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Ecological patterns of Odonata assemblages in karst springs in central Montenegro

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Abstract – Karstic springs are important habitats for maintaining freshwater biodiversity. However, little is known about Odonata larvae assemblages in karstic springs, and studies about the ecological factors that determine species distribution in these habitats are still lacking. In this study the composition of Odonata larvae communities from 91 springs located in the central part of Montenegro was investigated. The richest fauna was found in sublacustrine springs, followed by limnocrenes, while that of the rheocrenes was less rich. The results obtained confirm the main research hypothesis that Odonata larvae assemblages in the karstic springs in the central part of Montenegro were comparably influenced by the environmental parameters acting on the level of individual springs as well as the factors acting at the landscape level. Odonata larvae assemblages divided springs into four groups. On the other hand, the springs could be divided into three groups based on habitat and landscape characteristics. CCA indicates that disturbance factors such as the permanence and directness of human influence on springs for use as drinking water sources are foremost in determining Odonata assemblages at the level of individual springs. The habitat scale considered several factors that influence Odonate assemblages, including altitude and riparian vegetation. This study proves that further odonatological studies in springs should include both types of factors and their interactions.

Keywords: Odonata / Montenegro / springs / crenobiology / diversity

Résumé – Patterns écologiques des assemblages d'Odonates dans les sources karstiques du centre du Monténégro. Les sources karstiques sont des habitats importants pour le maintien de la biodiversité des eaux douces. Cependant, on sait peu de choses sur les assemblages de larves d'odonates dans les sources karstiques et des études sur les facteurs écologiques qui déterminent la répartition des espèces dans ces habitats font toujours défaut. Dans cette étude, la composition des communautés de larves d'odonates de 91 sources situées dans la partie centrale du Monténégro a été étudiée. La faune la plus riche a été trouvée dans les sources sublacustres, suivies par les limnocrènes, tandis que celle des rhéocrènes était moins riche. Les résultats obtenus confirment la principale hypothèse de recherche selon laquelle les assemblages de larves d'odonates dans les sources karstiques dans la partie centrale du Monténégro étaient influencés par les paramètres environnementaux agissant au niveau de chaque source ainsi que par les facteurs agissant au niveau du paysage. Les assemblages de larves d'odonates ont séparé les sources en quatre groupes. Par ailleurs, les sources pourraient être divisées en trois groupes en fonction des caractéristiques de l'habitat et du paysage. La CCA indique que des facteurs de perturbation tels que la permanence et l'influence humaine directe sur les sources utilisés comme sources d'eau potable sont essentiels pour déterminer les assemblages d'odonates au niveau de chaque source. À l'échelle de l'habitat plusieurs facteurs influent sur les assemblages d'odonates, dont l'altitude et la végétation riveraine. Cette étude montre que d'autres études odonatologiques dans les sources devraient inclure les deux types de facteurs et leurs interactions.

Mots-clés : Odonate / Monténégro / source / crénobiologie / diversité

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1 Introduction

Odonates are a significant component of aquatic ecosystems and they are often used as bioindicators of ecosystem health (Oertli, 2008; Dolný *et al.*, 2011). In addition, in aquatic ecosystems where they are the top predators, odonates can influence many other components as they have a wide range of interactions with different organisms (Knight *et al.*, 2005). odonates have a high dispersal capacity (Conrad *et al.*, 1999) and inhabit a wide range of aquatic habitats including lentic and lotic water bodies. In general, the Odonate fauna of Montenegro has been sufficiently studied and so far 67 species have been recorded for the country (Gligorović *et al.*, 2010; De Knijf *et al.*, 2013; Buczyński *et al.*, 2014).

Springs are considered as groundwater-surface ecotones which host specialized and often endemic or rare taxa (Di Sabatino *et al.*, 2003; Cantonati *et al.*, 2006; Savić *et al.*, in press). The lower and usually stable temperature creates optimal conditions for stenothermal cold-water organisms and thus springs can highly contribute to the regional biodiversity of freshwater ecosystems (Boulton 2005; Pešić *et al.*, 2016). Beside the temperature, the macroinvertebrate composition of springs is also influenced by various environmental factors such as hydrological conditions, physico-chemical parameters and substratum composition (Hahn, 2000; Ilmonen and Paasivirta, 2005; von Fumetti *et al.*, 2006; von Fumetti and Nagel, 2012). The relative importance of different factors in aquatic and terrestrial habitats during larval and adult life stages of odonates, respectively, is poorly understood (Remsburg and Turner, 2009). Despite relatively long duration of the larval stage it seems that the relative distribution of Odonata is not primarily associated with this stage (Harabiš and Dolný, 2010). Generally, water velocity, temperature, shading, disturbance, type of substrate, trophy, aquatic vegetation (its spatial structure and abundance) and predation risk are considered to be the most important factors shaping assemblages of Odonata larvae (Buchwald, 1992; Buss *et al.*, 2004; Johansson *et al.*, 2006; McCauley, 2007; Strange *et al.*, 2007; Buczyński, 2015). The regional distribution of Odonata seems to be mostly affected by dispersal at the adult stage (Hof *et al.*, 2006) while the local distribution is probably mainly affected by interactions at the larva stage (McCauley, 2007).

Little is known about the ecology of odonates in springs, and with exception of some rare papers (*e.g.*, Buczyński, 1999; Buczyński *et al.*, 2003; Borisov, 2015), studies about the ecological factors that determine species distribution in these habitats are still lacking. In this study we postulated that Odonata assemblages in springs might be affected not only by factors acting at the level of individual spring (in this paper "habitat" factors), but also by factors acting in the terrestrial environment ("landscape" factors).

The present study aims to determine which assemblages of Odonata larvae occur in spring habitats in Montenegro. Further, we evaluate the impact of selected environmental and habitat factors on the spatial pattern of these assemblages and check what factors – local habitat factors affecting an individual spring, or landscape factors affecting the broader scale – determine the formation of Odonata larvae assemblages in karstic spring habitats.

2 Material and methods

Odonata larvae were collected from 91 springs (78 rheocrenes, 11 limnocrenes and 2 sublacustrine springs, see Appendix 1) located in the central part of Montenegro. The studied area belongs to the drainage basin of Lake Skadar, the largest lake in the Balkan Peninsula with a surface area that seasonally fluctuates between 370 and 600 km^2. There are a number of temporary and permanent karstic springs, most of them rheocrenes and limnocrenes (for spring type definition see *e.g.*, Gerecke and Di Sabatino, 2003). Some of springs are sublacustrine (called cryptodepressions or 'okos') and they occur along the shores of Lake Skadar; these springs issue from underwater dolines.

The sampling was done from 2009 to 2015. Odonata larvae were sampled with a small Surber sampler (10×10 cm = 0.01 m^2, 350 μm mesh width). All samples were immediately preserved in 96% ethanol, and subsequently sorted and identified in the laboratory. The identification and counting of material collected was done on the last-instar larvae and preimagines.

At each site water temperature (in winter – T_w and in summer – T_s) and pH were measured with a pH-meter (HI 98127, accuracy 0.1). Three measurements were carried out and the median was used for each for further analysis. The springs were divided into four classes based on their size (SI): 1: <1 m^2, 2: 1–5 m^2, 3: $\geq$5–20 m^2, 4: >20 m^2. Water discharge was determined visually at each site in winter (Diw) and summer (Dis), and the springs were grouped into four classes: 1 (<1 L min^{-1}), 2: ($\geq$1 and <5 L min^{-1}), 3: ($\geq$5 and <25 L min^{-1}), 4: ($\leq$25 L min^{-1}) according to von Fumetti *et al.* (2006).

The substrate types (anoxic mud – AM, clay – CL, sand – SA, gravel – GR, stones – ST, rocks – RO) present within the sites were categorized into four classes of frequency based on the percentage cover (von Fumetti *et al.*, 2006): 0: 0%; 1: 1–25%; 2: 26–50%; 3: 51–75%; 4: 76–100%. The percentage cover of the aquatic vegetation present within the site (macrophyte – MC, algae – ALG, and mosses – MS) was categorized into four classes: 0: 0%; 1: 1–25%; 2: 26–50%; 3: 51–75%; 4: 76–100%. In total 16 parameters of physicochemical characteristics (discharge, spring size, temperature and pH), substrate composition, aquatic vegetation, spring permanence (CO) and direct anthropogenic impact (AI) on the springs were analysed at the habitat level.

Analysis of the landscape was based on buffer zones marked out as a circle around each sampling site with a radius of 50 m from the waterline of each studied spring. Different land use and land cover types were categorized into four classes of frequency based on the percentage of cover: 0: 0%; 1: 1–25%; 2: 26–50%; 3: 51–75%; 4: 76–100%. The following basic parameters of the landscape were measured and described for each sampling site: (1) altitude (AL), (2) distance to nearby bodies of water (DWB), (3) flooding area (FL) and (4) the surface area of the patches of different types present in the landscape: forest (FO), riparian vegetation (RI), meadows (ME), built-up area (BA), agricultural land (AG) and karst vegetation (KA). In total 9 parameters were analysed at the landscape level.

Statistical analyses were performed using PRIMER 7.0 (Clarke and Gorley, 2015), MVSP v3.21 (Kovach, 2007) and SPSS 19. Dominance (D) and frequency (F) indices were used to evaluate species. The distribution of data was tested with the Kolmogorov–Smirnov test. For cluster analysis based on environmental data, centered and standardized environmental data was classified by the Euclidean distance similarity index. For classification of biotic samples, the Bray–Curtis similarity index on square root transformed data was used. PCA was undertaken on centered and standardized environmental data of the site groups used in the previous cluster analysis. SIMPER analysis was performed to test differences within the faunal composition of clusters A, B, C and D, and I, II and III clusters of sites distinguished by habitat (H) and landscape (L) classification.

Using the SIMPER procedure, dissimilarities between, and similarities within the above-mentioned groups can be explained with individual species and the composition of Odonata assemblages. A repeated measured analysis of variance (ANOVA) and multiple range tests (Fisher's least significant difference (LSD) procedure) were applied to determine the significance of differences in species richness between groups of springs. CCA (ter Braak, 1986) was applied to test the influence of environmental variables on the assemblages investigated. We first performed a forward selection of environmental variables (Legendre *et al.*, 2011). Also, we used the unrestricted Monte Carlo permutation test (ter Braak and Wiertz, 1994) to test the null hypothesis that the selected variables are unrelated to Odonata assemblages in investigated springs.

