91	<0.0001	7.28 (7.09–7.46) ^{a}	7.11 (6.76–7.45) ^{ac}	5.29 (4.93–5.66) ^{b}	6.24 (5.86–6.62) ^{c}
Ca	$g \cdot kg^{-1}$	0.6–12.4	9.389	0.0001	6.2 (4.9–7.4) ^{a}	6.4 (4.1–8.7) ^{a}	2.3 (1.4–3.1) ^{b}	6.8 (5.2–8.4) ^{a}
K	$mg \cdot kg^{-1}$	47–340	6.887	0.0008	189 (157–221) ^{a}	145 (106–183) ^{ab}	103 (76–130) ^{b}	122 (67–176) ^{ab}
Mg	$mg \cdot kg^{-1}$	14–2148	45.44	<0.0001	1210 (956–1463) ^{a}	615 (58–1172) ^{b}	48 (23–72) ^{c}	144 (61–226) ^{b}
C_{tot}	%	2.8–30.7	19.35	<0.0001	22.1 (20.2–24.0) ^{a}	20.2 (15.7–24.7) ^{a}	9.3 (6.6–12.0) ^{b}	18.4 (13.6–23.2) ^{a}
N	%	0.23–2.65	8.665	0.0002	1.56 (1.29–1.83) ^{a}	1.37 (1.00–1.74) ^{a}	0.70 (0.51–0.89) ^{b}	1.39 (0.98–1.79) ^{ab}

3.2. Environmental Discrimination of Vegetation Groups

We tested the environmental differences of vegetation clusters using a series of simple models. Cluster A (alliance *Astero-Seslerion*) was well separated from all other clusters based on lime bedrock, lower altitudes, and higher temperatures (Table 1). The relevés from the alliance *Caricion firmae* (cluster B) occur in higher altitudes than those from the alliance *Astero-Seslerion*. Their soil characteristics are similar except for the content of magnesium, which is lower. Cluster C (alliance *Festucion versicoloris*) was a well-differentiated group typical for the highest rates of mean annual precipitation and lowest mean annual temperature. The plots occur on the most acidic soils, with the lowest content of nitrogen, carbon, phosphorus, and minerals. Cluster D represents stands from the alliance *Caricion firmae* from the highest altitudes, which show ecological transitions to the relevés from the alliance *Oxytropido-Elynion* and often forms contact vegetation. They differ from the typical stands of the alliance *Caricion firmae* by more acidic soils, milder slopes, higher rates of mean annual precipitation, and lower mean annual temperature [15,74].

The classification tree based on the environmental data showed that the vegetation clusters can be well separated using the information on geological bedrock and altitude (Figure 5). The tree model had a high classification power on out-of-sample data (cross-validated accuracy = 91%). In particular, cluster A was typical for lower altitudes (≤ 1552 m) and cluster C for mylonite bedrock, and were clearly separated. Classification tree based on soil data (not displayed) had considerably lower classification accuracy (68%) and showed a good discrimination power only for cluster C ($pH_{KCl} \leq 6.3$).

