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The influence of land use on dragonfly and damselfly (Odonata) community structure

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Abstract

Land-use change is a major driver of insect biodiversity loss, yet its effects on odonate assemblages remain understudied in Central Europe. We investigated the species richness, abundance, conservation value, and community composition of dragonflies across natural, agricultural, and urban land-use types in Slovakia, using data collected from 2000 to 2021. In total, 2,829 individuals representing 32 species—49% of the national fauna—were recorded. Agricultural sites supported the highest species richness (28), followed by urban (27) and natural sites (9). Despite this, the Dragonfly Biotic Index (DBI) did not differ significantly among land-use types, suggesting that species of conservation value can occur outside of natural habitats. Community composition differed significantly across land uses, with natural habitats supporting distinct assemblages, while generalist species were broadly distributed. Canonical correspondence analysis revealed significant effects of both land use and habitat traits on species distribution patterns. Our findings highlight the potential conservation value of anthropogenic habitats for odonates and showcase the importance of integrating diverse land-use types into regional conservation strategies.

Keywords: Aquatic insects, DBI, bioindication, conservation, Zygoptera, Anisoptera

Introduction

Over the past 50 years, the most significant negative impact on biodiversity involved changes in land use (IPBES 2019). The expansion of agricultural land and urban areas has occurred largely at the expense of natural habitats such as forests, grasslands, and wetlands. These changes often involve processes like deforestation, soil tillage, fertilization, cropping, and urban development, each of which leads to habitat degradation or destruction (Newbold et al. 2015). In particular, the conversion of land for intensive agriculture introduces enhanced nutrient inputs and pesticides and habitat degradation, which in turn jeopardizes the biodiversity (Collen et al. 2014; Reid

et al. 2019). Urbanization substantially alters geomorphological, hydrological, and biogeochemical conditions, often resulting in the spread of invasive species, the loss of native species, and an increase in widespread, generalist species (Goertzen and Suhling 2019).

Insects, the most diverse and abundant group of animals, are dramatically declining globally (Wagner 2020; Van Klink et al. 2024). They have long been central to water-quality assessments (Schindler et al. 2003; Dolný et al. 2021; Vilenica et al. 2025). A global meta-analysis showed that in insects, urbanization resulted in a mean decrease of 42 % in abundance, 40 % in richness, and 24 % in trait effects, compared to a conserved area (Vaz et al. 2023). Similarly, another meta-analysis examining agricultural land use and aquatic invertebrates showed that sensitive taxa decline under agricultural impact, while more tolerant taxa tend to benefit (Schürings et al. 2022). Within this broader group of aquatic macroinvertebrates, dragonflies (order Odonata) are recognized as a flagship group.

Dragonflies are divided into two suborders: damselflies (Zygoptera) and the true dragonflies (Anisoptera). Many odonate species are habitat specialists and are particularly susceptible to human-induced environmental changes, rendering them invaluable indicators in conservation ecology (Simaika and Samways 2009; Dolný et al. 2011; Buczyńska and Buczyński 2019; Vorster et al. 2020). Odonates respond sensitively to habitat alterations such as pollution, hydrological changes, and vegetation loss (Kalkman et al. 2010). Many species have specific habitat requirements, such as clear, oxygen-rich waters and developed riparian zones. The presence or absence of particular species can therefore provide critical insights into the ecological status of freshwater systems. The recent Red List of European dragonflies by De Knijf et al. (2024) assessed 137 species occurring across the European Union, classifying 30 as threatened. Given their sensitivity to habitat quality, dragonflies are increasingly used to assess the ecological impacts of land use (Satour et al. 2024).

Several recent studies across different regions have examined how land-use intensity and habitat transformation influence odonate diversity and community composition. The cross-country study in the Czech Republic, revealed that the level of naturalness significantly correlates with the occurrence of endangered dragonfly species (Dolný et al. 2021). The species richness remained stable across degraded habitats, while the occurrence of endangered species significantly declines with decreasing habitat naturalness. Similarly, a study in Germany reported lower odonate diversity in intensively farmed landscapes compared to urban areas. Urban assemblages were dominated by opportunistic and thermophilous species, whereas natural landscapes supported more habitat specialists (Goertzen and Suhling 2019). Comparable patterns have been observed in other regions. In Texas, surveys of ponds across multiple land-use types revealed that the highest species richness and the presence of habitat specialists occur in urban ponds, likely due to consistent water availability from urban runoff—unlike agricultural wetlands, which were more vulnerable to drought (Husband and McIntyre 2021). In Mexico, Rocha-Ortega et al. (2019) found that species richness was higher in agricultural and urban areas than in natural ones. The study of Raebel et al. (2012) demonstrated that odonate species richness is affected by land-use at different spatial scales of agri-environment schemes. These findings highlight the adaptability of generalist species, which possess broader ecological tolerances and stronger dispersal abilities than habitat specialists, allowing them to colonize and persist in anthropogenic environments.

