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Tuexenia 37: 431–446. Göttingen 2017.
doi: 10.14471/2017.37.017, available.g.le online at www.tuexenia.de

Simulation of long-term changes in environmental factors and grassland composition in three protected areas of Serbia

Simulierte Langzeitveränderungen von Umweltbedingungen und Graslandvegetation in drei Schutzgebieten in Serbien

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Abstract

Intense direct and indirect human pressure has been imposed on grasslands throughout their range. Mostly due to the constant need for more food production or due to changes in environmental conditions, grasslands as habitats are expected to become highly endangered. The aim of this study was to estimate the grasslands' ecological response to future climate and environmental changes.

The study took place in three ecologically different grassland communities in three protected natural areas of Serbia (Southeastern Europe), following the same methodology. The study sites were: 1) Peštersko polje Special Nature Reserve (SNR), 2) Deliblato sands SNR (its southern part: Labudovo okno) and 3) Zasavica SNR.

Climate change was simulated for mean temperatures and precipitations using the Eta Belgrade University-Princeton Ocean Model (EBU-POM) climate model, for the A1B Intergovernmental Panel on Climate Change (IPCC) emission scenario covering the 1951–2100 period and insolation and volumetric soil moisture content for the 1979–2100 period.

Grassland vegetation was analysed at all three sites. One representative plant community per site was selected for further analysis and simulation of ecological changes. One plot was positioned inside each of the above-mentioned communities, all vascular plant species inside the plot were recorded, and soil samples were taken. Ecological Optima (EO) for moisture and temperature were calculated from modified Ellenberg's plant indicator values of recorded species.

The plants' response to climate and environmental changes was simulated using the VSD+ model for the 2010–2100 period. The data obtained from the model were further analysed with Canonical Correspondence Analysis (CCA).

Overall results show that the temperature rise, along with the irregular precipitation at all three sites, will lead to a drop of the relative abundance of many native species in the period between 2040 and 2060. The low obtained Habitat Suitability Index for the future means that there will be either unfavourable environmental conditions for the development of grasslands, or the species we analysed were untypical. Cosmopolitans and xerothermic species will be more accustomed to the new conditions. Grasses will be the most resilient functional group according to our study.

It may be concluded that the functional group of grasses will also play the leading role in future grasslands at the studied sites.

Manuscript received 02 December 2016, accepted 30 June 2017
Co-ordinating Editor: Anikó Csecserics

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Keywords: climate change, habitat suitability index, plant community simulation, Serbian grasslands, VSD+ model

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

According to the Corine land cover map (CLC 2012), grasslands (pastures and natural grasslands) cover 5.08% of the total territory of Serbia. Zonal distribution of grasslands is related to orography. 25.4% of all grasslands are in the valleys of the lowland (up to 300 m), 37.8% are in the hilly region (300–1000 m) and 36.8% in the mountain region (above 1000 m). The grasslands of hilly and mountain region are similar with respect to their floristic composition and thus usually treated as a single group, namely as grasslands of the hilly-mountainous region. These are the floristically richest grasslands, especially in the forest zone (STOSIC & LAZAREVIC 2009). They are also of the greatest significance for livestock production since they are the main or even only source of livestock feed in this region. Nowadays natural grasslands in Serbia are seriously threatened. The abandonment of grasslands, poor management and insufficient grazing pressure lead to changes in species composition and to rapid spread of shrubs and tree species (DAJIĆ STEVANOVIĆ et al. 2008, AĆIĆ et al. 2013).

There have been very few studies that deal with the response of grasslands to climate change in Serbia (e.g., BELOICA et al. 2015), and grassland biodiversity is generally understudied throughout Southeastern Europe (DENGLER et al. 2014). On the other hand, a global study shows that grassland productivity will increase, especially in the humid temperate and Mediterranean biome (PARTON et al. 1995). Most native grasslands are likely to contain a high diversity of drought-tolerant species; hence local native species may help to maintain ecosystem functioning under changing drought regimes (CRAINE et al. 2013). However, there is also the risk that drought-tolerant invasive plants will extend their cover in the future (KELEMEN et al. 2016, WESCHE et al. 2016). Most recent studies including Coupled Model Intercomparison Project (CMIP5, in: IPCC 2014) have confirmed a tendency towards drier and warmer climate in the Mediterranean region (which includes Serbia) in the next century (MARIOTTI et al. 2015, DELL'AQUILA et al. 2016). Future rates of forced warming and drying (by greenhouse gasses, anthropogenic aerosols and natural forcing) in the Mediterranean are projected to be higher than in the past century (MARIOTTI et al. 2015). CRAINE et al. (2013) argued that drought will shift the functional composition of grasslands in ways we do not yet understand. However, species-rich grasslands will have sufficient functional diversity to help to maintain ecosystem functioning despite changes in climate.

JONES et al. (2016) cite evidence-based arguments that grassland ecosystems will be highly responsive to future changes in soil moisture availability caused by altered precipitation variability and increased duration and frequency of dry periods between rain events.

Grasslands will likely respond more rapidly to climate and environmental changes than forests, and changes in vegetation cover will be much easier to detect. Therefore, the aim of our study was to estimate the grasslands' response to future climate and environmental changes. First we tried to detect what changes in climate patterns are expected under the A1B scenario (IPCC 2014) for the studied region, according to the EBU-POM model. Then we analysed possible changes in the species composition of grassland vegetation in three selected plots in Serbia, which emerged as a result of the Very Simple Soil Dynamic model simulation (VSD+ v. 5.5, 2001, 2015, Alterra, CCE; MOL-DIJKSTRA & REINDS 2017).

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2. Materials and Methods

2.1 Study sites

Three sites in different parts of Serbia (Southeastern Europe) were selected to study; their basic characteristics are presented in Table 1. The criteria for the selection of sites were that all sites are under the national protection regime and designated as Ramsar sites, i.e. internationally important habitats for migratory birds (NAVID 1989).

All sites have distinct environmental conditions. The first site, Peštersko polje (PP) Special Nature Reserve, is located on the Pešter plateau, at an altitude of around 1200 m, with a climate for which the term "Serbian Siberia" has been coined: The average temperature of the warmest month is around 15.3 °C, summers are short and winters harsh (the lowest temperature ever measured in Serbia, -39.5 °C, was recorded at this location). The precipitation regime is continental, with a precipitation maximum in May, but the high altitude and the Mediterranean impact generate a secondary maximum in November (Republic Hydrometeorological Service of Serbia, RHMS, http://www.hidmet.gov.rs/ciril/meteorologija/klimatologija_srednjaci.php, accessed 2016–08–29). Grasslands are poorly researched at the PP site, and only little data is available. The studied community was determined as Ass. *Nardetum strictae* Grebenščikov 1950 (RAKONJAC et al. 2008) and therefore classified according to the European Nature Information System (EUNIS, http://eunis.eea.europa.eu/habitats/1218, accessed 2016–08–29) as "mat-grass swards" habitat type (LAKUŠIĆ et al. 2005). Natural grassland is the dominant land cover type, followed by pasture and complex cultivation pattern type (CLC 2012). Dominant influences are: climate, the river Boroštica (which sometimes floods the area) and grazing.

Table 1. Basic information on the studied sites. SNR – Special Nature Reserve. *Southern part of Deliblatska peščara (Deliblato sands) SNR.

Tabelle 1. Grundinformationen zu den drei serbischen Untersuchungsgebieten. SNR = Special Nature Reserve. *, Südteil des Delibater Sande (Deliblatska peščara)-SNR.