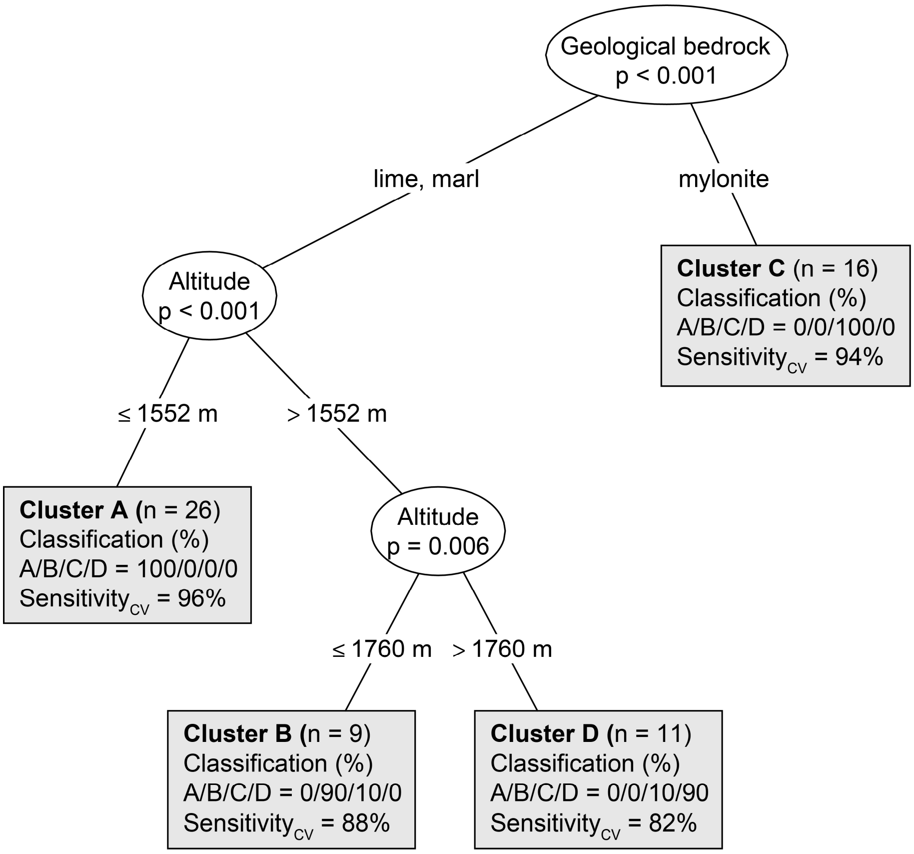

Figure 5. Conditional inference classification tree of vegetation clusters based on environmental data. Bonferroni adjusted probabilities (p), observed classification to clusters (%), and cross-validated sensitivity (Sensitivity_{CV}) are displayed for each cluster.

3.3. Distribution of *Carex rupestris*

An ensemble of 40 tuned bivariate models showed a high accuracy in predicting the occurrence of *C. rupestris* (cross-validated AUC ± SD = 0.90 ± 0.02). Predicted suitable habitat (probability of occurrence > 0.5) covers about 1.7% of the area of Slovakia and includes the highest part of the Western Carpathians (Tatra Mountains, Nízke Tatry Mountains, Malá and Veľká Fatra Mountains), which is consistent with the known geographic range of the species (Figure 6). More than 90% of the occurrence records matched with the two highest probability classes for the potential distribution (probability of occurrence > 0.8).