3 Results

3.1 General characteristics of Odonata fauna

We collected 2979 Odonata larvae during this study. In the material collected were 44 species belonging to 25 genera (Tab. 1). From one to 23 taxa were found per spring. The maximum α-diversity (23 and 22 species respectively) was found in S5 and S6–two large sublacustrine springs at Lake Skadar. In contrast, the lowest α-diversity (single species) was found in S47. The highest frequency was noted for *Cordulegaster bidentata* (present in 54 springs) and the most abundant species in the material was *Cordulegaster bidentata* (269 specimens).

The qualitatively richest fauna was found in sublacustrine springs (22.5 ± 0.71 species), followed by limnocrenes (14.8 ± 4.74), while that of the rheocrenes was less rich (6.51 ± 3.89). Using the one way ANOVA, it was confirmed that species richness ($F = 39.45$, $p < 0.001$) in different types of springs differed significantly. The LSD analysis revealed significant difference between sublacustrine springs and limnocrenes ($p = 0.013$) and rheocrenes ($p < 0.001$) as well between rheocrenes and limnocrenes ($p < 0.001$).

3.2 Faunistic similarity between springs

Figure 1 presents a dendrogram grouping springs based on faunistic similarity. The springs were clearly grouped in four clusters. Faunistic similarity between springs ranged from 2.91% to 92.31%. The first cluster includes limnocrenes and small rheocrenes springs at the higher altitude, characterized by their high content of anoxic mud and absence of riparian vegetation. The springs of the second cluster includes small rheocrenes at lower altitudes affected by drought (S11,16,34,38,66,68,82) or anthropogenic disturbance (S33,49,66,68).

Most springs belong to cluster C. This cluster includes most of rheocrenes at the lower and medium altitudes. The springs from this group manifest a wide variation in substrate composition (anoxic mud to limestone) and a greater distance from nearby water bodies. Cluster D consisted of two subclusters. The first one includes sublacustrine springs (S6–7) and limnocrenes (S1–3,7,13,36,44,60,74). The second one includes large lowland karstic springs (called “vrelo”, S4,22–23,41,44,46) and a small rheocrenes (S17,19–21,26–29,42,62) located on the river banks.

ANOVA showed significant difference ($F = 13.63$, $p < 0.001$) for the species richness between Odonata assemblages from site clusters A, B, C and D. The highest diversity reveal assemblage type C (12.12 ± 5.81), followed by assemblage type A (6.62 ± 2.92) and type D (6.23± 4.09). The lowest diversity reveal assemblage type B (4.1 ±1.60).

Appendix 2 presents taxa mostly associated with each of the site clusters and dissimilarity in the taxonomic composition between each of the clusters. It can be seen that the community groups separated on the basis of faunistic similarity are better defined, have a higher internal similarity and are more dissimilar to each other than the assemblages in the groups separated by habitat and landscape classification, respectively. *Enallagma cyathigerum* is a characteristic representative of type A assemblages, while *Orthetrum brunneum* is characteristic of type B assemblages. *Calopteryx splendens* and *Cordulegaster bidentata* are characteristic of springs from group C and D, respectively.

3.3 Habitat level

Figure 2A presents a dendrogram grouping springs based on habitat factors. Three clusters can be seen. Wilcoxon test ($Z = -6.037$, $p < 0.001$) revealed that the clusters of springs based on habitat characteristics were not consistent with those grouped according to faunistic similarity.

To recognize environmental patterns at the habitat level a PCA was undertaken. The first and second PCA axes explain 21.6% and 19.4% variation of the variables analyzed, respectively. The first PCA axis correlated negatively with the discharge (summer: −0.417; winter: −0.426) and the spring size (−0.367). The second PCA axis correlated positively with the percentage of anoxic mud (0.351) and clay (0.35) and correlated negatively with the percentage of stones (−0.353). The spring clusters were much less separated in the PCA plot than the clusters formed on the basis of landscape characteristics (Fig. 3).

Appendix 3 presents taxa mostly associated with each of the site clusters and dissimilarity in the taxonomic composition between each of the clusters. *Calopteryx splendens* is characteristic for the springs from cluster I(H), while *Cordulegaster bidentata* mostly contributes, to the assemblages in clusters II(H) and III(H).

Table 1. Quantitative occurrence of Odonata in springs in central part of Montenegro. Abbr. – abbreviation, *n* – number of specimens, *D* – dominance (%), *N* – number of springs in which species occurred, *F* – frequency (%).

Species	Abbr.	Material collected				Sublacustrine springs		Limnocrenes		Rheocrenes	
		n	*D*	*N*	*F*	*n*	*F*	*n*	*F*	*n*	*F*
Calopteryx virgo (Linnaeus)	Cavi	190	6.4	40	44.0	13	100.0	25	53.3	152	40.5
C. splendens (Harris)	Casp	259	8.7	36	39.5	22	100.0	65	60.0	172	33.8
Lestes barbarus (Fabricius)	Leba	56	1.9	13	14.3	8	100.0	23	26.7	25	9.5
L. sponsa (Hansemann)	Lesp	15	0.5	4	4.4	0	0.0	10	20.0	5	1.4
L. dryas Kirby	Ledr	36	1.2	9	9.9	9	100.0	26	40.0	1	1.4
Sympecma fusca (Vander Linden)	Syfu	33	1.1	15	16.5	3	100.0	10	26.7	20	12.2
Ischnura elegans (Vander Linden)	Isel	39	1.3	11	12.0	6	100.0	25	46.7	8	2.7
I. pumilio (Charpentier)	Ispu	63	2.1	21	23.0	7	100.0	26	46.7	30	16.2
Enallagma cyathigerum (Charpentier)	Ency	59	2.0	9	9.9	0	0.0	22	13.3	37	9.5
Coenagrion puella (Linnaeus)	Copu	103	3.5	25	27.5	10	100.0	48	66.7	45	17.6
Erythromma najas (Hansemann)	Erna	30	1.0	9	9.9	1	50.0	22	40.0	7	2.7
E. viridulum (Charpentier)	Ervi	93	3.1	25	30.8	8	100.0	38	46.7	47	21.6
Pyrrhosoma nymphula (Sulzer)	Pyny	24	0.8	6	6.6	0	0.0	11	13.3	13	5.4
Platycnemis pennipes (Pallas)	Plpe	167	5.6	31	34.1	5	100.0	55	53.3	107	28.4
Brachytron pratense (O.F. Müller)	Brpr	28	0.9	7	9.9	3	50.0	18	40.0	7	2.7
Aeshna juncea Linnaeus	Aeju	39	1.3	20	7.7	0	0.0	22	13.3	17	6.8
A. cyanea (O.F. Müller)	Aecy	98	3.3	14	22.0	3	50.0	67	73.3	28	10.8
A. affinis Vander Linden	Aeaf	52	1.7	18	15.4	7	50.0	44	80	1	1.4
A. mixta Latreille	Aemi	69	2.3	23	19.8	0	0.0	35	66.7	34	10.8
Anax imperator Leach	Anim	51	1.7	4	25.3	3	100.0	17	46.7	31	18.9
A. parthenope (Selys)	Anpa	18	0.6	4	4.4	9	100.0	9	13.3	0	0.0
A. ephippiger (Burmeister)	Anep	12	0.4	9	4.4	4	100.0	3	6.7	5	1.4
Caeliaeschna microstigma (Schneider)	Cami	78	2.6	27	29.7	0	0.0	0	0.0	78	36.5
Gomphus flavipes (Charpentier)	Gofl	3	0.1	2	3.3	0	0.0	3	13.3	0	0.0
G. schneiderii Selys	Gosc	87	2.9	26	28.6	5	100.0	4	13.3	78	29.7
Onychogomphus forcipatus (Linnaeus)	Onfo	120	4.0	32	35.2	4	50.0	7	20.0	109	37.8
Cordulia aenea (Linnaeus)	Come	17	0.6	4	4.4	0	0.0	9	6.7	8	4.1
Somatochlora meridionalis Nielsen	Some1	93	3.1	32	35.2	0	0.0	8	20.0	85	39.2
S. metalica (Vander Linden)	Some2	25	0.8	6	6.6	0	0.0	14	13.3	11	5.4
S. flavomaculata (Vander Linden)	Sofl	38	1.3	9	9.9	0	0.0	27	40.0	11	4.1
Cordulegaster bidentata (Selys)	Cobi	269	9.0	54	59.3	0	0.0	8	13.3	261	70.3
C. heros Theischinger	Cohe	96	3.2	24	26.4	0	0.0	0	0.0	96	32.4
Libelulla depressa Linnaeus	Lide	51	1.7	19	20.9	0	0.0	17	33.3	34	18.9
L. quadrimaculata Linnaeus	Liqu	33	1.1	11	12.1	0	0.0	28	60.0	5	2.7
L. fulva Müller	Lifu	24	0.8	8	8.8	5	100.0	11	20.0	8	4.1
Orthetrum coerulescens (Fabricius)	Orco	63	2.1	16	17.6	3	50.0	6	13.3	54	17.6
O. brunneum (Fonscolombe)	Orbr	82	2.8	31	34.1	0	0.0	4	13.3	78	39.2
Sympetrum sanquineum (O.F. Müller)	Sysa	59	2.0	21	23.1	4	100.0	26	46.7	29	16.2
S. flaveolum (Linnaeus)	Syfl	18	0.6	6	6.6	0	0.0	11	20.0	7	4.1
S. striolatum (Charpentier)	Syst	73	2.5	18	19.8	0	0.0	54	73.3	19	9.5
S. meridionale (Selys)	Syme	58	1.9	19	20.9	2	50.0	14	26.7	42	18.9
Crocothemis erythraea (Brullé)	Crer	73	2.5	16	17.6	11	100.0	57	86.7	5	1.4
Trithemis annulata (Palisot de Beauvois)	Tran	30	1.0	8	8.8	5	100.0	18	33.3	7	1.4
Lindenia tetraphylla (Vander Linden)	Lite	55	1.8	7	7.7	27	100.0	21	20.0	7	2.7