Site	PP	LO	ZAS
Name	Peštersko polje	Labudovo okno	Zasavica
Protection status	SNR	SNR*	SNR
Latitude (° N)	43.08050	44.797222	44.939611
Longitude (° E)	20.11475	21.227417	19.529333
Altitude (m)	1158	68	78
Annual mean temperature (°C)	6.09	14.73	10.84
Annual sum of precipitation (mm)	710.16	641.09	614.72
Parent material	Lacustrine/marsh sediments	Aluvium	Aluvium
Soil type WRB	Haplic Planosol (Eutric)	Gleyic Phaeosem (Eutric)	Gleyic Phaeosem (Eutric)
EUNIS habitat type	E1.71 Mat-grass swards	E2.54 Meadows of the steppe zone, dominated by *Agrostis stolonifera*	E2.55 Meadows of the steppe zone, dominated by *Alopecurus pratensis*
Association	*Nardetum strictae* Grebenščikov 1950	*Trifolio-Agrostietum stolonifere* Marković 1973	*Alopecuretum pratensis* Kojić, Mrfat-Vukelić, Dajić, Djordjević- Milošević 2003

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The Labudovo okno (LO) site is the southern part of the Deliblato sands Special Nature Reserve located in the South of the Banat (Pannonian Plain). The climate is Pannonian with a Danubian precipitation regime. "Košava", a strong, winter-specific south-eastern wind, has a special influence, with a wind force of 5.5 Beaufort (11 m/s) (RHMS). The grassland vegetation is described as Ass. *Trifolio-Agrostietum stolonifere* Marković 1973 with high anthropogenic influence, and classified according to EUNIS (LAKUŠIĆ et al. 2005) as "meadows of the steppe zone, dominated by *Agrostis stolonifera*". This site is frequently mowed and grazed. The dominant land cover is natural grassland, surrounded by transitional woodland-shrub and a complex cultivation pattern (CLC 2012).

The third site, Zasavica Special Nature Reserve (ZAS), is located between the Srem and Mačva regions. The climate is also Pannonian, influenced by the Danubian precipitation regime. The Valjevac pasture, where the research was conducted, is claimed to be the only natural pasture left in the area. It has been protected since 1997 and restored not long after (Institute for Nature Conservation of Vojvodina Province), so nowadays only grazing and occasional shrub removing is allowed. The grassland community at the studied site is defined as *Alopecuretum pratensis* Kojić, Mrfat-Vukelić, Dajić, Djordjević-Milošević 2003 and therefore classified as "meadows of the steppe zone dominated by *Alopecurus pratensis*" (LAKUŠIĆ et al. 2005). According to CLC (2012), the most dominant land cover type at the studied site is natural grassland, surrounded by land principally occupied by agriculture with significant areas of natural vegetation and by broadleaved forests.

2.2 Climate research

Data regarding the expected climate conditions were obtained by applying a dynamic downscaling technique using a coupled atmosphere-ocean regional climate model EBU-POM (DJURDJEVIC & RAJKOVIC 2008, KRZIC et al. 2011) and the moderate A1B scenario (IPCC 2014) for greenhouse gas emissions. The whole model simulation covers the 1951–2100 period. For initial and lateral boundary conditions, data from the ECHAM5/MPI-OM model (ROECKNER et al. 2003) simulation were used. ECHAM5 model results are available from the CERA database (http://cera-www.dkrz.de/, accessed 2016–08–29). For the surface air temperature and the daily precipitation model, bias was removed using observed daily time series of the same variables of the normal climate period 1961–1990 obtained from RHMS (Supplement E1), following the so-called bias correction statistical method (RUML et al. 2012). Climate data were extracted from geospatial files for the exact coordinates of the studied sites. The parameters for the simulation were: temperature, precipitation, insolation and soil moisture content.

2.3 Floristic and vegetation research

Grassland vegetation was studied at all three sites and under the different climate and environmental conditions. One permanent plot was selected per site and observed for three consecutive years (2010, 2011 and 2012). Each plot was selected in a way to represent the most dominant grassland type in the area. The plot size was 10 m × 10 m, and all vascular plants were recorded according to the BRAUN-BLANQUET (1965) method. Standard floristic research was conducted; species were determined according to JÁVORKA & CSAPODY (1975), and nomenclature followed the Euro+Med PlantBase (http://ww2.bgbm.org/EuroPlusMed/ accessed 2016–08–29). A cumulative table with relative species cover and ecological indices is presented in Supplement E2.

Modified Ellenberg's indicator values of plant species were determined according to KOJIĆ et al. (1997) and used for the calculation of Ecological Optima (EO). The Ecological Optimum for moisture (EO_m) and for temperature (EO_t) were calculated following the weighted averaging method also suggested by KOJIĆ et al. (1997). According to its EO, each community was positioned on a moisture and temperature gradient using a scale suggested by the authors (Supplement E3).

Habitat types were determined according to the EUNIS database and the Habitats of Serbia Handbook with descriptions and basic data (LAKUŠIĆ et al. 2005).

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2.4 Soil properties research

Soil samples were taken from each studied plot at 20 cm depth in order to test the chemical and physical soil properties. All analyses were conducted at the Faculty of Forestry, University of Belgrade, according to the following methods: pH (in H_2O) was measured electrometrically using a pH meter; the sum of exchangeable bases (EBc) was determined using the KAPPEN (1929) method; the total capacity of cation adsorption (T) and the degree of base saturation (V%) were calculated according to HISSINK (1925); the $CaCO_3$ content was measured with a Scheibler calcimeter; the total organic carbon content was determined by the TYURIN (1931) method; and total nitrogen was measured by the Kjeldahl macro method (BREMNER 1960). The analyses of the mechanical composition of the soil were performed by the pyrophosphate B method. Soil types were determined according to the WORLD REFERENCE BASE FOR SOIL RESOURCES (2006) following the nomenclature suggested by KNEŽEVIĆ et al. (2011).

2.5 Models for ecological simulation

Originally, VSD+ is a soil dynamic model for the estimation of soil property changes under the influence of air pollution and climate change. The VSD+ model that was used in this study for the simulation of changes in species occurrences from 2010 to 2100 is a soil-vegetation model. It is a dynamic soil chemistry model specifically made to calculate the effects of the deposition of nitrogen (N) and sulphur (S) on soil acidification and eutrophication (REINDS et al. 2014). We used a pre-processor model (MetHyd v1.5.1, 2010, 2013, Alterra, CCE; SLOOTWEG et al. 2010) in conjunction with the VSD+ model for calculating daily evapotranspiration, soil moisture, percolation (runoff) and parameters related to (de)nitrification and mineralisation.

The PROPS (Probability of Occurrence of Plant Species) module v.5.5.1. (Alterra, CCE; REINDS et al. 2015) has been used for the simulation of changes in plant communities as a post process model (VSD+PROPS). This model was developed to enable assessments of changes in plant species diversity, which occur as a response to changes in climate and air pollution (REINDS et al. 2015). The PROPS model estimates the occurrence probability (OP) of plant species as a function of abiotic conditions, such as N deposition, soil pH and C:N ratio in the soil, and climatic variables such as temperature and precipitation. The PROPS model (shortly described by REINDS et al. 2012) is based on a dataset of over 40,000 vegetation relevés with measured abiotic soil parameters from across Europe. Input variables for the VSD+PROPS model in our study were: climate parameters (temperature, precipitation, insolation and soil moisture content), physical and chemical soil properties and S and N depositions of the studied vegetation plots. The model output is an aggregate indicator for species occurrence in a habitat – the Habitat Suitability Index (HSI). In this study, besides HSI, the Bray-Curtis index is used as a measure of dissimilarity. The HSI is defined as an arithmetic mean of the normalised/log-transformed probabilities of occurrence of the species of interest (POSCH et al. 2014). While modelling the HSI, all plants species per site were included in the analysis. The other output of the model, the Bray-Curtis index, explains the dissimilarity in species composition (BRAY & CURTIS 1957). It was calculated by comparing the reference OP (obtained from the model for the time when the relevés were taken) to the future OP (obtained by the simulation). The relationship between observed abundance and modelled occurrence probabilities was analysed by Pearson's correlation.

After the simulation, a Canonical Correspondence Analysis (CCA) was performed using Past 3.14 (HAMMER et al. 2001) software. OP (as species scores) and environmental variables were obtained as a result of the simulation for the 2010–2100 period. In order to track changes in the communities that will occur over time, we used scores for every tenth year in the above-mentioned period of time.

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3. Results

3.1 Climate simulation

Results from the climate simulation are synthesised in Table 2, showing the differences between the normal observation period (1961–1990) obtained from RHMS (Supplement E1) and the last 30 years of the simulation period (2071–2100).