The present study investigates the relationship between land use and odonate conservation value. Given that land-use change remains a primary threat to dragonfly diversity, we focused on comparing natural, agricultural, and urban land-use types in terms of the conservation value for individual species. To this end, we analysed data

collected between 2000 and 2021. We aimed to evaluate whether different types of land use vary in their ability to support species-rich and conservation-relevant dragonfly assemblages. Specifically, we addressed the following hypotheses:

i. Agricultural and urban land uses will host less species with high conservation value than those situated in natural land use.
ii. The species richness will be the highest in agricultural land use due to the wide spectrum of sampled wetlands.

Materials and Methods

Study area

The Kysuce region is located in north-western Slovakia, bordering the Czech Republic to the west and Poland to the north. It also extends into the Beskydy Euroregion and encompasses an area of 935 km², of which 654 km² is designated as the Kysuce Protected Landscape Area. The region is characterised by a rugged terrain that is predominantly covered by coniferous forests. Remnants of the original forest cover, primarily composed of mixed deciduous and coniferous stands, are mainly represented by beech and fir-beech communities (Debnár 2021). The agricultural landscape is traditionally associated with dispersed settlements and consists of arable land, grasslands, and pastures, accounting for only 12% of the total area (Barančok and Barančoková 2016).

The selected study sites included large areas of relatively undisturbed natural and transformed but extensively used agricultural area (Fig. 1).

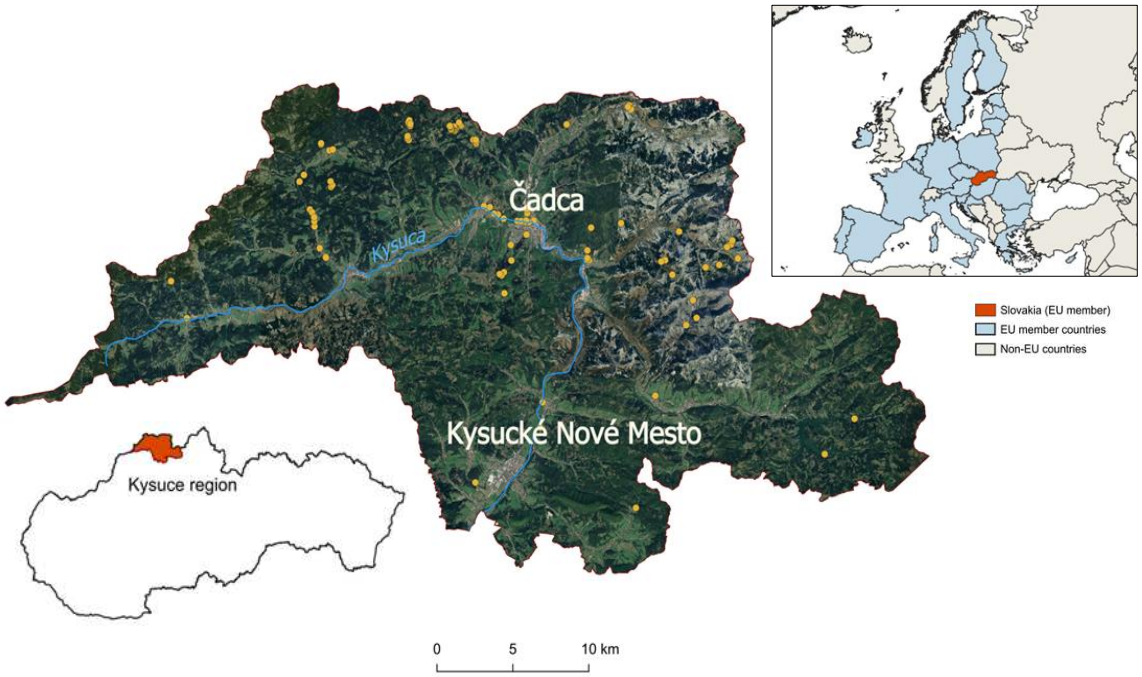


Fig. 1 Location of Kysuce region and the study sites (Sources: Administrative boundaries: ZBGIS®, Úrad geodézie, kartografie a katastra Slovenskej republiky, © EuroGeographics for the administrative boundaries; Imagery: Google ©2024 TerraMetrics; Orthophoto: GKÚ Bratislava, NLC).