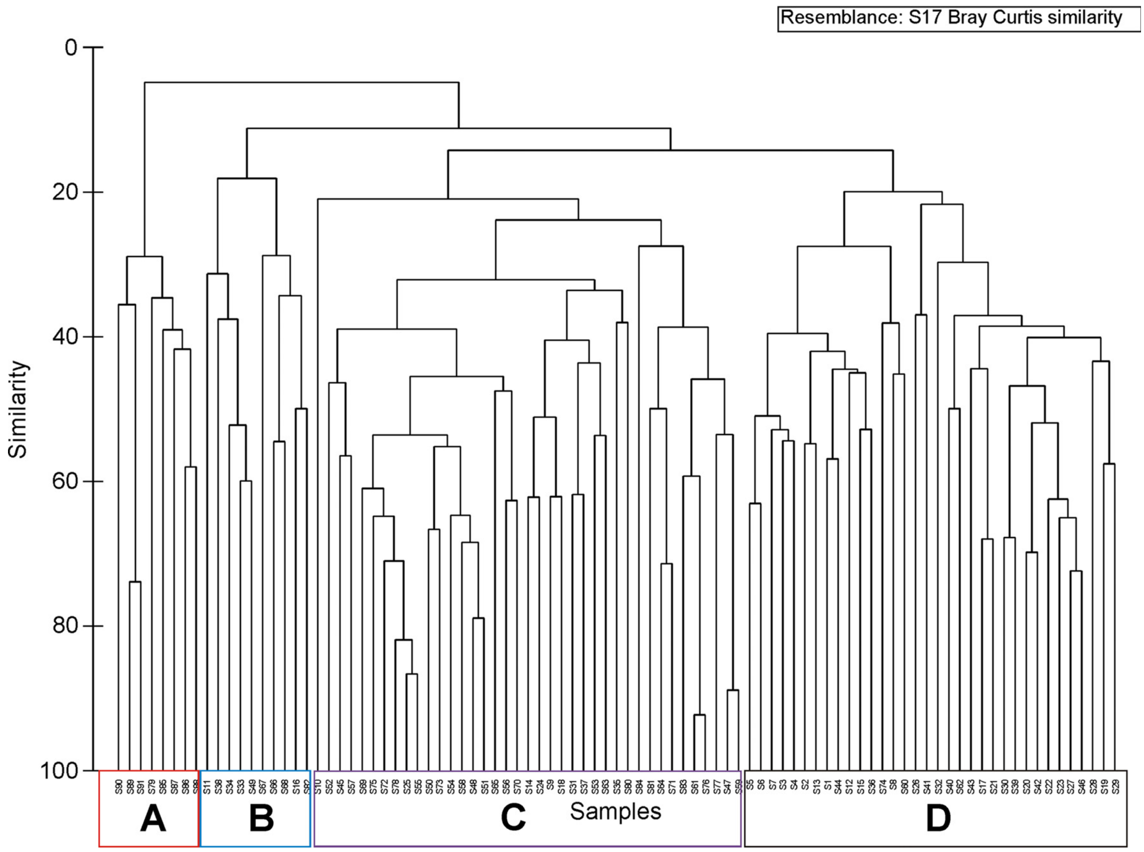

Fig. 1. Bray–Curtis similarity of Odonata assemblages within investigated springs.

The results of the CCA analysis summarize the main trends in the relationship between Odonata and habitat factors. The first and second axes explain 30.57% and 24.41% of species variation of the variables analyzed, respectively. The results of CCA analysis revealed that the habitat variables used in ordination explain 37.49% of the total variation in Odonata species. Of the 15 statistically significant parameters shaping the structure of the assemblages, the influence of the parameter "permanence" was the greatest (explaining 4.54% of variation). However, an analysis of the correlations showed that only some species were significantly associated with this factor – *Calopteryx virgo* correlated positively, while *Lestes barbarus* and *Sympetrum sanguineum* correlated negatively with spring permanence. The next parameter having the greatest influence on the formation of Odonata assemblages was "anthropogenic impact" (explaining 4.46% of variation). Figure 4 illustrating the CCA results the species which avoid anthropogenic influence are concentrated in the lower left-hand corner of the diagram. This variable correlated negatively with most species (with the strongest correlations for *Calopteryx splendens*, *Platycnemis pennipes*, *Onychogomphus forcipatus*, and *Coenagrion puella*), but correlated positively with *Orthetrum brunneum*, *Cordulegaster bidentata* and *Somatochlora meridionalis*.

Another group of species was associated with a set of co-occurring substrate factors – the percentage of the stones, rocks and the gravel (upper left-hand corner of the diagram). The most important factor among them, based on the number of statistically significant correlations between particular species, was the percentage of stones (19 species), while the percentage of rocks (8) and gravel (5) were less important. On other hand, species which showed affinities to springs with a higher content of anoxic mud, clay, algae and macrophyte were concentrated in lower right-hand corner of the diagram. Within this set of co-occurring factors the most important (based on the number of statistically significant correlation between particular species and this parameter) was the percentage of anoxic mud and algae (18 species), followed by the percentage of macrophytes (17), mosses and clay (14).

3.4 Landscape level

Figure 2C presents a dendrogram grouping springs based on landscape factors. Three clusters can be seen. Outliers encompass one spring (S48) which not belong to any of the clusters. Wilcoxon test ($Z = -7.07$, $p < 0.001$) revealed that the clusters of springs formed on the basis of landscape characteristics were not consistent with the grouping based on faunistic similarity.

To recognize the environmental patterns at the landscape level a PCA was undertaken. The first and second PCA axes explain 24.7% and 22.8% variation of the variables analyzed, respectively. The first PCA axis correlated negatively with parameter "meadow" (−0.606). The second PCA axis correlated positively with the percentage of riparian vegetation (0.461) and agricultural land (0.465) and correlated negatively with the altitude (−0.411). The results revealed that spring clusters were clearly separated in the PCA plot. The springs in

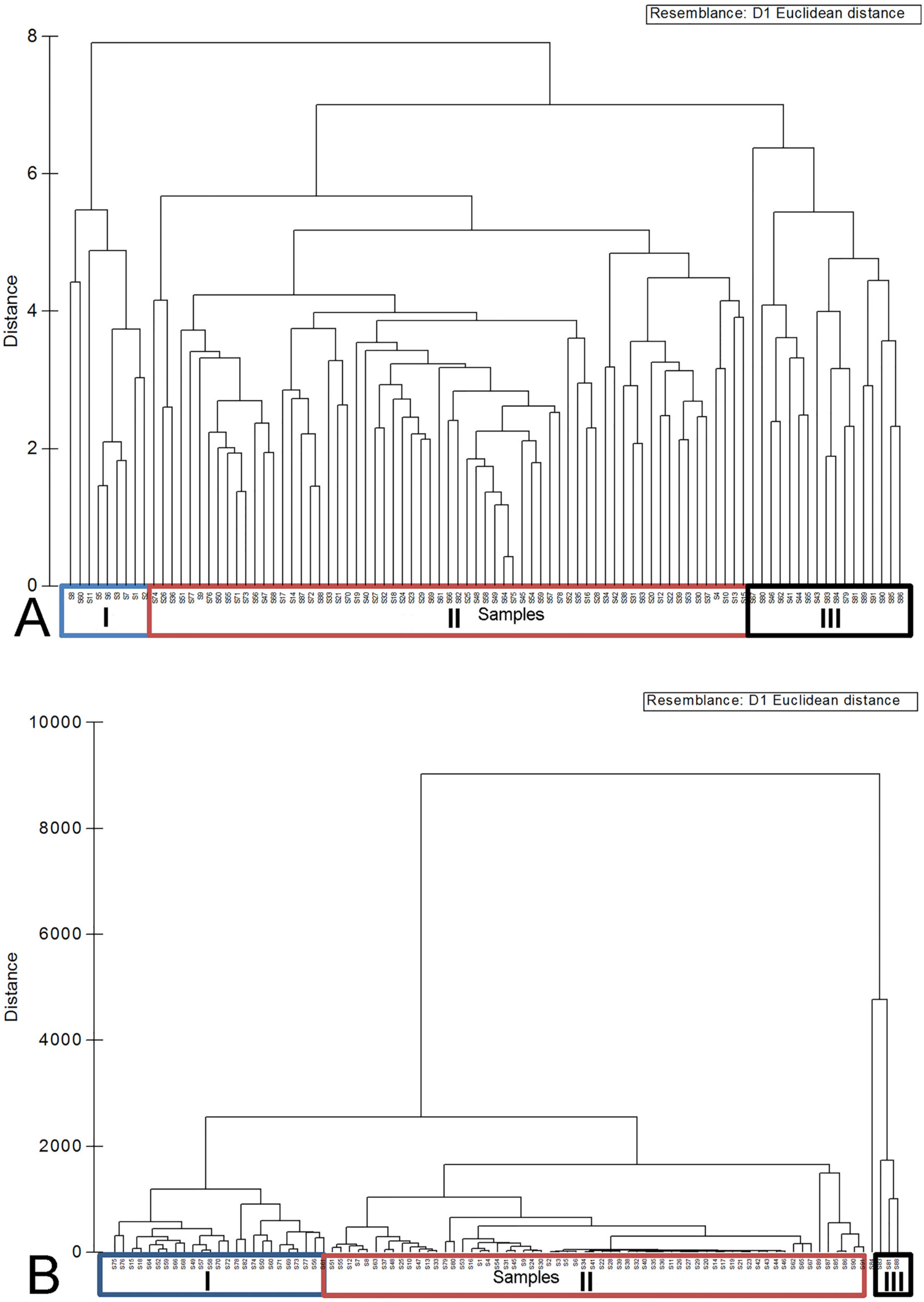

Fig. 2. (A) Similarity distance between sites in clusters I, II, and III reflecting habitat (H) characteristics of investigated springs. (B) Similarity distance between sites in clusters I, II, and III reflecting landscape (L) characteristics of investigated springs.