For the analysed A1B scenario, the average annual temperature will increase by nearly 2.6 °C at all sites. It is projected that July will be the warmest month. According to the simulation, the biggest change in temperature is projected exactly for the warmest month, July (average increase of 7.37 °C). The precipitation amount will decrease by 55.3 mm on an annual level (Table 2). Reference values (Supplement E1) indicate that June will be the month with the highest amount of precipitation in both regions, with Danubian (LO, ZAS) and Continental (PP) precipitation regimes. However, the projected values of precipitation are quite different. The monthly distribution of precipitation will change significantly, with low values in summer and high values in winter. Particularly, the growing season will apparently become the driest season. The annual amount of precipitation in the region with Danubian regime (LO, ZAS) will decrease considerably, by 50.14 mm and 47.21 mm, respectively. In the region with Continental regime (PP), there will also be a marked change in the amount of precipitation in June (-22.42 mm), but more importantly, the secondary November maximum will disappear (Table 2). Insolation is not about to change much; it will increase on average by 336.4 h/year. Soil moisture content will experience a slight decrease of 0.22 m^3 m^{-3}/year on average at all sites.

The increase of the mean annual temperature will affect all three sites equally (+2.6 °C). The warmest site will remain LO, with a mean temperature of 28.9 °C during the warmest month (July). PP will remain the coldest site (8.7 °C annual temperature), with the lowest July temperature increase (+6.44 °C). The driest site will remain ZAS (568 mm), although the biggest decline of precipitation in the driest month will occur at the LO site (-50.14 mm).

Table 2. Changes of climate parameters. PP – Peštersko polje, LO – Labudovo okno, ZAS – Zasavica, Av. – average value. All results were obtained by comparing data for the reference period (1961–1990) with data from the simulation for the period 2071–2100 according to the A1B scenario. Temperatures were calculated as annual averages. The biggest changes of temperatures and precipitations are on monthly average level. Precipitation, insolation and soil water changes were calculated as average of annual sums.

Tabelle 2. Prognostizierte Klimaveränderungen nach Simulationswerten (nach dem A1B-Szenario) für 2071–2100. Die drei serbischen Untersuchungsgebiete waren: PP = Peštersko polje, LO = Labudovo okno, ZAS = Zasavica; Av. = Mittelwert über die drei Gebiete. Die Referenzperiode umfasste den Zeitraum von 1961–1990. Die Temperaturwerte wurden als Jahresmittel berechnet. Die größten Temperatur- und Niederschlagsänderungen zeigten die Monatsmittel. Die Veränderungen von Niederschlag, Einstrahlung und Bodenwassers wurden als mittlere Jahressummen berechnet.

Sites	Temperature (°C)	Biggest temp. change (°C) / month	Precipitation (l m^{-2})	Biggest prec. change (l m^{-2}) / month	Insolation (h/year)	Soil water (m^3 m^{-3}/year)
PP	↗ 2.58	+6.44 /July	↘ 67.7	-26.08 / Nov.	↗ 480.4	↘ 0.15
LO	↗ 2.55	+7.97 / July	↘ 52.5	-50.14 / June	↗ 337.6	↘ 0.24
ZAS	↗ 2.57	+7.71 / July	↘ 45.8	-47.21 / June	↗ 191.1	↘ 0.28
Av.	↗ 2.57	+7.37	↘ 55.3	-41.38	↗ 336.4	↘ 0.22

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Even with a significant decrease in annual precipitation (-67.7 mm), PP will remain the wettest site (642 mm/year). The highest increase in sunshine duration (+480 h/year) will occur at this site, and it will have the lowest surplus in soil moisture.

3.2 Ecological optima

EO_m and EO_t of species were calculated for each plot. Therefore, each community was positioned on a moisture and temperature gradient (according to Supplement E3), giving us information about the ecological conditions of sites.

An EO_m of 3.92 describes the PP plot as mesic (on the moisture gradient). EO_t is 3.15, which places this community in the mesothermic/thermophilic section. The LO plot has a score of 2.85 for EO_m and 3.27 for EO_t. The community was declared submesic and mesothermic/thermophilic like the previous community. An EO_m score of 3.05 places the ZAS plot between the PP and the LO site. An EO_t of 3.5 makes this community mesothermic/thermophilic as well.

It can be stated for the PP site that EO scores follow the climate data (Table 2): The grassland at the PP site is the coldest and the wettest. As for the other two sites, permutation occurred to a certain extent: The grassland at the LO site is the driest, and the grassland at ZAS is the warmest (despite the climate data).

3.3 Soil properties

According to the soil data (Table 1, 3), the soil at PP is classified as Haplic Planosol (Eutric) (WRB). It is alkaline with a soil pH of 8.01. The soil at the LO site is Gleyic Phaeosem (Eutric) (WRB), also alkaline with a pH of 8.18. The ZAS soil is also Gleyic Phaeosem (Eutric) (WRB), and it is alkaline with a soil pH of 7.78. Regarding the soil texture, the PP site has a higher sand fraction than the other two sites. Soils at the LO and ZAS sites are loamier.

Table 3. Physical and chemical soil properties. PP – Peštersko polje, LO – Labudovo okno, ZAS – Zasavica. The soil was sampled at 20 cm depth. pH was determined from the H_2O solution; EBc represents the sum of exchangeable cations in the soil; T is the cation exchange capacity of the soil (CEC); V is the base saturation of the soil; $CaCO_3$ is the content of calcium carbonate; C is the carbon content and C/N the carbon/nitrogen ratio. In case of active carbonate presence, the soil adsorption complex was not measured. 0* indicates that the soil does not contain any active carbonate.

Tabelle 3. Physikalisch-chemische Bodeneigenschaften der drei serbischen Untersuchungsgebiete: PP = Peštersko polje, LO = Labudovo okno, ZAS = Zasavica. Es wurde Boden in 20 cm Tiefe beprobt; die pH-Werte beziehen sich auf eine wässrige Suspension; S = Summe der austauschbaren Kationen des Bodens, T = Kationenaustauschkapazität (KAK) des Bodens, V = Basensättigung des Bodens, CaCO3 = Kalziumkarbonatgehalt des Bodens, C = Kohlenstoffgehalt des Bodens, C/N = Kohlenstoff/Stickstoffverhältnis des Bodens; „-“ bedeutet: S und T wurden wegen aktiver Karbonatpräsenz nicht gemessen; „0*“ bedeutet: Boden enthält kein aktives Karbonat.

Site	Depth (cm)	pH (H_2O)	EBc (cmol/kg)	T	V (%)	$CaCO_3$ (%)	C (%)	C/N	Sand (%)	Silt (%)	Clay (%)
PP	20	8.01	32.6	33.8	96.9	0*	1.8	11.3	38.1	29.5	32.4
LO	20	8.13	-	-	100	11.4	2.1	11.3	80.1	15.8	4.10
ZAS	20	7.78	-	-	100	4.8	7.3	8.5	7.5	61.2	31.3

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3.4 Species and vegetation changes (model simulation)

Changes of the OP of species per site are given in Figure 1a, b, c, and HSI and B-C index are in Supplement E4. For the PP site, a very low OP is found for all species. The highest OP is only 0.08 in 2010, and it gradually rises to 0.25 towards the last two decades of the 21st century (Fig. 1a). The species can be divided into three groups, relative to their OP: species that will disappear between 2040 and 2060 (e.g., *Galium palustre*, *Veronica scutellata* and *Ranunculus flammula*); species with an OP that will remain on the same low level (e.g., *Lysimachia nummularia*, *Rorippa sylvestris* and *Ranunculus sardous*); and species with an OP that will rise until the year 2100 (only *Agrostis capillaris*, *Leontodon autumnalis* and *Potentila reptans*). For the LO site, values of OP are in the range from 0.01 to 0.49 in 2010. For the majority of species, OP values decrease towards the end of the simulation period. In the year 2100, they are all below 0.2 (Fig. 1b). The OP will rise for the following species: *Lolium perenne* (0.83 in 2100), *Plantago lanceolata* (0.68 in 2100) and *Trifolium pratense* (0.62 in 2100). At the ZAS site (Fig. 1c), only two species have a high OP at the beginning as well as at the end of the simulation period (2010–2100), namely *Dactylis glomerata* (0.62 in 2010; 0.75 in 2100) and *Plantago lanceolata* (0.67 in 2010; 0.68 in 2100). The rest of the species at this site have low starting OP values (below 0.25), which will further decrease below 0.15 in 2100.