The surrounding local land use differed between natural (forest ecosystems), agricultural (predominately meadows and pastures) and urban (predominantly towns and villages).

Study sites were situated within a hilly landscape, between coordinates 18°19'21.39" to 19°9'37.93"E and 49°14'51.01" to 49°49'11.81"N (Table 1).

Table 1 Study sites (1–110) and biotope types (Ružičková et al., 1996) in the studied area, with coordinates and land use.

Site number	Typ of biotope	Coordinates		Land use
1	stream	49°25'7.51"N	18°54'59.76"E	natural
2	stream	49°25'34.67"N	18°54'26.64'E	natural
3	stream	49°25'35.68"N	18°54'32.82"E	natural
4	stream	49°25'32.26"N	18°54'20.19"E	natural
5	stream	49°25'32.30"N	18°54'20.31"E	natural
6	stream	49°25'35.07"N	18°57'30.15"E	natural
7	spring	49°26'17.82"N	18°58'2.68"E	agricultural
8	stream	49°26'26.49"N	18°58'7.01"E	natural
9	stream	49°25'50.97"N	18°58'29.41"E	natural
10	stream	49°24'2.17"N	18°45'57.25"E	agricultural
11	stream	49°24'44.34"N	18°45'50.51"E	agricultural
12	stream	49°25'42.53"N	18°50'17.12"E	agricultural
13	stream	49°23'28.24"N	18°55'56.63"E	agricultural
14	spring	49°24'19.68"N	18°56'12.83"E	natural
15	stream	49°26'18.04"N	18°35'2.17"E	natural
16	stream	49°28'31.21"N	18°35'22.79"E	agricultural
17	stream	49°28'33.34"N	18°35'23.08"E	natural
18	stream	49°28'33.03"N	18°35'22.51"E	natural
19	stream	49°29'32.72"N	18°42'54.27"E	natural
20	stream	49°29'34.57"N	18°42'50.88"E	natural
21	stream	49°29'38.39"N	18°42'47.09"E	natural
22	stream	49°29'26.42"N	18°42'38.67"E	agricultural
23	stream	49°29'27.56"N	18°42'36.16"E	natural
24	stream	49°29'28.58"N	18°42'34.08"E	natural
25	stream	49°29'29.73"N	18°42'31.73"E	natural
26	stream	49°29'20.88"N	18°42'34.40"E	agricultural
27	stream	49°29'21.57"N	18°42'31.78"E	natural
28	stream	49°29'21.97"N	18°42'28.94"E	natural
29	stream	49°29'22.32"N	18°42'25.90"E	natural
30	stream	49°29'22.64"N	18°42'24.07"E	natural
31	stream	49°29'23.40"N	18°42'22.87"E	natural
32	stream	49°29'24.62"N	18°42'22.61"E	agricultural