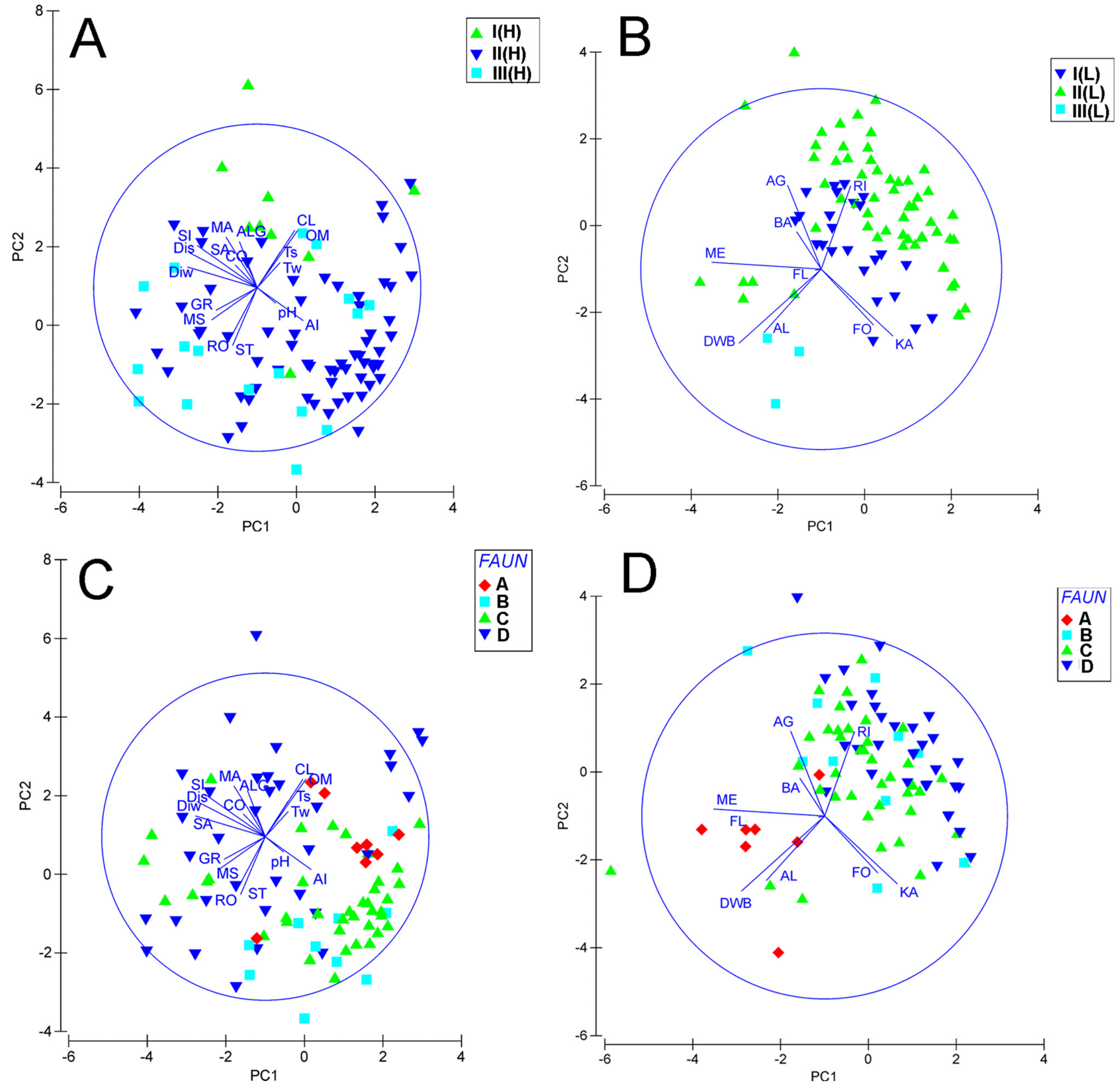

Fig. 3. (A and B) Results of PCA showing habitat (Fig. A) and landscape (Fig. B) characteristics of investigated springs respectively under habitat (H) and landscape (L) classification into clusters I, II and III. (C and D) Results of PCA showing habitat (Fig. C) and landscape (Fig. D) characteristics into faunistic defined clusters A, B, C and D.

cluster I(L) were more isolated due to the higher altitude. On other hand, springs from clusters II(L) and III(L) are more scattered over the biplot (more variable) but with a clear tendency for separation, with a stronger preference for riparian vegetation in the latter cluster.

Appendix 3 presents taxa mostly associated with each of the site clusters and dissimilarity in the taxonomic composition between each of the clusters. *Calopteryx splendens* is characteristic representative for the springs from cluster I(H), while *Cordulegaster bidentata* mostly contributes, to the assemblages in clusters II(H) and III(H).

The results of the CCA analysis summarize the main trend in the relationship between Odonata and the landscape factors. The first and second axes explain 47.34% and 18.92% variation of the variables analyzed, respectively. The results of CCA analysis revealed that the variables used in ordination explain 24.12% of the total variation in Odonata species. Of the 8 statistically significant parameters shaping the structure of the assemblages, the influence of altitude was greatest (explaining 6.2% of variation). Figure 5 illustrating the CCA results there is a large group of species which prefer lower altitude (upper and lower left-hand corner of the diagram).

Another group of species was associated with higher altitude (right-hand side of the diagram). This group includes *Cordulia aenea, Aeshna juncea, Pyrrhosoma nymphula, Enallagma cyathigerum* and *Somatochlora mettalica*. All

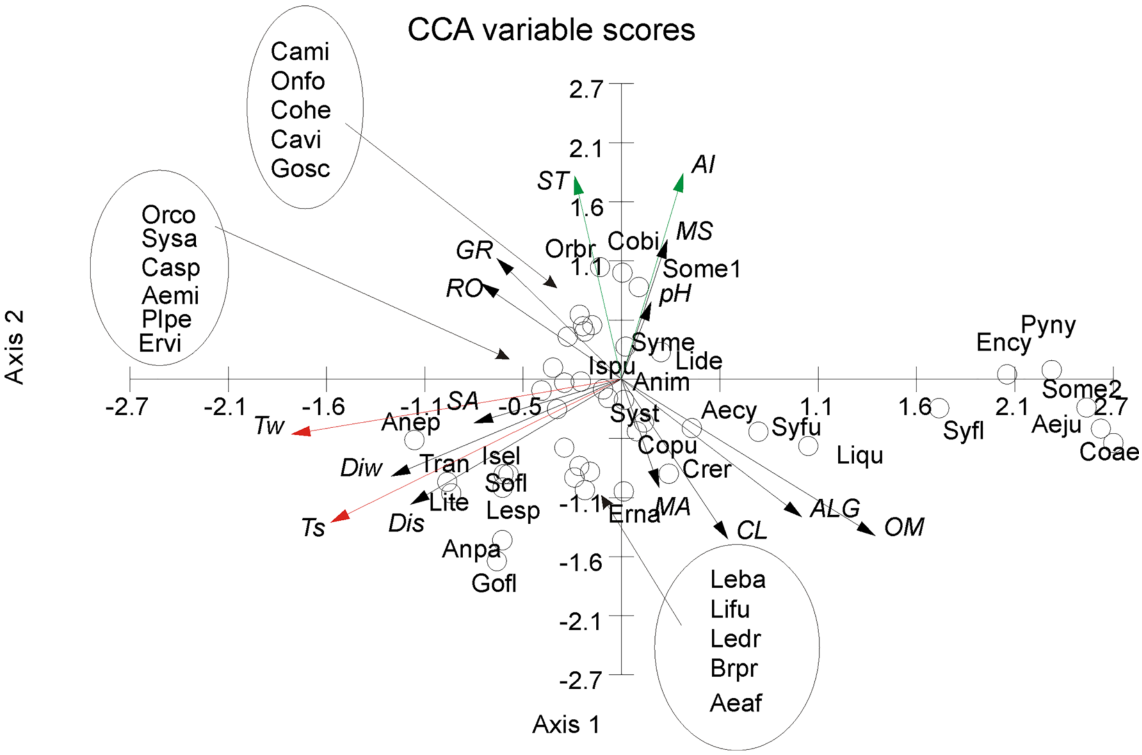

Fig. 4. CCA bioplot of species by habitat variables based on 91 investigated springs.

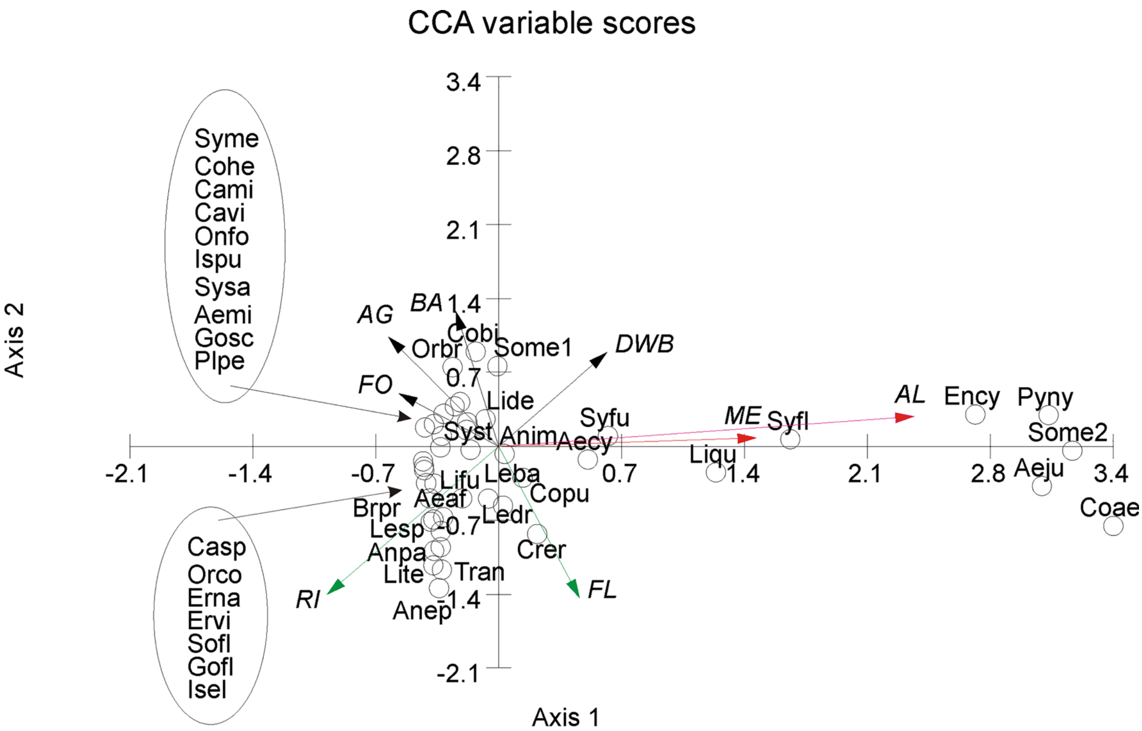

Fig. 5. CCA bioplot of species by landscape variables based on 91 investigated springs.

these species showed positive, statistically significant correlations with altitude. In the lower left hand corner of the diagram there is a group of species whose distribution mainly depends on riparian vegetation. Most species correlated positively with this factor, with the strongest correlations for *Brachytron pratense*, *Calopteryx splendens*, *Erythromma viridulum*, *Ischnura elegans, Aeshna affinis*, *Crocothemis erythraea*, *Platycnemis pennipes*, *Somatochlora flavomaculata*, *Trithemis annulata*, *Libellula fulva*, and *Orthetrum coerulescens*. In the upper left-hand quarter of the diagram there are species whose distribution is determined by the presence of the built-up areas, with the strongest correlation for

Cordulegaster bidentata and to a lesser extent for *Orthetrum brunneum* and *Somatochlora meridionalis*.