The correlation between OP and observed abundance is low: For PP it ranges from 0.32 to 0.46, for LO from 0.30 to 0.39, and for ZAS it is even negative (-0.29 to -0.05).

The minimum HSI is 0.23 (for the PP site in 2010), and the maximum is only 0.55 (for the LO site in 2093). B-C will remain the highest at the ZAS site (0.95 in 2010; 0.84 in 2100). For the other two sites (PP and LO), B–C will decrease considerably (Supplement E4).

Output variables from the model (as environmental variables) and OP (as species scores) were used in CCA ordination. According to the CCA graphs (Supplements E5 a, b, c), the only increasing parameter is temperature, while all the other parameters are expected to decrease at all three sites. Also, the environment at the time of this research was cooler and wetter for the grassland communities (Supplements E5a, b, c, position of 2010 site). It is apparent that the species placed closer to the sites named 2100, 2090 and 2080 will be more accustomed to the new conditions.

4. Discussion

Comparing and analysing data from the RHMS (Supplement E1) with the data obtained from EBU-POM for the three sites, we found differences in temperature and precipitation (Table 2) that correspond to trends in temperature (increasing) and precipitation (decreasing) on a broader scale (MARIOTTI et al. 2015, DELL'AQUILA et al. 2016). However, it is important to emphasise the very high standard deviation of the precipitation data, implying irregularity and uncertainty of precipitation itself.

The change of precipitation patterns may have a greater impact on plant communities than the change of temperature, but not necessarily a straightforward impact (MORECROFT & PATERSON 2006). In particular, the seasonal distribution and variability of precipitation can be more important than its total amount (WELTZIN et al. 2003). The soil moisture content change from our study is in accordance with the results of the simulation undertaken by MIHAILOVIĆ et al. (2016) for the entire territory of Serbia.

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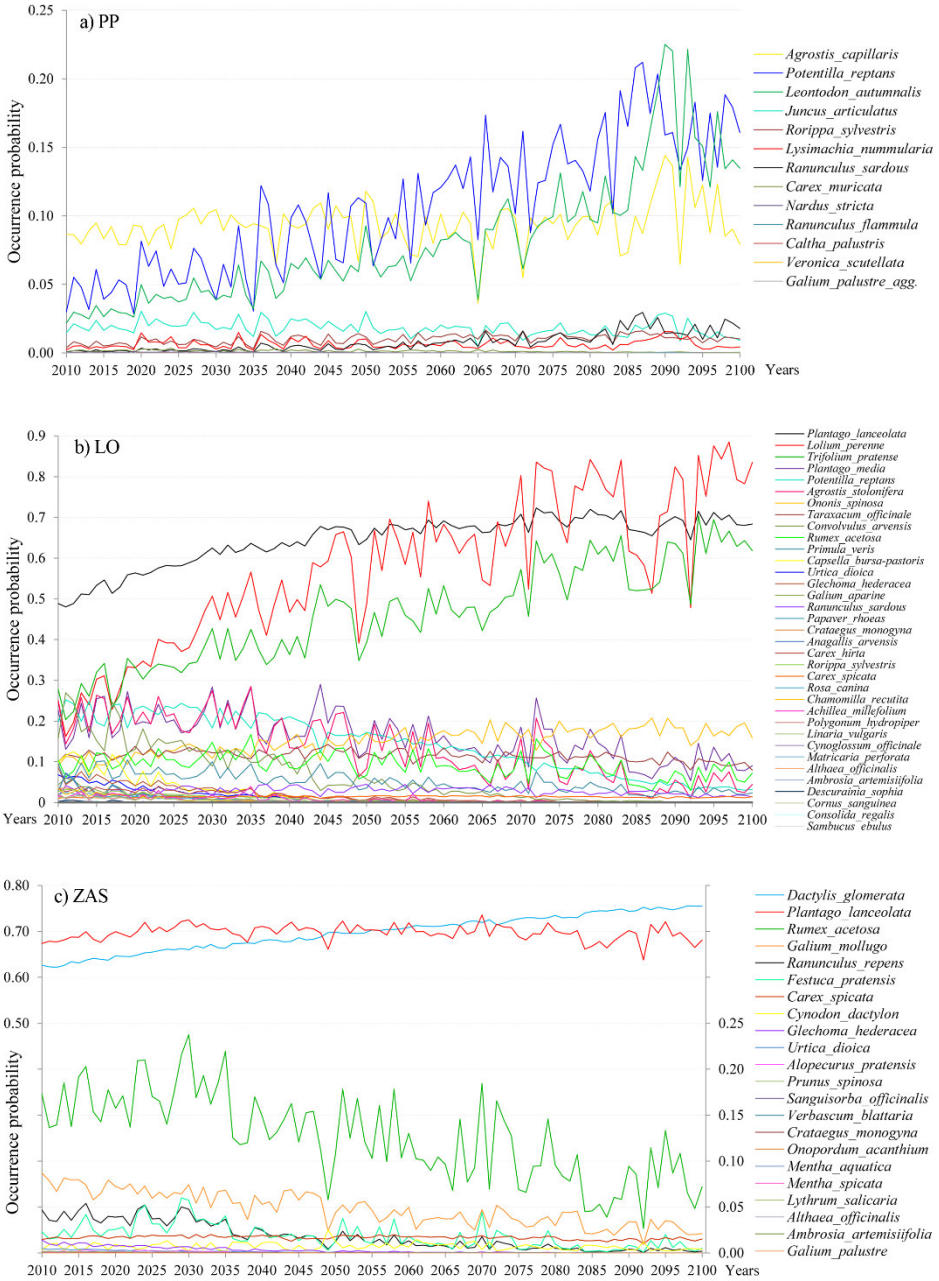

Fig. 1. Occurrence probability (OP) of species for the 2010–2100 period for **a)** the PP (Peštersko polje) site, **b)** the LO (Labudovo okno) site and **c)** the ZAS (Zasavica) site obtained from the VSD+PROPS model.

Abb. 1. Vorkommenswahrscheinlichkeit (OP) von Pflanzenarten im Zeitraum 2010–2100 auf Grundlage des VSD+PROPS-Modells. Die drei serbischen Untersuchungsgebiete waren: **a)** PP = Peštersko polje, **b)** LO = Labudovo okno, **c)** ZAS = Zasavica.

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Regarding the EO_m of species, the PP site is categorised as mesic, meaning that its species prefer moderate moist habitats without a dry period. The other two sites (LO and ZAS) are submesic, with species that prefer mesic conditions, but can survive in xeric conditions as well. Regarding the EO_t, the species of all three sites belong to a mesothermic/ thermophilic ecological group, and a majority are sub-Mediterranean species. The summer period is critical for the survival of certain ecological groups of plants. Comparing the ecological groups at our sites with future climate data (Table 2), we can conclude that the submesophilic ecological group of plants at LO and ZAS should be able to overcome projected hot and dry summers. Similarly, the mesophilic ecological group of plants at PP should overcome the hot summer, since there is no dry period projected for this site. The precipitation pattern is emphasised as the key driver of grassland changes (MORECROFT & PATERSON 2006, FRY et al. 2013), therefore species from the subxerophilic ecological group are more desirable in grasslands. Species from the named group are represented with 28.33% at all three studied sites (Supplement E2); that percentage should be higher in order to overcome such climate conditions. The projected climate pattern (precipitation in the first place) will have a negative impact on plants from the mesophilic and hydro-helophilic ecological group, which are represented with 21.67% at all three sites.