Site number	Typ of biotope	Coordinates		Land use
33	stream	49°29'28.24"N	18°42'21.54"E	natural
34	stream	49°29'29.33"N	18°42'19.56"E	natural
35	stream	49°29'30.39"N	18°42'18.01"E	natural
36	stream	49°17'11.20"N	18°53'57.00"E	agricultural
37	stream	49°27'07.20"N	18°36'36.00"E	agricultural
38	stream	49°27'10.80"N	18°36'39.60"E	agricultural
39	stream	49°27'18.00"N	18°36'43.20"E	agricultural
40	stream	49°28'55.20"N	18°40'37.20"E	agricultural
41	stream	49°28'58.80"N	18°40'22.80"E	agricultural
42	stream	49°29'02.40"N	18°40'22.80"E	agricultural
43	epirhithral	49°29'24.00"N	18°40'58.80"E	agricultural
44	epirhithral	49°29'27.60"N	18°40'58.80"E	agricultural
45	epirhithral	49°29'27.60"N	18°40'55.20"E	agricultural
46	epirhithral	49°29'31.20"N	18°40'51.60"E	agricultural
47	epirhithral	49°29'34.80"N	18°40'44.40"E	agricultural
48	epirhithral	49°29'27.60"N	18°40'58.80"E	agricultural
49	stream	49°25'40.80"N	18°46'26.40"E	urban
50	temporary water	49°24'39.74"N	18°45'37.34"E	agricultural
51	temporary water	49°24'37.94"N	18° 45'43.46"E	agricultural
52	temporary water	49°24'40.03"N	18°45'37.06"E	agricultural
53	temporary water	49°26'28.98"N	18°50'23.49"E	agricultural
54	temporary water	49°23'44.42"N	18°56'29.11"E	natural
55	temporary water	49°27'26.45"N	18°34'34.64"E	agricultural
56	stream	49°26'18.15"N	18°35'2.03"E	natural
57	pond	49°29'0.01"N	18°43'47.87"E	agricultural
58	stream	49°29'6.33"N	18°43'37.98"E	agricultural
59	marshland	49°28'20.40"N	18°35'51.50"E	natural
60	stream	49°26'47.42"N	18°46'51.98"E	urban
61	stream	49°26'17.70"N	18°35'3.10"E	natural
62	stream	49°26'33.83"N	18°47'14.92"E	urban
63	stream	49°26'55.61"N	18°46'48.36"E	urban
64	stream	49°26'29.65"N	18°46'59.62"E	urban
65	stream	49°26'30.20"N	18°46'21.43"E	urban
66	stream	49°26'32.70"N	18°45'36.42"E	urban
67	stream	49°26'40.10"N	18°45'16.87"E	urban
68	stream	49°26'50.98"N	18°44'50.71"E	urban
69	stream	49°26'53.41"N	18°44'48.91"E	urban
70	stream	49°26'54.54"N	18°44'28.98"E	urban
71	stream	49°26'29.43"N	18°46'47.46"E	urban

Site number	Typ of biotope	Coordinates		Land use
72	stream	49°26'12.34"N	18°57'51,22"E	agricultural
73	stream	49°28'22.71"N	18°36'2.36"E	agricultural
74	spring	49°26'4.40"N	18°46'54.60"E	urban
75	stream	49°19'37.57"N	18°48'25.62"E	agricultural
76	marshland	49°30'42.32"N	18°51'57.97"E	agricultural
77	marshland	49°30'35.07"N	18°52'5.10"E	agricultural
78	marshland	49°30'34.34"N	18°52'5.34"E	agricultural
79	stream	49°29'3.91"N	18°43'47.96"E	agricultural
80	stream	49°26'30.52"N	18°46'34.26"E	urban
81	temporary water	49°26'32.61"N	18°46'50.10"E	urban
82	marshland	49°25'23.03"N	18°50'24.95"E	agricultural
83	stream	49°25'23.67"N	18°50'17.82"E	agricultural
84	pond	49°17'35.48"N	18°45'9.13"E	agricultural
85	pond	49°24'45.51"N	18°36'6.16"E	agricultural
86	temporary water	49°25'1.53"N	18°35'44.44"E	agricultural
87	stream	49°25'27.94"N	18°56'46.26"E	natural
88	pond	49°19'30.38"N	19°3'57.87"E	natural
89	stream	49°26'40.92"N	18°45'4.07"E	urban
90	stream	49°22'17.19"N	18°28'50.08"E	urban
91	stream	49°24'43.57"N	18°36'7.31"E	urban
92	temporary water	49°25'44.65"N	18°35'22.05"E	agricultural
93	stream	49°25'54.96"N	18°35'19.85"E	agricultural
94	spring	49°23'28.95"N	18°27'48.89"E	natural
95	temporary water	49°27'12.32"N	18°34'21.86"E	urban
96	temporary water	49°25'9.55"N	18°46'12.12"E	natural
97	pond	49°26'35.70"N	18°55'11.55"E	agricultural
98	temporary water	49°20'28.61"N	18°48'28.34"E	urban
99	temporary water	49°21'0.63"N	18°54'33.25"E	urban
100	marshland	49°25'27.22"N	18°50'18.95"E	urban
101	pond	49°29'6.68"N	18°43'46.05"E	agricultural
102	marshland	49°30'39.05"N	18°51'54.54"E	agricultural
103	stream	49°29'53.21"N	18°48'38.47"E	agricultural
104	temporary water	49°26'12.31"N	18°35'10.84"E	urban
105	temporary water	49°26'2.99"N	18°35'18.55"E	urban
106	stream	49°8'5.54"N	22°20'42.08"E	natural
107	stream	49°26'34.89"N	18°45'42.85"E	agricultural
108	temporary water	49.26'42.92"N	18.52'0.00"E	agricultural
109	pond	49°26'41.73"N	18°52'18.24"E	agricultural
110	stream	49°19'40.40"N	18°48'33.21"E	urban