4 Discussion

In 91 springs situated in the central part of Montenegro, a total of 44 species of odonates were recorded. This total is over 60% of the total recorded for Montenegro (De Knijf *et al.*, 2013; Buczyński *et al.*, 2014). The highest numbers of species were caught in two sublacustrine springs. This can be explained by the larger surface area and the standing water body nature of these springs which is primarily induced by the spatial factor, *i.e.*, the location of these water bodies within the lake. Studies on other taxa, such as aquatic Heteroptera (Gligorović *et al.*, 2016) and aquatic gastropods (Pešić and Glöer, 2013) confirm that sublacustrine springs contain the most diverse assemblages. Similarly, limnocrene springs showed considerably higher Odonata diversity when compared to rheocrenes, indicating the importance of lentic habitats in the study area for maintaining the regional biodiversity of Odonata spring populations.

Our research on Odonata larvae assemblages in the karstic springs of the central Montenegro showed that environmental and faunistical classification may not be related. Similar differences in classification of the Dynaric karst springs based on the faunistical and environmental factors affecting the individual springs were pointed out by Płóciennik *et al.* (2016) and Gligorović *et al.* (2016).

In the dendrogram of faunistic similarities (Fig. 1) four clusters can be seen: cluster A groups sites from higher altitudes, cluster B includes springs affected by disturbance factors including drought but also a human influence, while cluster C groups aggregates most of the small rheocrenes at lower and medium altitudes. Cluster D is more diverse and encompasses limnocrenes and sublacustrine springs on one side, and a large karstic rheocrenes as well as small riparian springs on the other side. On the other hand, habitat factors divide spring sites into three groups, but no clear trends were observed. The PCA analysis revealed that the spring clusters formed on the basis of habitat parameters were much less differentiated than those clusters formed on the basis of landscape characteristics, suggesting that the impact of habitat factors is blurred by factors acting outside the level of individual springs. The research on karstic springs proves that Odonata communities separated on the basis of faunistic similarity are much better defined and more dissimilar than springs, according, respectively, to their habitat and landscape characters. Faunistic dissimilarity between springs, even on a small spatial scale, was indicated for some groups such as chironomids (Płóciennik *et al.*, 2016) and water bugs (Gligorović *et al.*, 2016).

At the habitat level 19 factors were analyzed. The results of the CCA showed that the greatest influence on Odonata communities have the parameter of "permanence" followed by the "anthropogenic influence". The latter parameter includes various kinds of anthropogenic modification of the spring habitat for use as drinking water sources, from spring boxes (concrete or wooden boxes placed over the spring to collect and store the water) to piped springs (spring water emerging from an artificial pipe). Both parameters should be considered as disturbance factors, which, as shown in some studies (for example Dmitrović *et al.*, 2016; Płóciennik *et al.*, 2016) may become important factors in shaping spring assemblages especially in karstic springs.

Several studies show that factors outside the aquatic environment have significant impact on spring assemblages. The landscape factors most used in similar studies of macroinvertebrate fauna in springs were altitude, the type and the structure of the landscape, and how it is used, and the proximity of nearby water bodies (Křoupalová *et al.*, 2011; Dumnicka *et al.*, 2007; Martin and Brunke, 2012; Pakulnicka *et al.*, 2016; Stryjecki *et al.*, 2016).

At the landscape level, 9 parameters were analyzed. According to the landscape characteristics, the springs were divided into three groups. The results of the CCA analysis revealed altitude as most important landscape factor. In our study the species most closely associated with the latter factor (the highest correlations with *Cordulia aenea, Aeshna juncea, Pyrrhosoma nymphula, Enallagma cyathigerum* and *Somatochlora mettalica*) prefer higher altitude (see De Knijf *et al.*, 2013). According to Harabiš and Dolný (2010) species that prefer higher biotopes are generally scarcer because there is less availability of water biotopes at higher than at lower altitudes. This is in agreement with results of our study which revealed that most species prefer springs at lower altitudes.

The other landscape factors influencing Odonata larvae communities in our study were riparian vegetation and urban environment. Many researchers (*e.g.*, Schindler *et al.*, 2003; Remsburg and Turner, 2009; Buczyński, 2015; Oliveira-Junior *et al.*, 2015) stressed the importance of riparian vegetation on the species richness and distribution of Odonata species. On the other hand, various studies emphasized the negative influence of human activities caused by urbanization and agricultural activities on the distribution and diversity of Odonata, which generally lead to a decrease and homogenization in the richness of Odonata species (Buczyński and Lewandowski, 2011; Willigalla and Fartmann, 2012; Harabiš and Dolný, 2012; Monteiro-Junior *et al.*, 2015). Nevertheless, Goertzen and Suhling (2013) showed that moderately disturbed ruderal and pioneer ponds in residential and agricultural areas increase the number of Odonata species. However, in comparison with the species from springs which are more stenotopic, species from ponds are more eurythermic and thus less susceptible to changes in environment.

The results of the CCA suggest that the presence of *Cordulegaster bidentata* was related to built-up areas, so this species can be considered an indicator of disturbed habitat. The colonization of this species may be the results of the habitat preferences of this species for small watercourses (Buczyński *et al.*, 2014) and the availability of suitable habitats affected by water regulation and deforestation. These changes, such as the introduction of concrete or wooden spring boxes, results in a reduction in the flow and the formation of large areas of still water, leading to the transformation of these environments into semi-lotic habitats suitable for colonization by the latter species.

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Appendix 1 General characteristics of the studied springs.

Code	Longitude	Latitude	Altitude [m]	Spring type	Permanence	Anthropogenic impact	Spring classification		
							Faunal	Landscape	Habitat
S1	42°18′50.6″N	19°21′12.9″E	5	Limnocrene	Permanent	No	4	2	1
S2	42°16′59.4″N	19°14′36.8″E	6	Limnocrene	Permanent	No	4	2	1
S3	42°22′01.6″N	19°09′11.8″E	9	Limnocrene	Permanent	No	4	2	1
S4	42°19′30.5″N	19°21′47.0″E	9	Rheocrene	Permanent	No	4	2	2
S5	42°21′29.8″N	19°06′20.8″E	12	Sublacustrine	Permanent	No	4	2	1
S6	42°21′30.7″N	19°06′31.0″E	16	Sublacustrine	Permanent	No	4	2	1
S7	42°22′28.31″N	19°08′58.6″E	17	Limnocrene	Permanent	No	4	2	1
S8	42°22′28.3″N	19°08′58.6″E	17	Limnocrene	Permanent	No	4	2	1
S9	42°18′22.2″N	19°03′14.6″E	19	Rheocrene	Permanent	No	3	2	2
S10	42°18′18.9″N	19°03′05.8″E	23	Rheocrene	Permanent	No	3	2	2
S11	42°29′03.0″N	19°07′20.9″E	35	Rheocrene	Temporary	No	2	2	1
S12	42°28′48.2″N	19°10′55.6″E	38	Limnocrene	Permanent	No	4	2	2
S13	42°29′3.76″N	19°09′14.95″E	38	Limnocrene	Permanent	No	4	2	2
S14	42°30′17.4″N	19°13′17.6″E	39	Rheocrene	Permanent	Pipe	3	2	2
S15	42°29′09.6″NN	19°10′25.2″E	39	Limnocrene	Permanent	No	4	1	2
S16	42°30′31.1″N	19°13′20.0″E	40	Rheocrene	Temporary	Pipe	2	2	2
S17	42°30′38.3″N	19°12′00.7″E	40	Rheocrene	Temporary	No	4	2	2
S18	42°28′50.8″N	19°10′52.5″E	40	Rheocrene	Permanent	No	3	1	2
S19	42°28′07.2″N	19°17′18.4″E	41	Rheocrene	Permanent	No	4	2	2
S20	42°28′04.7″N	19°15′28.8″E	42	Rheocrene	Permanent	No	4	2	2
S21	42°33′15.1″N	19°06′20.4″E	43	Rheocrene	Permanent	No	4	2	2
S22	42°35′57.4″N	19°03′55.6″E	43	Rheocrene	Permanent	No	4	2	2
S23	42°36′16.0″N	19°04′01.8″E	43	Rheocrene	Permanent	No	4	2	2
S24	42°28′52.3″N	19°08′44.2″E	44	Rheocrene	Permanent	No	3	2	2
S25	42°31′28.6″N	19°10′29.7″E	46	Rheocrene	Permanent	Pipe	3	2	2
S26	42°29′00.2″N	19°14′34.5″E	47	Rheocrene	Temporary	No	4	2	2
S27	42°29′05.0″N	19°14′15.4″E	47	Rheocrene	Permanent	No	4	2	2
S28	42°28′37.3″N	19°18′19.8″E	48	Rheocrene	Temporary	No	4	2	2
S29	42°28′59.4″N	19°14′35.5″E	48	Rheocrene	Permanent	No	4	2	2
S30	42°37′26.6″N	19°01′09.2″E	50	Rheocrene	Permanent	No	4	2	2
S31	42°37′56.1″N	19°00′40.3″E	50	Rheocrene	Permanent	No	3	2	2
S32	42°26′14.2″N	19°17′50.9″E	51	Rheocrene	Permanent	No	4	2	2
S33	42°31′40.9″N	19°12′21.4″E	53	Rheocrene	Permanent	Concrete box	2	2	2
S34	42°31′12.7″N	19°05′54.6″E	53	Rheocrene	Temporary	No	2	2	2
S35	42°31′32.1″N	19°11′30.9″E	54	Rheocrene	Permanent	No	3	2	2
S36	42°31′50.9″N	19°05′41.1″E	54	Limnocrene	Permanent	No	4	2	2
S37	42°38′18.2″N,	19°00′26.3″E	55	Rheocrene	Permanent	No	3	2	2
S38	42°26′10.7″N	19°17′57.1″E	55	Rheocrene	Temporary	Pipe	2	2	2
S39	42°37′50.7″N	19°01′58.1″E	56	Rheocrene	Permanent	No	4	2	2
S40	42°37′25.9″N	19°02′33.5″E	56	Rheocrene	Permanent	No	4	2	2
S41	42°31′52.5″N	19°05′33.1″E	56	Rheocrene	Temporary	No	4	2	3
S42	42°29′51.8″N	19°18′40.5″E	64	Rheocrene	Temporary	No	4	2	2
S43	42°37′29.2″N	19°02′35.6″E	68	Limnocrene	Permanent	No	4	2	3
S44	42°39′59.8″N	18°59′23.3″E	68	Limnocrene	Permanent	No	4	2	3
S45	42°11′58.0″N	19°05′11.4″E	69	Rheocrene	Permanent	No	3	2	2
S46	42°40′29.5″N	18°59′48.7″E	78	Rheocrene	Permanent	No	4	2	3
S47	42°31′39.3″N	19°13′08.5″E	89	Rheocrene	Permanent	Concrete box	3	2	2
S48	42°13′13.7″N	19°06′24.3″E	91	Rheocrene	Permanent	Wood box	3	2	2
S49	42°30′20.5″N	19°15′25.7″E	103	Rheocrene	Permanent	Wood box	2	1	2
S50	42°30′23.9″N	19°15′46.6″E	106	Rheocrene	Permanent	Wood box	3	1	2