All three sites have alkaline soils, which is typical for the Vojvodina province (LO, ZAS) according to CIRIC et al. (2012). The very high pH value (8) and saturation with bases (96%) at the PP site could origin from the surrounding parent material. MESIĆ et al. (2012) suggest that the optimal C content for grasslands of similar type should be between 1 and 3%. The PP and LO sites have a C content of around 2, which complies with their findings. Considering the C:N ratio, values at PP and LO are in agreement with those found by MESIĆ et al. (2012) (around 11). The ZAS site stands out as an exception because of the high C content (7.3%) and the lower C:N ratio (8.5). Those results imply that the nitrogen content in soils of the ZAS site is also very high, possibly due to fertilisation from the surrounding arable fields (CLC 2012). Decrease of other soil nutrients will not be significant, but in synergy with the lack of soil moisture, it might contribute to change in grassland composition at all three sites.

It has been noticed for all three sites that species that prefer more humid conditions are at the low bottom of the graphs (Figs. 1a, b, c) and gradually fade away. Grasses will be the dominant functional group at all three sites. We found that the relation between OP and abundance is weak, and generally correlations rank below 0.5 (GOMEZ 2014). Such low correlation, especially at the ZAS site, could be explained by the high presence of undesired species (e.g., invasive plants, non-native plants, shrubs) (ČAVLOVIĆ et al. 2012). Thus, drought-tolerant invasive plants may extend their cover (KELEMEN et al. 2016, WESCHE et al. 2016) at the expense of declining native species.

The low HSI value also indicates that there are either unfavourable environmental conditions for the development of grasslands or that untypical species were chosen for the analysis. Nevertheless, simulation shows that HSI will rise towards the end of the century, implying better conditions for grasslands (Supplement E4). However, there are differences between studied sites. In contrast, the Bray-Curtis index of dissimilarity decreases over time, meaning that the species composition is changing (some species are disappearing while the others are expanding their population). Some authors (e.g., VARGA 1997) argue that the dry grasslands of the lowlands of the Pannonian region are the least vulnerable in Europe with respect to climate change, because their species are highly adapted to drought and heat. However, a turnover is possible, with conditions becoming more Mediterranean – forest steppe specialists and forest generalists may decrease, while Mediterranean species are pre-

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dicted to increase (KOVÁCS-LÁNG et al. 2000; THUILLER et al. 2005, WESCHE et al. 2016). Plant species that require higher amounts of soil moisture (e.g., *Galium palustre*, *Veronica scutellata*, *Caltha palustris*) are expected to decline and potentially disappear. According to our simulation, between 2040 and 2060, species with a narrow range of tolerance, especially towards moisture and temperature, will probably start to disappear. The species-poor sites, such as PP, will probably become more open and ruled by only a few dominant species. The stabilisation of the occurrence and non-occurrence (based on the OP) of the species in species-rich grasslands, such as LO, may occur near the end of the century, assuming mowing and grazing pressure of the same intensity.

A decline of similarity indices (e.g., B–C) under climate change and nitrogen deposition scenarios has been confirmed in forest habitats as well (RIZZETTO et al. 2016).

An actual experiment of climate manipulation at Buxton grasslands (GRIME et al. 2008) shows that overall composition and relative abundance of species resisted all 13 years during the experiment. Summer droughts and soil moisture changes resulted in minor species loss or change in species abundances.

Neither dynamical species-habitat models (such as VSD+) nor species distribution models (SDMs) include relations inside the communities of interest (with the possibility of upscaling). On landscape level, CZÚCZ et al. (2011) suggest the implementation of the adaptive capacity of ecosystems as indicator framework, in compliance with SDMs or other types of ecological studies that deal with climate change impact, adaptation and vulnerability.

Management regime has not been included in this study, but it should be part of future research, since it was found that low intensity grazing management is necessary for maintaining the high cover of grassland specialists (TÖRÖK et al. 2016). Land use change and overexploitation, rather than climate change per se, establish the primary threats to the grasslands (GRIME et al. 2008).

5. Conclusion

According to our simulation, the temperature will increase, and precipitations will be irregular and slightly decrease in the studied regions. Similar results have been obtained with global models. Sunshine duration and soil moisture will not change drastically. Grasses (e.g., *Agrostis capillaris*, *Lolium perenne*, *Dactylis glomerata*) will be the ones to adapt the fastest to the new environmental conditions. Plant species with high indicator values for humidity will be the most vulnerable ones (e.g., *Veronica scutellata*, *Rorippa sylvestris* and *Mentha aquatica*).

Erweiterte deutsche Zusammenfassung

Einleitung – In Serbien sind vor allem natürliche Grasländer stark gefährdet. Bislang liegen nur sehr wenige Studien zur Auswirkung von Klimaveränderungen auf Grasländer in Serbien vor (z. B. BELOICA et al. 2015). Zudem wurde die Biodiversität des Graslands in Südosteuropa bislang insgesamt kaum untersucht (DENGLER et al. 2014). Das Ziel dieser Studie ist ein Beitrag zur Kenntnis, inwieweit Pflanzengesellschaften auf veränderte Klimabedingungen reagieren.

Material und Methoden – Die Untersuchung wurden in drei Schutzgebieten in Serbien durchgeführt; untersucht wurden drei ökologisch verschiedene Graslandgesellschaften. Die drei Untersuchungsgebiete waren das Peštersko polje-*Special Nature Reserve* (SNR), das Delibater Sande-SNR (dessen südlicher Teil zum Gebiet Labudovo okno gehört) und das Zasavica-SNR. Zunächst wurde die

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Graslandvegetation der drei Gebiete analysiert. In jedem Gebiet wurde eine repräsentative Pflanzengesellschaft ausgewählt um die ökologischen Veränderungen zu simulieren. Die ökologischen Optima der Arten hinsichtlich Feuchte und Temperatur wurden auf Grundlage von Zeigerwerten (nach KOJIĆ et al. 1997) berechnet. Die Bodeneigenschaften wurden an den gleichen Orten bestimmt, wo die Aufnahmen erstellt wurden. Die Namen der Pflanzenarten entsprechen der EURO+MED-Datenbank und die Habitattypen EUNIS. Die Veränderungen der mittleren Temperatur und des mittleren Niederschlags nach dem A1B-(IPCC 2014)-Szenario wurden auf Grundlage des Zeitraums 1951–2100 mit Hilfe von EBU-POM-Klimamodellen simuliert. Die Einstrahlung und der volumetrische Bodenwassergehalt wurden auf Grundlage des Zeitraums 1979–2100 simuliert. Die Reaktion der Pflanzen auf die Klima- und Umweltveränderungen wurde mit Hilfe von VSD+ (Version 5.5, 2001, 2015 Alterra, CCE; MOL-DIJKSTRA & REINDS 2017) für den Zeitraum 2010–2100 simuliert. Eine kanonische Korrespondenzanalyse der Pflanzengesellschaften für denselben Zeitraum wurde mit Hilfe von Past 3.14 (HAMMER et al. 2001) durchgeführt.