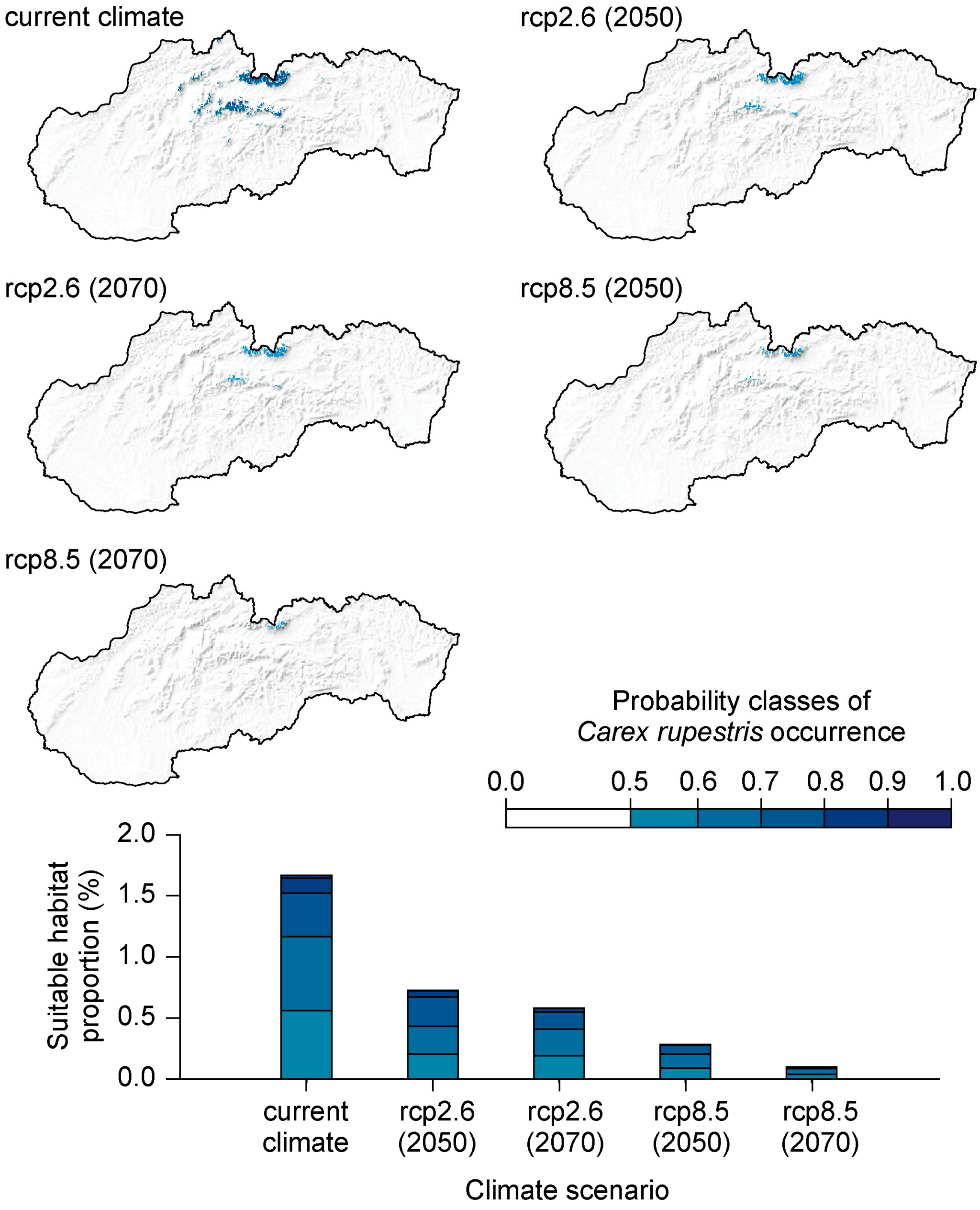

Figure 6. Habitat suitability maps showing the spatial extent of relatively favorable environmental conditions for *C. rupestris* (predicted probability of occurrence > 0.5) under current climate and under two climate change scenarios (rcp2.6, rcp8.5) in the year 2050 and 2070. Elevation hillshade is shown in gray. The barplot displays relative proportion of suitable habitat (percentage of the total area of Slovakia) for the current climate and possible future conditions.

Suitable habitat proportion is expected to decline steeply under all investigated climate change scenarios (Figure 6). Even the mildest rcp2.6 alternative expects a shrinkage of suitable habitat to be 40% in 2050 and the almost complete disappearance of suitable conditions at the known occurrence sites in Nízke Tatry Mountains, Malá, and Veľká Fatra Mountains until 2050. Under rcp8.5, it is expected that there will be an extensive loss of environmental suitability (a decrease to 17% and 6% of the original suitable habitat extent until 2050 and 2070, respectively) and the vanishing of favorable environmental conditions at more than 90% of sites with currently known presence of *C. rupestris*. The Tatra Mountains is expected to be the only mountain range retaining potentially suitable habitats in 2070.

4. Discussion

4.1. Vegetation Classification and Environmental Differentiation of Plots with Carex rupestris

We found that *C. rupestris* in the Western Carpathians occurs in four vegetation types with significantly different environmental settings: alliance *Astero-Seslerion* (cluster A), alliance *Caricion firmae* (cluster B), transition community from *Caricion firmae* to the alliance *Oxytropido-Elynion* (cluster D), and alliance *Festucion versicoloris* (cluster C). The range of communities span relatively wide gradient of altitudes (1297–2012 m asl), bedrock (from lime to mylonite), and associated soil conditions, such as pH (4.0–7.7) or nitrogen (0.2–2.7%). Apparently, the species is able to tolerate a relatively broad spectrum of habitats. On the other hand, occurrence sites cover a relatively narrow window of temperatures (mean annual temperature 0.4–4.0 °C) suggesting cold-adaptation and a restricted thermal niche of the species.

The geographical distributions of the cold-adapted arctic-alpine species with narrow thermal niches are often very constrained in extrazonal areas. In fact, *C. rupestris* was considered to be one of the rarest plant species in the former Czechoslovakia [75]. It is believed that the species migrated along the Carpathians from the northern regions of the Holarctic in the Pleistocene [9] and survived the last glacial maximum in a way leading to a disjunctive arctic-alpine occurrence with a distinctive pattern with steep mountain peaks serving as a barrier to migration and often harboring glacial relicts [76].