Appendix 1 (continued)

Code	Longitude	Latitude	Altitude [m]	Spring type	Permanence	Anthropogenic impact	Spring classification		
							Faunal	Landscape	Habitat
S51	42°27′46.7″N	19°18′32.1″E	115	Rheocrene	Permanent	Wood box	3	2	2
S52	42°19′07.6″N	19°02′00.9″E	164	Rheocrene	Permanent	Da pipe	3	1	2
S53	42°15′51.9″N	18°59′17.2″E	181	Rheocrene	Permanent	No	3	2	2
S54	42°15′25.3″N	19°02′21.3″E	186	Rheocrene	Permanent	Wood box	3	2	2
S55	42°31′44.7″N	19°13′29.0″E	192	Rheocrene	Permanent	Wood box	3	2	2
S56	42°33′19.7″N	19°11′35.5″E	194	Rheocrene	Permanent	Wood box	3	1	2
S57	42°33′44.2″N	19°10′42.8″E	202	Rheocrene	Temporary	Pipe	3	1	2
S58	42°33′44.8″N	19°10′43.9″E	204	Rheocrene	Permanent	Wood box	3	1	2
S59	42°14′11.7″N	19°02′37.9″E	209	Rheocrene	Permanent	Concrete box	3	1	2
S60	42°23′19.8″N	19°06′44.6″E	213	Limnocrene	Permanent	No	4	1	1
S61	42°33′33.5″N	19°11′32.2″E	256	Rheocrene	Permanent	Wood box	3	1	2
S62	42°43′50.1″N	19°20′15.6″E	258	Rheocrene	Permanent	No	4	2	3
S63	42°15′14.2″N	18°59′25.7″E	279	Rheocrene	Permanent	Wood box	3	2	2
S64	42°30′38.3″N	19°17′17.8″E	280	Rheocrene	Permanent	Wood box	3	1	2
S65	42°46′00.4″N	19°23′26.1″E	308	Rheocrene	Permanent	No	3	2	3
S66	42°31′45.7″N	19°14′06.6″E	378	Rheocrene	Temporary	Concrete box	2	1	2
S67	42°44′19.0″N	19°19′44.9″E	403	Rheocrene	Permanent	No	2	2	3
S68	42°32′02.3″N	19°13′59.9″E	404	Rheocrene	Temporary	Concrete box	2	1	2
S69	42°32′47.1″N	19°13′16.0″E	405	Rheocrene	Permanent	Wood box	3	1	2
S70	42°32′39.7″N	19°13′21.2″E	406	Rheocrene	Permanent	Wood box	3	1	2
S71	42°36′33.5″N	19°06′13.9″E	417	Rheocrene	Permanent	Wood box	3	1	2
S72	42°32′25.2″N	19°13′40.7″E	443	Rheocrene	Permanent	Wood box	3	1	2
S73	42°31′03.3″N	19°15′09.0″E	448	Rheocrene	Permanent	Wood box	3	1	2
S74	42°27′51.7″N	19°20′40.5″E	457	Limnocrene	Temporary	No	4	1	2
S75	42°38′35.3″N	19°02′47.1″E	516	Rheocrene	Permanent	Wood box	3	1	2
S76	42°38′48.3″N	19°02′48.0″E	563	Rheocrene	Permanent	Wood box	3	1	2
S77	42°28′00.3″N	19°20′34.6″E	567	Rheocrene	Temporary	Concrete box	3	1	2
S78	42°26′42.8″N	19°21′52.7″E	651	Rheocrene	Permanent	Concrete box	3	1	2
S79	42°51′15.5″N	18°56′41.3″E	658	Rheocrene	Permanent	No	1	2	3
S80	42°51′26.7″N	18°56′31.5″E	663	Rheocrene	Permanent	No	3	2	3
S81	42°19′28.2″N	18°55′25.3″E	717	Rheocrene	Permanent	Concrete box	3	4	3
S82	42°26′40.3″N	19°22′19.8″E	775	Rheocrene	Temporary	No	2	1	2
S83	42°22′39.3″N	18°50′23.7″E	1247	Rheocrene	Permanent	Concrete box	3	4	3
S84	42°29′19.0″N	19°31′57.0″E	1368	Rheocrene	Permanent	Wood box	3	3	3
S85	42°40′28.5″N	19°16′01.3″E	1419	Rheocrene	Permanent	No	1	2	3
S86	42°40′29.6″N	19°15′59.8″E	1421	Rheocrene	Permanent	No	1	2	3
S87	42°36′35.5″N	19°33′15.3″E	1472	Rheocrene	Permanent	Pipe	1	2	2
S88	42°31′11.4″N	19°31′52.5″E	1511	Rheocrene	Permanent	Pipe	1	4	2
S89	42°48′15.9″N	19°12′54.9″E	1607	Limnocrene	Permanent	No	1	2	3
S90	42°48′46.5″N	19°13′40.5″E	1706	Rheocrene	Permanent	No	1	2	3
S91	42°48′22.96″N	19°14′42.84″E	1786	Limnocrene	Permanent	No	1	2	3

Appendix 2 Results of SIMPER analysis of Odonata assemblages of site groups A, B, C and D.

Group 1 Average similarity: 34.90 Group 2 Average similarity: 25.71 Group 3 Average similarity: 28.65 Group 4 Average similarity: 30.00	Group 1 and 2 Average dissimilarity: 97.05 Group 1 and 3 Average dissimilarity: 95.12 Group 2 and 3 Average dissimilarity: 89.66 Group 1 and 4 Average dissimilarity: 94.53 Group 2 and 4 Average dissimilarity: 80.07 Group 3 and 4 Average dissimilarity: 86.14

Species	Av. Abund	Av. Sim	Sim/SD	Contrib %	Cum %
Group 1					
Ency	6.5	16.37	1.28	46.92	46.92
Aeju	4.5	5.07	0.82	14.54	61.45
Some1	3.13	4.86	0.92	13.93	75.38
Pyny	2.38	3.02	0.62	8.65	84.04
Coae	2.13	1.7	0.44	4.86	88.9
Aecy	2.38	1.44	0.45	4.13	93.03
Group 2					
Orbr	3.2	13.97	1.02	54.32	54.32
Cobi	2.9	4.9	0.52	19.07	73.39
Sysa	0.9	1.9	0.38	7.39	80.78
Leba	1.3	1.47	0.26	5.72	86.5
Syst	0.9	1.22	0.26	4.74	91.24
Group 3					
Casp	7	8.5	1.06	29.67	29.67
Plpe	3.71	3.03	0.81	10.58	40.25
Onfo	2.56	2.96	0.61	10.34	50.59
Ervi	2.21	1.48	0.46	5.18	55.77
Cavi	2.06	1.37	0.5	4.77	60.54
Copu	2	1.09	0.48	3.81	64.34
Gosc	1.74	1.06	0.42	3.71	68.05
Syst	1.74	0.95	0.36	3.32	71.38
Crer	1.82	0.69	0.38	2.41	73.79
Orco	1.35	0.64	0.29	2.23	76.02
Cobi	1.59	0.6	0.27	2.11	78.12
Aeaf	1.53	0.58	0.37	2.04	80.16
Aecy	1.76	0.56	0.29	1.95	82.12
Ispu	1.29	0.43	0.32	1.5	83.62
Sysa	1.06	0.4	0.32	1.39	85.01
Leba	1.26	0.38	0.26	1.32	86.32
Anim	0.94	0.36	0.36	1.26	87.58
Cami	0.79	0.34	0.26	1.2	88.79
Isel	1.06	0.34	0.28	1.19	89.98
Aemi	1.15	0.32	0.31	1.13	91.11
Group 4					
Cobi	4.69	16.97	1.4	56.57	56.57
Cavi	2.87	3.79	0.53	12.63	69.2
Some2	1.82	3.56	0.55	11.88	81.07
Orbr	0.87	1.2	0.38	4.01	85.09

Appendix 2 (continued)

Group 1 Average similarity: 34.90 Group 2 Average similarity: 25.71 Group 3 Average similarity: 28.65 Group 4 Average similarity: 30.00	Group 1 and 2 Average dissimilarity: 97.05 Group 1 and 3 Average dissimilarity: 95.12 Group 2 and 3 Average dissimilarity: 89.66 Group 1 and 4 Average dissimilarity: 94.53 Group 2 and 4 Average dissimilarity: 80.07 Group 3 and 4 Average dissimilarity: 86.14

Species	Av. Abund	Av. Sim	Sim/SD	Contrib %	Cum %
Cohe	1.67	0.83	0.3	2.76	87.85
Cami	1.1	0.66	0.32	2.18	90.03

Appendix 3 Results of SIMPER analysis for Odonata assemblages of site groups I, II and III (habitat classification), and of site groups I, II, III and outlier (landscape classification).