Ergebnisse und Diskussion – Unsere Ergebnisse auf Basis der EBU-POM-Berechnungen zeigen für alle drei Gebiete eine Zunahme der Temperatur und Abnahme der Niederschläge; Letztere werden nach unseren Berechnungen zudem zunehmend unregelmäßig stattfinden (Tab. 2). Nach unserer Vorhersage wird Juli der wärmste Monat werden, wobei unsere Simulierung für diesen wärmsten Monat auch die stärkte Temperaturzunahme zeigt. Zudem wird die Vegetationsperiode die trockenste Zeit werden. Auch die Einstrahlung wird nach unserer Vorhersage leicht zunehmen, während der Bodenwassergehalt dagegen abnehmen wird. Nach einem Abgleich der ökologischen Gruppen der Pflanzen in unseren Gebieten mit dem zukünftigen Klima (Tab. 2) kommen wir zu dem Schluss, dass die submesophilen Pflanzen die vorhergesagten heißen und trockenen Sommer in den beiden Gebieten Labudovo okno und Zasavica überstehen könnten. Dies gilt auch für die ökologische Gruppe der mesophilen Pflanzenarten im Gebiet Peštersko polje, für das unsere Simulationen keine Trockenperiode vorhersagen. Dagegen werden Pflanzenarten mit engem Toleranzbereich hinsichtlich Feuchte und Temperatur nach unseren Simulation auf Basis des VSD+-Models zwischen 2040 und 2060 wahrscheinlich verschwinden (Abb. 4). Die artenarmen Flächen, wie sie im Gebiet Peštersko polje existieren, dürften in ihrer Struktur zukünftig offener und auch zunehmend von einigen wenigen dominanten Arten beherrscht werden. Kosmopolitische und xerotherme Pflanzenarten werden an die hier vermutlich entstehenden Bedingungen am besten angepasst sein. Gräser (z. B. *Dactylis glomerata*, *Lolium perenne* und *Agrostis capillaris*) werden als die stabilste funktionelle Gruppe in der zukünftigen Artenzusammensetzung der Grasländer eine Führungsrolle einnehmen. Zudem könnten sich trockentolerante invasive Pflanzenarten in ihrer Deckung (KELEMEN et al. 2016, WESCHE et al. 2016) auf Kosten der abnehmenden heimischen Arten ausbreiten. Unsere Simulation zeigte ebenfalls, dass gegen Ende des Jahrhunderts der *Habitat Suitability Index* ansteigt, was sogar bessere Bedingungen für Grasländer insgesamt impliziert (s. Anhang E4). Umgekehrt nahm der Bray-Curtis-Ähnlichkeitsindex mit der Zeit ab, was ebenfalls auf eine Veränderung der Artenzusammensetzung hindeutet weil einige Arten verschwinden während andere Arten zunehmen werden. Eine nach der Simulation durchgeführte CCA (s. Anhang E5) zeigt, dass die Temperatur als einziger Parameter ansteigen wird, während alle anderen untersuchten Parameter abnehmen werden. Das Managementregime wurde in unserer Studie nicht berücksichtigt. Da jedoch gezeigt wurde, dass eine extensive Beweidung für den Erhalt der Graslandspezialisten notwendig ist (TÖRÖK et al. 2016), sollte das Managementregime in zukünftigen Untersuchungen berücksichtigt werden.

Acknowledgement

This research was part of the project 'Studying climate change and its influence on the environment: impacts, adaptation and mitigation' (43007) financed by the Ministry of Education and Science of the Republic of Serbia within the framework of integrated and interdisciplinary research for the period 2011–2017.

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Supplements

Additional supporting information may be found in the online version of this article.

Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.

Supplement E1. Mean monthly temperature (t), mean monthly sum of precipitation (p), and mean annual temperature and annual precipitation sum obtained from RHMS for the period 1961–1990.

Anhang E1. Monatsmittel der Temperatur (t) und des Niederschlags (p) sowie Jahresmittel (Year) der Temperatur und des Niederschlags nach Angaben des RHMS für den Zeitraum 1961–1990.

Supplement E2. Relative species percent cover and modified indicator values for the sites Zasavica (C_ZAS), Labudovo okno (C_LO), and Peštersko polje (C_PP).

Anhang E2. Relative Prozentdeckung und modifizierte Zeigerwerte der Arten in den Gebieten Zasavica (C_ZAS), Labudovo okno (C_LO) und Peštersko polje (C_PP).

Supplement E3. Ecological optima (EO) of species regarding moisture (EO_m) and temperature (EO_t), and their corresponding ecological groups according to KOJIĆ et al. (1997).

Anhang E3. Ökologische Optima der Arten bezüglich Feuchte (EO_m) und Temperatur (EO_t) und die entsprechende ökologische Artengruppe nach KOJIĆ et al. (1997).

Supplement E4. Bray-Curtis index for Peštersko polje (B-C_PP), Labudovo okno (B-C_LO) and Zasavica (B-C_ZAS); Habitat Suitability Indices for Peštersko polje (HSI_PP), Labudovo okno (HSI_LO) and Zasavica (HSI_ZAS).

Anhang E4. Bray Curtis-Index für die Gebiete Peštersko polje (B-C_PP), Labudovo okno (B-C_LO) und Zasavica (B-C_ZAS); Habitat-Eignungsindex für Peštersko polje (HSI_PP), Labudovo okno (HSI_LO) und Zasavica (HSI_ZAS).

Supplement E5. Species occurrence probabilities from the VSD+PROPS model are taken as the species scores for CCA.

Anhang E5. CCA der drei Gebiete a) PP = Peštersko polje, b) LO = Labudovo okno und c) ZAS = Zasavica.

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Supplement E1. Mean monthly temperature (t), mean monthly sum of precipitation (p), and mean annual temperature and annual precipitation sum obtained from RHMS for the period 1961–1990. The extremes are displayed as bold; secondary precipitation maximum is underlined. Study sites are: PP = Peštersko polje site, LO = Labudovo okno site, ZAS = Zasavica site.

Anhang E1. Monatsmittel der Temperatur (t) und des Niederschlags (p) sowie Jahresmittel (Year) der Temperatur und des Niederschlags nach Angaben des RHMS für den Zeitraum 1961–1990. Minima/Maxima sind fett dargestellt; der zweithöchste Monatsniederschlag ist unterstrichen. Die Untersuchungsgebiete sind: PP = Peštersko polje, LO = Labudovo okno und ZAS = Zasavica.

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Year
PP	t (°C)	**-4.94**	-2.70	1.32	6.15	10.89	13.67	**15.31**	14.98	11.65	6.98	2.26	-2.53	6.09
	p (mm)	48.26	**38.01**	38.56	48.72	73.86	**85.23**	68.53	67.25	59.94	57.21	<u>71.47</u>	53.12	710.16
LO	t (°C)	**-0.50**	1.88	6.28	11.67	16.54	19.39	**20.89**	20.60	17.06	11.84	6.35	1.59	11.13
	p (mm)	44.39	40.96	41.69	55.29	72.17	**88.25**	67.88	56.41	49.67	**39.61**	48.02	56.12	660.45
ZAS	t (°C)	**-0.77**	1.76	6.22	11.51	16.54	19.32	**20.74**	20.15	16.46	11.23	5.75	1.17	10.84
	p (mm)	40.4	**37.3**	40.8	51.1	58.2	**84.3**	64.6	54.2	44.1	38.2	52.0	49.4	614.7

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Supplement E2. Relative species percent cover for the sites Zasavica (C_ZAS), Labudovo okno (C_LO), and Peštersko polje (C_PP); modified indicator values for soil moisture (SM), soil acidity (pH) (SA), nutrients (SN), light (LC), and temperature (T). Relevé size was 10 m × 10 m.

Anhang E2. Relative Prozentdeckung der Arten in den Gebieten Zasavica (C_ZAS), Labudovo okno (C_LO) und Peštersko polje (C_PP). Modifizierte Zeigerwerte für Bodenfeuchte (SM), Bodenreaktion (pH) (SA), Nährstoffe (SN), Licht (LC) und Temperatur (T). Die Größe der Aufnahmeflächen betrug 10 × 10 m.