All streams and some rivers had untransformed sections of natural vegetation, as well as sections of cultivated land. All streams and several rivers included both unaltered segments with natural vegetation and sections influenced by human activity. Untransformed sites were generally located in the upper reaches of streams and rivers, whereas agricultural sites were found in the middle reaches. The selection of a gradient of habitats, from highly transformed to entirely natural, was intended to capture the range of dragonfly responses to varying degrees of disturbance.

Sampling

We examined the distribution and habitat preferences of dragonfly species under specific ecological conditions, with the aim of applying the Dragonfly Biotic Index (Simaika and Samways 2009; Samways and Simaika 2016). Intensive surveys of aquatic habitats were conducted from 2000 to 2021, during the period from early May to late October. Fieldwork was undertaken on sunny days, between 10:00 a.m. and 6:00 p.m. Habitat types at each site were classified based on morphological characteristics, mode of origin and use, and hydrological properties. These criteria included water body size, cross-sectional profile, bottom substrate, and hydrological regime. Sampling sites were deliberately selected to represent the principal types of freshwater ecosystems in the region.

A total of 110 study sites were surveyed, encompassing ten habitat types and two main aquatic systems — lentic (standing water) and lotic (flowing water), within both protected and unprotected areas. The lentic systems included wetlands (n = 9), non-peat-forming swamp (n = 140), peatland swamp (n = 3), fishpond (n = 5), temporary pools (n = 125), pond (n = 41). The lotic systems comprised mountain streams (n = 6), foothill river (n = 89), foothill brook (metarhithral zone) (n = 64), springs on non-calcareous bedrock (n = 7).

Wetlands are ecosystems where the land is permanently or seasonally saturated with water. Water levels fluctuate seasonally, and this variability influences the composition of plant and animal communities. Wetlands are typically rich in organic matter due to slow decomposition rates in saturated soils. Vegetation ranges from emergent plants such as sedges, reeds, and cattails to mosses and shrubs, depending on water depth and nutrient availability. *Non-peatbog wetlands* are shallow depressions with fluctuating water levels, often eutrophic to dystrophic, supporting a diverse range of plant species. *Peatland swamp* are nutrient-poor, acidic wetlands dominated by peat-forming plants like *Sphagnum* mosses. They typically have low pH values (2.8–4.5) and are oligotrophic. *Fishpond* is artificial or semi-natural water bodies created for fish farming. They support a variety of aquatic life, including fish species such as carp (*Cyprinus carpio*) and perch (*Perca fluviatilis*), as well as various invertebrates and plants.

Temporary pools are wet meadows and grasslands, often found in floodplains or depressions. *Ponds* are small artificial water bodies (< 5 ha) constructed for various purposes, including irrigation, flood control, and recreation. *Mountain streams* occur in high-altitude areas, typically above 1000 meters above sea level. These streams are characterized by cold, nutrient-poor (oligotrophic) water with a relatively stable temperature regime ranging between 3 to 6°C. The current is fast and turbulent, and the streambed is composed mainly of coarse substrates such as gravel, stones, and boulders. *Foothill rivers* (hyporhithral zone) are situated in the submontane region, usually between 200 and 800 meters in elevation. These rivers exhibit moderate to fast flow, and the water is cool, with slightly acidic to neutral pH and low to moderate nutrient levels. The substrate typically consists of a mixture of gravel, sand, and occasionally boulders. *Foothill brooks* representing the metarhithral zone, occur in the lower montane belt, generally between 600 and 1000 meters elevation. These streams have cooler water temperatures, ranging from 6 to 10°C, and show moderate current velocities. The water tends to be neutral to slightly alkaline

and contains moderate levels of nutrients. The streambed is typically formed by gravel and sand. *Springs* located on non-calcareous bedrock are found in the colline to montane zones and are characterized by cold, oligotrophic water that is slightly acidic to neutral in pH. These springs are often stable in terms of hydrology, with constant or seasonally stable water discharge.