Habitat

Group I Average similarity: 31.68 Group II Average similarity: 21.56 Group III Average similarity: 13.37	Group I and II Average dissimilarity: 86.26 Group I and III Average dissimilarity: 88.66 Group II and III Average dissimilarity: 85.75

Species	Av. Abund	Av. Sim	Sim/SD	Contrib %	Cum %
Group 1					
Casp	6.11	3.35	0.78	10.57	10.57
Copu	3.33	2.9	1.06	9.16	19.73
Isel	2.78	2.6	1.03	8.21	27.93
Crer	3.44	2.47	0.97	7.8	35.74
Lite	5.33	2.34	0.59	7.39	43.12
Aeaf	3.22	1.92	0.72	6.06	49.19
Tran	2.56	1.87	1.01	5.9	55.08
Leba	2.67	1.78	0.8	5.61	60.7
Plpe	3.78	1.42	0.58	4.49	65.19
Cavi	2.67	1.38	0.77	4.36	69.55
Syst	2.56	1.34	0.4	4.22	73.77
Ervi	2.22	1.03	0.56	3.27	77.04
Aecy	2.89	0.91	0.41	2.89	79.92
Ledr	2.11	0.83	0.38	2.62	82.55
Anpa	2	0.7	0.44	2.2	84.75
Sofl	2.11	0.61	0.41	1.92	86.67
Ispu	1.67	0.61	0.49	1.91	88.58
Anim	1.11	0.49	0.5	1.55	90.14
Casp	6.11	3.35	0.78	10.57	10.57

Landscape

Group I Average similarity: 28.27 Group II Average similarity: 19.11 Group III Average similarity: 16.44	Group I and II Average dissimilarity: 84.01 Group I and III Average dissimilarity: 81.77 Group II and III Average dissimilarity: 91.23 Outlier & I; II; III Average dissimilarity: 83.02; 93.14; 74.74

Species	Av. Abund	Av. Sim	Sim/SD	Contrib %	Cum %
Group 1					
Cobi	3.8	16.76	1.33	59.29	59.29
Cavi	1.76	3.31	0.45	11.72	71
Some1	1.52	2.92	0.46	10.34	81.34
Orbr	1.12	1.7	0.38	6.01	87.36
Lide	0.52	0.66	0.16	2.32	89.68
Sysa	0.76	0.63	0.2	2.23	91.91
Group 2					
Casp	4.18	3.26	0.55	17.07	17.07
Cobi	2.71	2.66	0.4	13.94	31.01
Cavi	2.35	1.58	0.42	8.29	39.3
Onfo	1.79	1.55	0.42	8.09	47.39
Plpe	2.48	1.42	0.43	7.41	54.8
Orbr	0.87	0.87	0.27	4.57	59.37
Ervi	1.32	0.73	0.32	3.8	63.17
Gosc	1.32	0.72	0.35	3.78	66.95
Cami	1.06	0.62	0.31	3.26	70.21
Copu	1.5	0.62	0.34	3.24	73.45
Cohe	1.37	0.61	0.26	3.17	76.62

Appendix 3 (continued)

Habitat						Landscape					
Group I Average similarity: 31.68 Group II Average similarity: 21.56 Group III Average similarity: 13.37			Group I and II Average dissimilarity: 86.26 Group I and III Average dissimilarity: 88.66 Group II and III Average dissimilarity: 85.75			Group I Average similarity: 28.27 Group II Average similarity: 19.11 Group III Average similarity: 16.44			Group I and II Average dissimilarity: 84.01 Group I and III Average dissimilarity: 81.77 Group II and III Average dissimilarity: 91.23 Outlier & I; II; III Average dissimilarity: 83.02; 93.14; 74.74		
Species	Av. Abund	Av. Sim	Sim/SD	Contrib %	Cum %	Species	Av. Abund	Av. Sim	Sim/SD	Contrib %	Cum %
						Some2	0.85	0.58	0.27	3.05	79.67
Group 2						Syst	0.84	0.34	0.18	1.8	81.47
Cobi	3.57	8.12	0.72	37.66	37.66	Orco	0.97	0.33	0.21	1.72	83.19
Cavi	2.14	2.23	0.41	10.32	47.98	Anim	0.76	0.3	0.3	1.57	84.76
Orbr	1.09	1.49	0.35	6.91	54.89	Ispu	0.85	0.29	0.25	1.5	86.26
Casp	2.62	1.46	0.31	6.77	61.67	Aemi	0.97	0.26	0.19	1.36	87.62
Some2	1.15	1.39	0.35	6.46	68.13	Crer	1.13	0.24	0.21	1.27	88.89
Onfo	1.45	1.02	0.35	4.71	72.84	Sysa	0.65	0.24	0.19	1.26	90.15
Plpe	1.89	0.91	0.32	4.23	77.06						
Cohe	1.34	0.64	0.26	2.98	80.04	*Group 3*					
Cami	1.06	0.63	0.3	2.91	82.95	Cobi	1.33	11.11	0.58	67.57	67.57
Gosc	0.97	0.53	0.29	2.45	85.41	Ency	3.67	5.33	0.58	32.43	100
Syme	0.83	0.45	0.22	2.1	87.5						
Sysa	0.75	0.42	0.2	1.95	89.45						
Ervi	0.98	0.39	0.21	1.83	91.28						
Group 3											
Cobi	2.18	2.5	0.42	18.19	18.19						
Ency	2.71	2.36	0.37	17.21	35.4						
Aeju	2.18	1.09	0.3	7.94	43.33						
Onfo	1.29	0.87	0.27	6.3	49.63						
Casp	2	0.83	0.3	6.07	55.71						
Pyny	1.24	0.77	0.24	5.61	61.32						
Cavi	1.59	0.68	0.27	4.94	66.26						
Aecy	1.41	0.64	0.32	4.65	70.91						
Some1	0.65	0.48	0.19	3.46	74.37						
Copu	1.53	0.39	0.24	2.84	77.21						
Coae	1	0.35	0.19	2.55	79.76						
Some	1.12	0.32	0.2	2.34	82.09						
Anim	0.82	0.28	0.27	2.05	84.14						

Appendix 4 Physicochemical characteristics (discharge, spring size, temperature and pH), substrate composition and aquatic vegetation of 91 investigated springs.

Spring	Spring	Discharge (L min^{-1})		T (°C)		pH (value)	Substrate composition						Aquatic vegetation		
code	size (m^2)	Summer	Winter	Summer	Winter		Organic mud	Clay	Sand	Gravel	Stones	Rocks	Mosses	Macrophyte	Algae
S1	>20	>25	>25	21.1	11.1	7.12	1	1	1	0	1	1	0	2	2
S2	>20	>25	>25	19.4	12.2	6.97	2	2	2	0	0	0	0	2	2
S3	>20	5–25	>25	18.4	12.1	7.23	1	1	1	0	1	1	0	1	1
S4	>20	5–25	>25	15.2	10.2	7.2	0	0	2	2	1	1	1	0	1
S5	>20	>25	>25	17.4	11.5	7.1	2	1	0	0	1	2	0	1	1
S6	>20	>25	>25	17.5	11.2	7.12	2	2	0	0	1	1	0	1	1
S7	>20	5–25	>25	18.6	11.6	7.21	2	1	0	0	1	2	0	1	1
S8	>20	0–1	0–1	21.2	11.1	7.24	2	3	0	0	0	0	0	0	1
S9	>1	1–5	1–5	17.2	10.1	6.95	1	1	0	0	1	1	0	1	1
S10	>20	5–25	>25	16.6	11.2	7.22	1	1	1	1	1	1	2	1	2
S11	5–20	0–1	>25	17.7	11.3	7.06	1	0	0	0	1	3	1	0	0
S12	5–20	1–5	5–25	13.1	10.5	7.29	1	1	1	1	1	1	1	3	1
S13	5–20	1–5	>25	15.6	11.3	7.18	2	1	0	0	1	2	1	3	1
S14	>1	1–5	5–25	13.5	10.2	7.49	2	1	1	0	1	0	1	0	1
S15	>20	>25	>25	14.2	12.8	7.26	1	1	1	1	1	2	2	2	2
S16	1–5	0–1	1–5	16.1	11.2	7.21	1	1	1	2	2	1	1	0	1
S17	>1	0–1	1–5	13.1	10.8	7.19	3	2	0	0	0	0	1	1	1
S18	1–5	0–1	1–5	12.4	9.5	7.32	0	1	1	1	2	2	1	1	1
S19	1–5	0–1	1–5	13.1	11	7.22	1	0	2	0	1	2	2	0	1
S20	5–20	1–5	5–25	12.6	10.3	7.41	1	0	1	2	2	0	2	1	1
S21	>1	0–1	1–5	14.3	11.2	7.25	2	1	0	0	2	0	1	1	1
S22	1–5	5–25	>25	13.2	10.8	7.19	1	0	0	1	1	1	2	3	1
S23	1–5	1–5	5–25	13.2	10.6	7.34	1	1	0	1	1	1	0	1	1
S24	>1	1–5	5–25	13.4	9.6	7.26	0	0	0	1	2	2	1	1	1
S25	>1	0–1	1–5	15.2	10.1	7.28	1	1	0	0	1	1	1	1	1
S26	>1	0–1	1–5	16.3	11.2	7.18	2	2	1	0	0	0	0	3	1
S27	1–5	1–5	1–5	13.6	11.1	7.38	0	0	0	1	2	1	2	2	1
S28	1–5	0–1	1–5	16.1	10.7	7.32	0	0	1	2	1	1	0	0	1
S29	1–5	1–5	5–25	14.1	10.2	7.46	1	1	0	1	2	2	1	2	1
S30	5–20	5–25	>25	14.3	9.8	7.36	1	1	1	1	1	1	2	2	2
S31	5–20	5–25	>25	12.3	9.1	7.29	0	1	1	1	2	3	3	2	1
S32	1–5	0–1	1–5	14.2	10.2	7.11	0	0	0	2	2	2	2	1	1
S33	>1	0–1	1–5	16.3	11.2	7.41	2	2	2	0	2	0	1	1	1
S34	5–20	0–1	>25	14.1	12	7.32	0	0	0	0	3	3	2	0	1
S35	5–20	0–1	1–5	15.2	10.4	7.41	1	1	1	1	1	0	0	1	1
S36	1–5	0–1	1–5	16.2	10.4	7.45	3	3	0	0	0	0	0	2	1
S37	5–20	1–5	>25	14.3	9.7	7.24	1	0	0	2	2	1	2	2	1
S38	1–5	1–5	>25	12.1	8.4	7.36	0	1	1	1	2	2	2	1	1
S39	5–20	5–25	>25	13.6	9.3	7.16	0	0	0	2	2	2	2	1	1
S40	>1	0–1	1–5	13.1	9.2	7.09	0	0	0	0	3	1	0	0	1
S41	>20	1–5	>25	10.1	7.5	7.32	0	0	0	1	2	3	1	1	1
S42	5–20	0–1	>25	13.2	9.3	7.41	0	0	0	0	3	2	3	0	1
S43	5–20	1–5	>25	10.1	8.7	7.1	0	0	1	3	1	1	0	0	1
S44	>20	>25	>25	10.2	8.4	7.21	1	1	0	0	2	2	1	2	2
S45	>1	0–1	1–5	14.1	10.1	7.23	1	0	0	1	2	1	1	1	1
S46	>20	>25	>25	11	7.8	7.24	1	0	0	1	2	3	3	1	1
S47	>1	0–1	1–5	16.7	11.3	7.18	0	1	1	1	1	2	1	0	1
S48	>1	0–1	1–5	13.6	9.7	7.32	1	1	0	0	1	2	1	1	1