Species name	C_ZAS	C_LO	C_PP	SM	SA	SN	LC	T
Achillea millefolium	.	3.3	.	2	3	3	4	3
Agrostis capillaris	.	.	11.5	3	2	2	3	3
Agrostis stolonifera	.	5.3	.	3	2	2	3	3
Alopecurus pratensis	9.2	.	.	3	3	4	3	3
Althaea officinalis	2.6	1.3	.	3	3	3	4	5
Ambrosia artemisiifolia	6.6	1.3	.	2	3	3	4	4
Anagallis arvensis	.	3.3	.	3	3	3	3	3
Caltha palustris	.	.	3.3	5	3	3	3	3
Capsella bursa-pastoris	.	2	.	2	3	3	4	3
Carex hirta	.	2	.	3	3	3	3	3
Carex muricata	.	.	11.5	3	3	2	3	4
Carex spicata	6.6	3.3	.	3	3	2	3	3
Cerinthe minor	2.6	.	.	2	4	3	4	5
Chamomilla recutita	.	3.3	.	3	3	2	3	3
Chenopodium album	.	2	.	2	3	4	3	3
Consolida regalis	.	3.3	.	3	3	3	4	4
Convolvulus arvensis	.	4.7	.	2	4	3	4	3
Cornus sanguinea	.	1.3	.	3	4	3	3	3
Crataegus laevigata	.	1.3	.	3	3	3	3	3
Crataegus monogyna	6.6	2	.	3	4	3	4	3
Cynodon dactylon	6.6	.	.	2	3	3	4	5
Cynoglossum officinale	.	3.3	.	2	4	4	4	3
Dactylis glomerata	3.9	.	.	3	3	4	3	3
Descurainia sophia	.	2	.	2	3	3	4	3
Festuca pratensis	6.6	.	.	3	3	3	4	3
Galium mollugo	3.9	.	.	3	3	3	3	3
Galium palustre	3.9	2	8.2	5	3	2	3	3
Glechoma hederacea	3.9	2	.	3	3	3	3	3
Juncus articulatus	.	.	8.2	4	2	3	3	3
Leontodon autumnalis	.	.	4.9	3	3	3	4	3
Linaria vulgaris	.	3.3	.	2	4	3	3	4
Lolium perenne	.	3.3	.	3	3	4	4	3
Lysimachia nummularia	.	.	8.2	4	3	3	2	3
Lythrum salicaria	2.6	.	.	4	3	3	3	3
Matricaria perforata	.	2	.	3	3	5	3	4
Mentha aquatica	2.6	.	.	5	3	3	3	3
Mentha spicata	3.9	3.3	.	4	4	4	3	3
Nardus stricta	.	.	13.1	3	1	2	4	3
Ononis spinosa	.	2	.	2	3	2	4	5
Onopordum acanthium	2.6	.	.	2	3	5	4	4
Papaver rhoeas	.	1.3	.	3	4	3	3	3
Plantago lanceolata	2.6	2	.	3	3	3	3	3
Plantago media	.	1.3	.	2	4	2	4	3
Polygonum hydropiper	.	2	.	4	2	3	3	3
Potentilla reptans	.	3.3	8.2	3	3	4	4	3
Primula veris	.	1.3	.	2	4	2	4	3
Prunus spinosa	6.6	.	.	2	4	3	4	4
Ranunculus flammula	.	.	4.9	5	2	1	4	3
Ranunculus polyanthemos	3.9	2	.	2	3	2	3	4
Ranunculus sardous	.	3.3	8.2	4	3	3	4	4
Rorippa sylvestris	.	2	4.9	4	4	3	4	4
Rosa canina	.	1.3	.	3	3	2	3	3
Rumex acetosa	2.6	3.3	.	3	3	3	4	3
Sambucus ebulus	.	2	.	3	4	4	4	4
Sanguisorba officinalis	2.6	.	.	4	3	2	4	3
Taraxacum officinale	.	3.3	.	3	3	3	4	3
Trifolium pratense	.	4.7	.	3	3	3	3	3
Urtica dioica	3.9	2	.	3	3	5	3	3
Verbascum blattaria	2.6	.	.	2	4	3	4	4
Veronica scutellata	.	1.3	4.9	5	2	2	3	2

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Supplement E3. Ecological optima (EO) of species regarding moisture (EO_m) and temperature (EO_t), and their corresponding ecological groups according to KOJIĆ et al. (1997).

Anhang E3. Ökologische Optima der Arten bezüglich Feuchte (EO_m) und Temperatur (EO_t) und die entsprechende ökologische Artengruppe nach KOJIĆ et al. (1997).

EO_m	Ecological group of plants relative to moisture	EO_t	Ecological group of plants relative to temperature
1	Xerophytes	1	Arctic and Alpine plants (frigoriphilic)
2	Subxerophytes	2	Frigoriphilic/mesothermic
3	Submesophytes	3	Mesothermic (Middle-European)
4	Mesophytes	4	Mesothermic/thermophilic
5	Hydro-helophytes	5	Thermophilic (Mediterranean)
6	Amphibious and floating hydrophytes		
7	Submerged hydrophytes		

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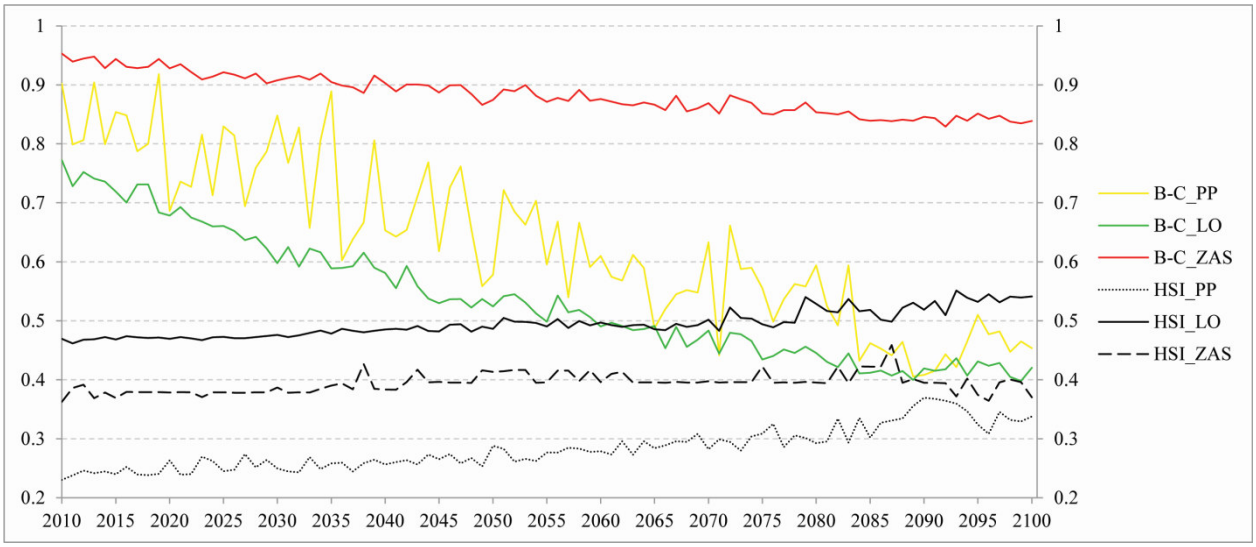
Supplement E4. Bray-Curtis index for Peštersko polje (B-C_PP), Labudovo okno (B-C_LO) and Zasavica (B-C_ZAS); Habitat Suitability Indices for Peštersko polje (HSI_PP), Labudovo okno (HSI_LO) and Zasavica (HSI_ZAS). Period under simulation: 2010-2100. Values for both indices may range from 0 to 1 (as value of HSI rises, a habitat becomes more suitable; as value of B-C rises, the species composition changes).

Anhang E4. Bray Curtis-Index für die Gebiete Peštersko polje (B-C_PP), Labudovo okno (B-C_LO) und Zasavica (B-C_ZAS). Habitat-Eignungsindex für Peštersko polje (HSI_PP), Labudovo okno (HSI_LO) und Zasavica (HSI_ZAS). Simulationsperiode 2010–2100. Die Werte der beiden Indices können von 0 bis 1 reichen (je höher der HSI-Wert liegt, desto geeigneter ist das Habitat, und je höher der B-C-Wert liegt, desto mehr ändert sich die Artenzusammensetzung).