The distributions of the cold-adapted arctic-alpine species are probably further limited by local evolution, by historical factors, and random events [77], although recent studies based on the measures of palynological richness assume no evident sensitivity of biodiversity at high elevations to past climate changes during the late-glacial/early Holocene period [78]. It seems that the most important limiting factor affecting the distribution of arctic-alpine species is the existence of suitable sites for these species and vegetation during the climatic optimum in the Holocene [79]. On the other hand, the existence of suitable habitats might not be sufficient, as this would assume that species could easily colonize the localities with appropriate conditions. Hence, the species traits controlling its dispersal ability (e.g., the length of pre-flowering and flowering stages, seed productivity, seed size, way of dispersal, clonality, seed germination, mortality of seedlings, need for suitable micro-loci for recruitment) should be considered as well. *C. rupestris* is a tufted graminoid perennial herb with an extensive, densely branched rhizome, which serves as an efficient local vegetative reproduction. Inflorescence comprises of one terminal spike with wind-pollinated flowers. Seeds show very low germination rates [80]. Moreover, many individuals remain sterile, the size of the populations does not increase and some populations are heavily infected by rust [10,81]. All these characteristics might be considered a competitive disadvantage resulting in a weak ability to colonize new arising habitats.

There was a strong relation between the soil properties and bedrock type of the stands with *C. rupestris*, which is probably strengthened by the fact that much of the rock in such relatively shallow soils is derived from the underlying bedrock brought near the surface by frost action [82]. The soil reaction is often a key factor influencing the species richness of the high-altitude vegetation and the presence of alpine species, as has been observed in the Alps [83] and other parts of Europe, North America, and Arctic [84–88].

4.2. The Fate of *Carex rupestris* in the Western Carpathians

The bioclimatic and topologic variables included in ESMs efficiently described the current distribution pattern of *C. rupestris* and predicted excessive loss of suitable environmental conditions under both of the investigated climate change scenarios. Although some suitable habitats of *C. rupestris* are predicted to occur even under a pessimistic rcp8.5 scenario, it seems that many current presence sites of the species will lack favorable conditions in the future. Remembering the Ukrainian story [30], even the current elevation of temperatures might inevitably cause the decline or even the extinction of *C. rupestris* in some current localities, mainly in the peripheral zones of its current distribution. A progressive decline of cold mountain habitats and the thermophilization of mountain plant communities mirroring the degree of recent warming have been already observed also in many European mountain systems [8,31,32].

Although, the highest probability classes of the ESMs further include a number of grid cells for which the occurrence of the species is very likely, the colonization of new suitable habitats is merely hypothetical, reflecting the species traits (see above), isolation of peripheral localities and the size and vitality of the populations. Still, one should bear in mind the limitations of climate-based HSMs. Notably, the models are blind to the ability of a species to track suitable environments, while the understanding of migration processes, the dynamics of shifting populations, and inter-specific interactions may be crucial for accurate spatio-temporal projections of HSMs [89]. Also, direct human activities, such as trampling (Figure 1C), reduce the species richness, diversity, as well as the percentage cover of cold-adapted species in the alpine environment [90]. Heavier disturbances could, therefore, lead to the direct destruction of the alpine environment, significantly eliminate suitable habitats of the species, and increase the risk for upward shifts of warm-tolerant species. The projected decline of *C. rupestris* in the Western Carpathians may be further exacerbated by the competitive overgrowing of larger plants, which are expected to shift their ranges towards higher altitudes, following elevated temperatures [76]. *Pinus mugo* (Figure 1C) is considered as one of such plants, significantly changing its frequency and overgrowing sites that were historically covered by high-altitude grasslands [31]. Finally, as stems from the concept of an extinction debt [91,92], the effects of global environmental changes, especially in small populations of long-lived perennials might be underestimated and may cause the delayed extinction of even recently stable-looking populations.

From the spatio-temporal projections of HSM, it is clear that *C. rupestris* will be restricted to higher elevations and it is expectable that the Tatra Mountains will be the only mountain range retaining potentially suitable habitats and providing possible refugia for this cold-adapted species in the future. Thus, these core refugia are of high conservation concern and deserve strict protection excluding any human actions that might further impair the habitats. Since this is the first attempt to explicitly model the spatial extent of suitable conditions for a rare arctic-alpine species in the Western Carpathians, the temporal trend in other relic arctic-alpine species needs to be estimated to inform the prioritization of conservation targets. Nevertheless, the predicted severe shrinkage of distribution ranges and associated geographic isolation raises serious concerns for the fate of the arctic-alpine species in the Western Carpathians.

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