Natural areas with low levels of anthropogenic disturbance—primarily located along the peripheries of core urban and agricultural zones and adjacent to streams and rivers—cover 64.02% of the total study area. Urban land use, representing the highest level of anthropogenic disturbance, accounts for 6.04% of the area. Agricultural land, which is subject to intermediate disturbance levels, covers 5,641.54 hectares.

All adult odonates, including recently emerged adults and mating pairs (counted as two individuals), as well as larvae, were recorded (Table 2).

Table 2 Odonata species recorded in Kysuce region with their occurrence in three types of land use.

Species	**IUCN**	**Land use**		
		agricultural	natural	urban
Aeshna affinis Vander Linden, 1820	LC	1	x	x
Aeshna cyanea (Müller,1764)	LC	225	20	82
Aeshna mixta Latreille, 1805	LC	2	x	1
Anax imperator Leach, 1815	LC	3	1	x
Calopteryx splendens (Harris, 1782)	LC	14	x	26
Calopteryx virgo (Linnaeus, 1758)	LC	30	x	41
Coenagrion puella (Linnaeus, 1758)	LC	284	17	46
Cordulegaster bidentata Selys, 1854	NT	56	115	6
Enallagma cyathigerum (Charpentier, 1840)	LC	91	20	22
Chalcolestes viridis (Vander Linden, 1825)	LC	36	x	5
Ischnura elegans (Vander Linden, 1820)	LC	11	x	2
Ischnura pumilio (Charpentier, 1825)	LC	4	x	1
Lestes barbarus (Fabricius, 1798)	LC	2	x	3
Lestes dryas Kirby, 1890	LC	1	x	x
Lestes sponsa (Hansemann, 1823)	LC	369	61	30
Lestes virens vestalis Rambur, 1842	LC	x	x	4
Libellula depressa Linnaeus, 1758	LC	204	x	5
Libellula quadrimaculata Linnaeus, 1758	LC	x	x	1
Onychogomphus forcipatus (Linnaeus, 1758)	LC	8	x	68
Orthetrum albistylum (Selys, 1848)	LC	1	x	x
Orthetrum brunneum (Fonscolombe, 1937)	LC	x	x	2
Orthetrum cancellatum (Linnaeus, 1758)	LC	3	x	1
Platycnemis pennipes (Pallas, 1771)	LC	145	2	278
Pyrrhosoma nymphula (Sulzer, 1776)	LC	76	5	21
Sympetrum danae (Sulzer, 1776)	LC	16	x	10
Sympetrum flaveolum (Linnaeus, 1758)	LC	8	x	15

Species	IUCN	Land use		
		agricultural	natural	urban
Sympetrum meridionale (Selys, 1841)	LC	x	x	1
Sympetrum pedemontanum (Allioni, 1766)	LC	3	x	41
Sympetrum sanguineum (Müller, 1764)	LC	19	8	189
Sympetrum striolatum (Charpentier, 1840)	LC	7	x	19
Sympetrum vulgatum (Linnaeus, 1758)	LC	12	x	26
Cordulia aenea (Linnaeus, 1758)	LC	3	x	x
Number of species		**28**	**9**	**27**
Number of individuals		**1634**	**249**	**946**

Surveys of both males and females were conducted by walking along the littoral zone and visually recording adults (Kadlec et al. 2012). Adults were mostly sampled using an entomological net and identified in the field. Some species were observed visually, identified by eye. Most adult specimens were captured using an entomological net and identified in the field. Some individuals were identified visually without capture. Species that could not be reliably identified in the field were collected and later determined in the laboratory using identification key of Dijkstra and Lewington (2014).

The data included both species presence/absence and relative abundance. In addition to species composition, local communities were characterized by species richness, defined as the total number of species recorded during a site visit. To assess the conservation value of the study sites, we applied the Dragonfly Biotic Index (DBI) developed by Simaika and Samways (2009). The DBI assigns scores from 0 (generalist species) to 9 (specialist species), incorporating factors such as regional distribution, national red list status, and sensitivity to habitat disturbance. DBI values for Central European odonate species followed the classification by Dolný et al. (2016).