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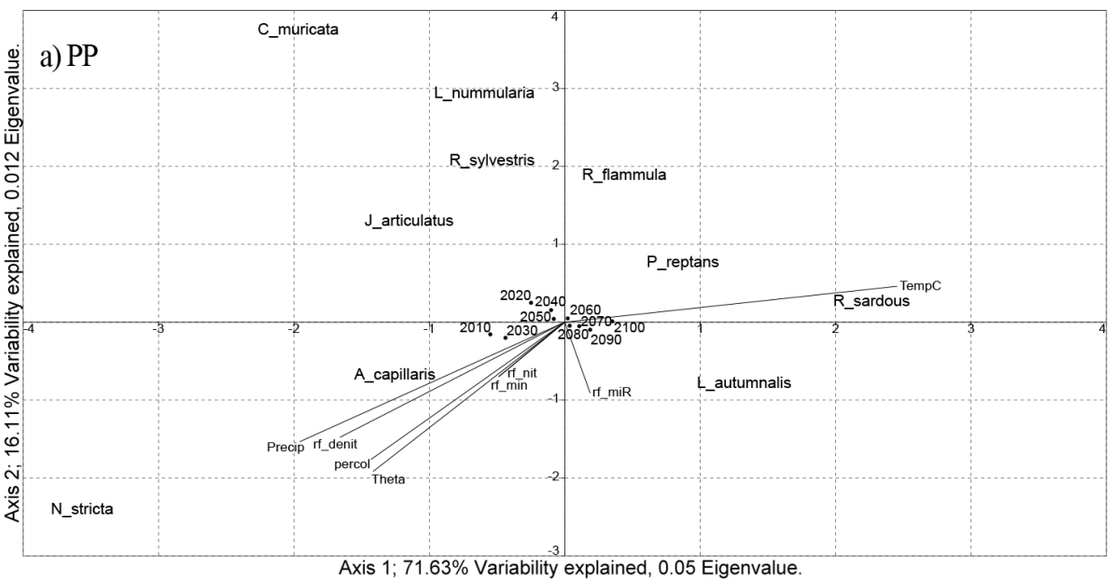
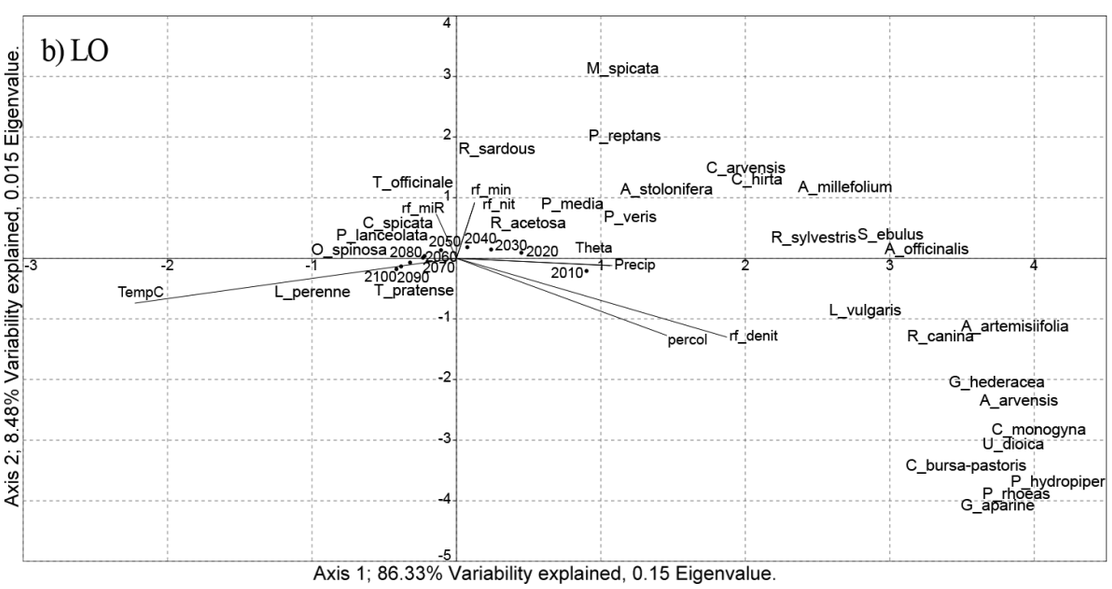
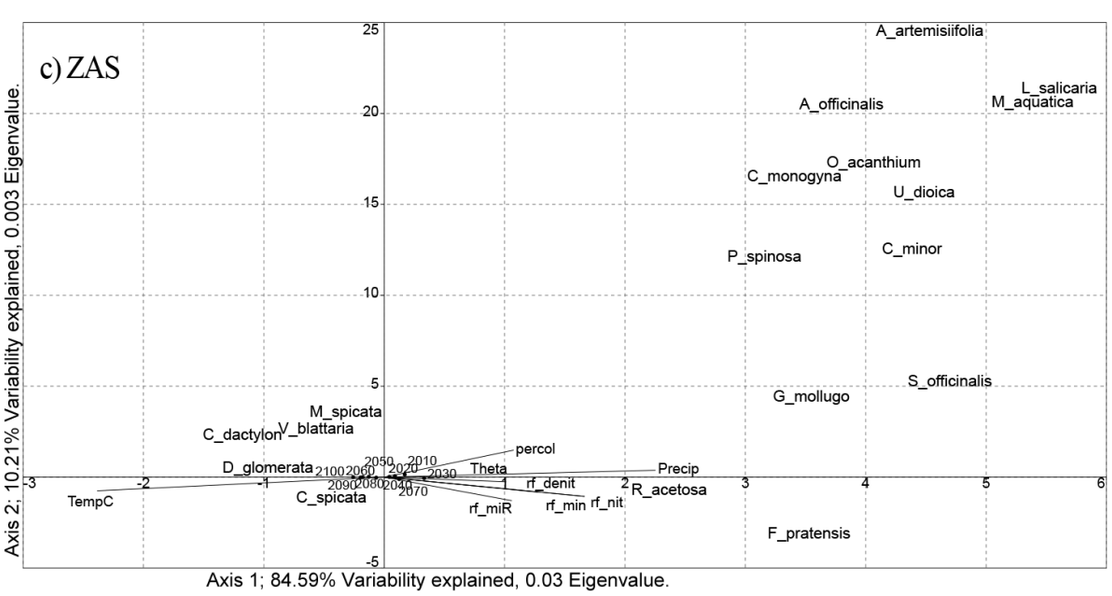
Supplement E5. CCA of the three areas a) PP (Peštersko polje) site, b) LO (Labudovo okno) site, c) (ZAS) Zasavica site. Species occurrence probabilities from the VSD+PROPS model are taken as the species scores for CCA. Output parameters from the model are taken as environmental variables (**rf min** = Reduction factor of mineralization rates due to moisture and temperature; **rf nit** = Reduction factor of nitrification rates due to moisture and temperature; **rf denit** = Reduction factor of denitrification rates due to moisture and temperature; **miR** = Reduction factor of mineralization rates due to moisture and temperature (input for the RothC component of the latest VSD+ model); **Percol** = Precipitation surplus mm/yr; **TempC** = Average temperature per year; **Precip** = Sum of precipitation per year; **Theta** = Soil water content). Years from the simulation are taken as sites (every 5 years in 2010-2100 period). p = 0.001, 0.003, 0.002 in 999 permutation test for all sites respectively.

Anhang E5. CCA der drei Gebiete a) PP = Peštersko polje, b) LO = Labudovo okno und c) ZAS = Zasavica.
Die Artwerte stellen die Vorkommenswahrscheinlichkeiten der Arten nach dem VSD+PROPS-Model dar. Ergebnisparameter aus dem Model wurden als Umweltvariablen genutzt (**rf min** = Reduktionsfaktor der Mineralisationsrate nach der Feuchte und Temperatur; **rf nit** = Reduktionsfaktor der Nitrifikationsrate nach der Feuchte und Temperatur; **rf denit** = Reduktionsfaktor der Denitrifikationsrate nach der Feuchte und Temperatur; **miR** = Reduktionsfaktor der Mineralisationsrate nach der Feuchte und Temperatur (Input der RothC-Komponente des letzten VSD+-Models); **Percol** = Niederschlagsüberschuss in mm pro Jahr; **TempC** = Jahresmitteltemperatur; **Precip** = Jahresniederschlag; **Theta** = Bodenwassergehalt. Die Jahre aus der Simulation wurden als Gebiete genutzt (alle 5 Jahre der Periode 2010–2100). p = 0,001, 0,003, 0,002 in 999 Permutationstests für alle Gebiete.







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Jahr/Year: 2017

Band/Volume: NS_37

Autor(en)/Author(s): Cavlovic Dragana, Beloica Jelena, Obratov-Petkovic Dragica, Durdevic Vladimir, Kosanin Olivera

Artikel/Article: Simulation of long-term changes in environmental factors and grassland composition in three protected areas of Serbia 431-446