Appendix 4 (continued)

Spring	Spring	Discharge (L min^{-1})		T (°C)		pH (value)	Substrate composition						Aquatic vegetation		
code	size (m^2)	Summer	Winter	Summer	Winter		Organic mud	Clay	Sand	Gravel	Stones	Rocks	Mosses	Macrophyte	Algae
S49	>1	0–1	1–5	15.3	10.4	7.43	1	1	0	0	1	2	1	0	1
S50	>1	0–1	1–5	16.1	11.7	7.35	2	0	0	0	2	2	1	1	1
S51	1–5	0–1	1–5	16.1	13.4	7.59	0	1	0	1	3	1	1	0	1
S52	1–5	0–1	1–5	14.2	11.1	6.92	2	1	1	2	2	1	1	2	2
S53	5–20	>25	>25	13.8	10.5	7.12	0	0	0	2	2	2	2	2	2
S54	>1	0–1	1–5	14.2	10.7	7.19	1	0	0	1	1	2	1	1	1
S55	>1	0–1	1–5	16.2	11.3	7.3	1	1	0	1	2	1	1	1	1
S56	>1	0–1	1–5	17.2	12.4	7.14	1	0	0	1	2	3	1	0	1
S57	>1	0–1	1–5	14.8	11.4	7.31	1	1	0	1	2	1	0	0	1
S58	>1	0–1	1–5	14.3	11.1	7.42	1	1	0	0	2	2	1	0	1
S59	>1	0–1	1–5	13.3	10.1	7.23	1	0	1	1	1	2	1	0	1
S60	>20	1–5	1–5	21.4	12.3	7.24	1	1	0	0	1	3	0	0	2
S61	>1	0–1	1–5	13	8.1	7.31	1	1	0	0	1	2	1	0	1
S62	5–20	>25	>25	10.3	8.1	6.92	0	0	0	0	2	3	4	0	1
S63	5–20	5–25	>25	12.8	10.1	7.22	1	1	1	1	2	2	3	2	1
S64	>1	0–1	1–5	14.2	10.6	7.32	1	1	0	0	1	2	1	0	1
S65	5–20	>25	>25	10.1	8.5	7.58	1	0	1	1	2	2	1	1	1
S66	>1	0–1	1–5	14.6	9.3	7.42	0	0	0	0	2	2	0	0	1
S67	>1	0–1	5–25	10.3	8.1	7.39	0	0	0	0	1	4	4	0	1
S68	>1	0–1	1–5	16.4	12.1	7.16	0	0	1	1	2	2	1	0	1
S69	1–5	1–5	5–25	13.5	9.8	7.42	1	1	1	1	1	2	1	1	1
S70	1–5	0–1	1–5	15.2	11.5	7.19	3	1	0	0	1	0	0	0	1
S71	>1	0–1	1–5	16.1	10.8	7.25	1	1	0	0	1	2	1	1	1
S72	>1	0–1	1–5	12.3	9.7	7.41	2	2	0	0	2	0	1	1	1
S73	>1	0–1	1–5	16.3	11.7	7.26	1	1	0	0	1	2	1	0	1
S74	5–20	0–1	1–5	17.8	12.7	7.52	3	1	0	0	1	0	0	1	2
S75	>1	0–1	1–5	14.1	10.2	7.38	1	1	0	0	1	2	1	0	1
S76	>1	0–1	1–5	15.1	12.4	7.26	2	1	0	0	1	2	1	0	1
S77	>1	0–1	1–5	18.2	10.1	7.19	1	0	0	0	1	3	1	0	1
S78	>1	0–1	1–5	13	11.1	7.25	1	1	1	1	2	1	1	0	1
S79	1–5	1–5	5–25	10.1	8.3	7.16	1	0	0	1	2	2	1	0	1
S80	>20	>25	>25	8.4	7.1	7.13	1	1	1	1	1	1	3	2	1
S81	5–20	1–5	5–25	11.4	9.1	7.33	1	0	0	1	1	2	1	0	1
S82	1–5	0–1	1–5	15.3	9.8	7.28	1	0	0	1	2	2	1	0	1
S83	>1	0–1	1–5	9.4	8.3	7.02	1	0	0	1	2	2	1	1	1
S84	>1	0–1	1–5	9.3	7.1	7.29	1	0	0	1	2	2	0	0	1
S85	>1	0–1	1–5	9.2	7.8	7.22	2	3	0	0	1	1	1	0	1
S86	>1	0–1	1–5	10.2	8.4	7.14	1	3	0	1	1	1	0	1	1
S87	>1	0–1	1–5	11.7	9.8	7.16	2	1	0	0	1	1	1	1	2
S88	>1	0–1	1–5	13.2	10.1	7.08	2	2	0	0	1	0	1	1	1
S89	>20	0–1	1–5	10.1	6.8	7.42	3	1	0	0	1	0	1	2	2
S90	>1	0–1	1–5	8.3	6.5	7.33	3	1	0	0	1	1	0	1	1
S91	1–5	0–1	1–5	11.3	8.2	7.21	3	1	0	0	1	0	2	2	2

Appendix 5 Landscape characteristics: distance to nearby bodies of water, flooding area ([+] present and [−] absent) and the surface area of the patches of different types present in the landscape of 91 investigated springs.

Spring code	Distance to nearby bodies of water (m)	Surface area of the patches of different types present in the landscape						Flooding area
		Karst vegetation	Forest	Riparian vegetation	Meadows	Agricultural land	Built-up area	
S1	612	2	2	2	0	0	0	+
S2	0	0	1	2	2	1	0	+
S3	0	1	1	1	1	1	0	+
S4	634	1	1	2	1	0	0	+
S5	0	2	1	2	0	0	2	+
S6	0	2	1	1	0	0	0	+
S7	1470	1	2	1	2	0	0	−
S8	1430	0	3	2	2	0	0	−
S9	388	1	2	2	1	0	1	+
S10	983	2	2	1	0	0	1	−
S11	0	3	1	1	1	1	0	+
S12	1340	2	1	2	0	0	1	−
S13	890	1	1	1	2	2	1	−
S14	7	0	2	0	2	1	1	+
S15	2150	2	1	1	2	1	0	−
S16	569	1	1	0	2	2	1	−
S17	6	2	0	1	1	1	1	+
S18	2209	1	1	1	2	1	0	−
S19	3	3	1	1	0	0	0	+
S20	8	3	1	1	0	0	0	+
S21	4	0	0	2	2	2	2	+
S22	32	2	1	2	1	0	1	−
S23	5	2	1	2	2	1	1	+
S24	397	2	1	1	2	2	1	−
S25	769	0	1	1	2	1	1	−
S26	2	2	2	1	1	0	0	+
S27	4	2	2	1	0	0	0	+
S28	42	3	1	0	0	0	0	+
S29	4	2	2	1	1	0	0	+
S30	413	1	2	1	2	2	0	−
S31	493	1	1	1	2	1	1	−
S32	0	2	0	0	2	1	0	+
S33	899	0	0	0	3	3	0	−
S34	22	2	1	1	1	1	0	+
S35	0	0	1	2	1	1	1	+
S36	0	0	1	3	1	1	0	+
S37	1092	2	2	1	1	0	0	−
S38	5	1	0	1	0	1	2	+
S39	35	2	1	1	0	0	2	+
S40	0	2	2	1	1	1	0	+
S41	21	3	1	0	1	1	0	+
S42	9	3	1	0	0	0	0	+
S43	13	2	2	1	1	1	0	+
S44	0	2	2	1	1	0	0	−
S45	499	2	3	0	0	0	0	−
S46	0	2	3	0	0	0	0	−
S47	920	3	2	0	1	1	1	−

Appendix 5 (continued)

Spring code	Distance to nearby bodies of water (m)	Surface area of the patches of different types present in the landscape						Flooding area
		Karst vegetation	Forest	Riparian vegetation	Meadows	Agricultural land	Built-up area	
S48	1094	2	1	0	1	1	1	−
S49	2652	2	2	0	1	1	0	−
S50	3641	2	3	0	1	0	1	−
S51	1439	2	1	0	1	1	2	−
S52	2278	1	2	1	1	1	1	−
S53	308	2	2	0	0	1	2	−
S54	503	3	1	0	1	1	1	−
S55	1434	3	3	0	0	0	0	−
S56	3197	2	1	1	1	1	1	−
S57	2589	1	1	1	1	1	1	−
S58	2563	1	1	1	1	1	1	−
S59	2285	3	1	0	0	0	2	−
S60	3805	4	1	0	0	0	0	−
S61	3446	1	1	1	1	1	1	−
S62	6	3	3	0	0	0	0	+
S63	1105	2	3	1	1	1	0	−
S64	2374	2	2	0	1	1	0	−
S65	148	1	2	1	1	1	2	−
S66	2164	1	1	0	1	1	1	−
S67	35	3	3	0	0	0	0	−
S68	2327	1	1	0	2	1	1	−
S69	2995	1	1	0	2	1	1	−
S70	2811	1	1	1	2	1	1	−
S71	3120	2	2	0	1	0	0	−
S72	2609	1	2	0	1	1	0	−
S73	2983	2	2	0	1	1	0	−
S74	3708	2	0	1	2	0	0	−
S75	1843	2	2	0	2	1	1	−
S76	2140	2	1	0	1	1	2	−
S77	3372	3	2	0	0	0	0	−
S78	4048	2	1	0	1	1	2	−
S79	321	1	2	0	2	1	1	−
S80	132	2	2	1	1	0	2	−
S81	9105	2	2	0	2	0	0	−
S82	4245	3	2	0	1	0	0	−
S83	7745	2	2	0	2	0	2	−
S84	13595	0	0	0	4	0	1	−
S85	9	0	2	0	3	0	0	+
S86	14	0	2	0	3	0	0	+
S87	528	2	1	0	2	0	1	−
S88	9708	2	3	0	2	0	0	−
S89	1590	1	0	0	4	0	0	−
S90	48	2	0	0	3	0	1	−
S91	11	2	0	0	3	0	0	+

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