Study sites were classified into three land-use categories: natural, agricultural, and urban. We calculated an abundance-weighted DBI in which we summed the DBI values of the recorded species multiplied by their current local abundance to account for the relative dominance of common or specialist species at a given site. This approach yielded three values of species richness, site-specific DBI and site-specific abundance-weighted DBI for each locality.

Statistical analyses

The data analysed in this research covered the data of species abundance (N), species richness index (S), species diversity index (H') Shannon entropy, and species evenness index (E). All of the indices were calculated with the aid of program Past.3 (Hammer 2015). All univariate analysis and data visualizations were implemented in R software version 3.6.3 (R Core Team, 2020) (Shapiro-Wilk W-test ($p = 0.001$), Kruskal-Wallis' test).

Multivariate analysis (CCA traits analysis) was run in CANOCO 5 (ter Braak and Šmilauer 2012). CCA analysis was employed to determine the dependencies between objects – odonates and type of land use. The number of individuals was used as a matrix, surrounding local land use (defined as the area immediately beyond the sampling site (natural, agricultural or urban) were recorded as categorical variables. Statistical significance of ordination analysis was tested by a Monte Carlo permutation test (iterations = 499, at the level of statistical significance $p\alpha = 0.05$). Natural sites were located largely in forest ecosystems in protected areas, agricultural sites were located on meadows and pastures, and urban sites occurred at the towns. We generated rarefaction curves via

Past.3 for a subset of 9 species with DBI > 0 to exclude the impact of widely distributed generalist species (Hammer, 2015).

Results

Species abundance and richness

A total of 2,829 individuals of 32 dragonfly species (19 Anisoptera and 13 Zygoptera) were recorded throughout the study, representing 49% of the entire Slovak odonate fauna (David and Šácha, 2019) (Table 1). The most numerous species was *Lestes sponsa* which was also most frequently recorded at agricultural sites. *Cordulegaster bidentata* was the most numerous species at natural sites, while *Platycnemis pennipes* was the most numerous species at urban sites. The highest species richness was recorded in agricultural land-use areas (28 species), followed closely by urban areas (27 species), while natural land-use areas exhibited the lowest species richness (9 species) (Fig. 2).

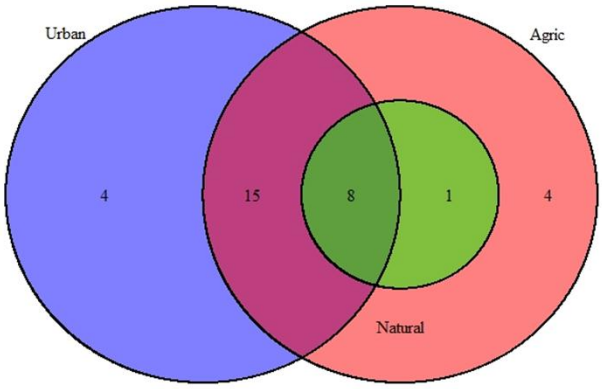


Fig. 2 Odonata species richness distribution among land use: urban land use (27 species), agricultural land use (28 species) and natural land use (9 species).

Eight species were found to be common across all three land-use categories. Four species were unique to agricultural land use (*Cordulia aenea*, *Aeshna affinis*, *Lestes dryas*, *Orthetrum albistylum*) and urban land use (*Lestes virens vestalis*, *Orthetrum brunneum*, *Libellula quadrimaculata*, *Sympetrum meridionale*). Fifteen species were common to the agricultural and urban land use only. There were no species common to the natural and urban land use.

The three types of land use differed significantly in site-specific species richness ($p = 0.000004$, $F(2.34) = 24.6235$, $df = 2$). The species richness was significantly less diverse in natural land use habitats compared to agricultural and urban land use. The highest species richness was at agricultural land use, while urban land use being intermediate (Fig. 3).

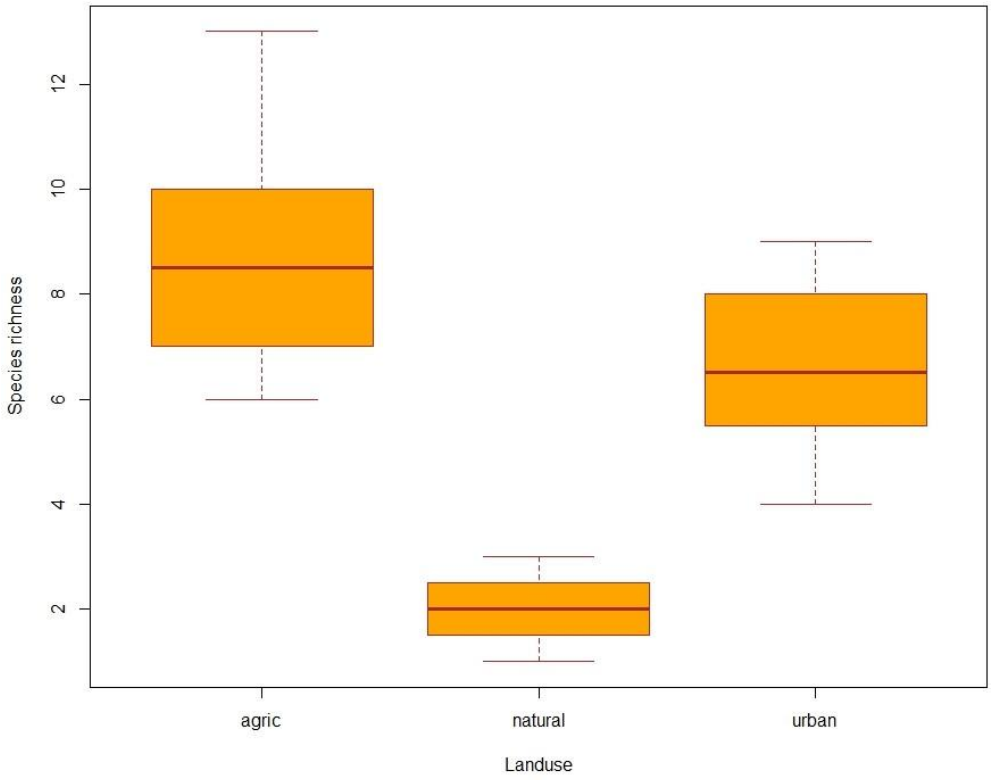


Fig. 3 Site-specific species richness of local odonate communities.

The site-specific DBI did not differ significantly between the land use ($p = 0.5154$, $F(2.36) = 1.3255$, $df = 2$, Fig. 4).

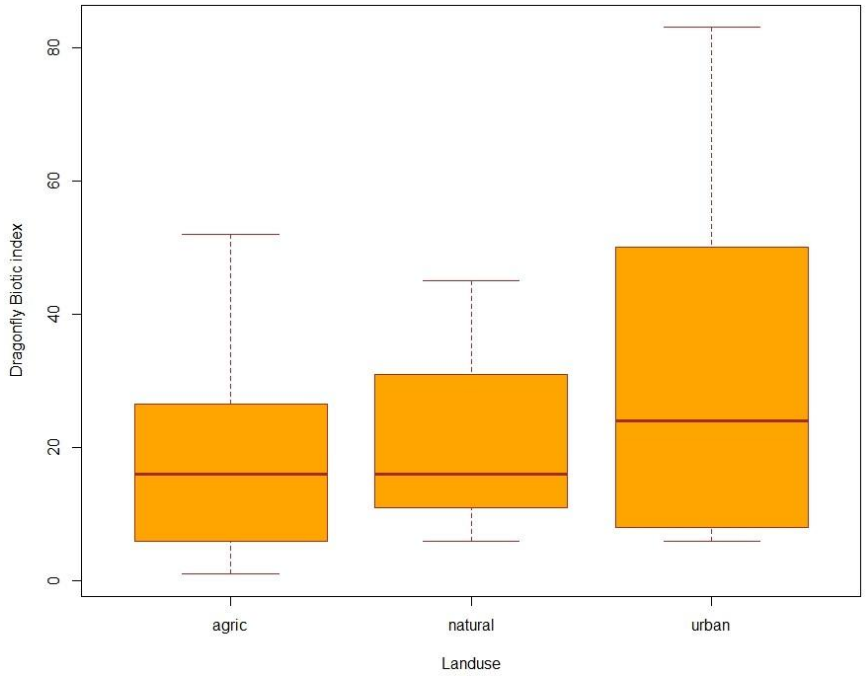


Fig. 4 Conservation value of the studied land use types based on local odonate assemblages.

We also confirmed a marginally significant difference ($p = 0.05$) in the number of species richness and habitats (Fig. 5).

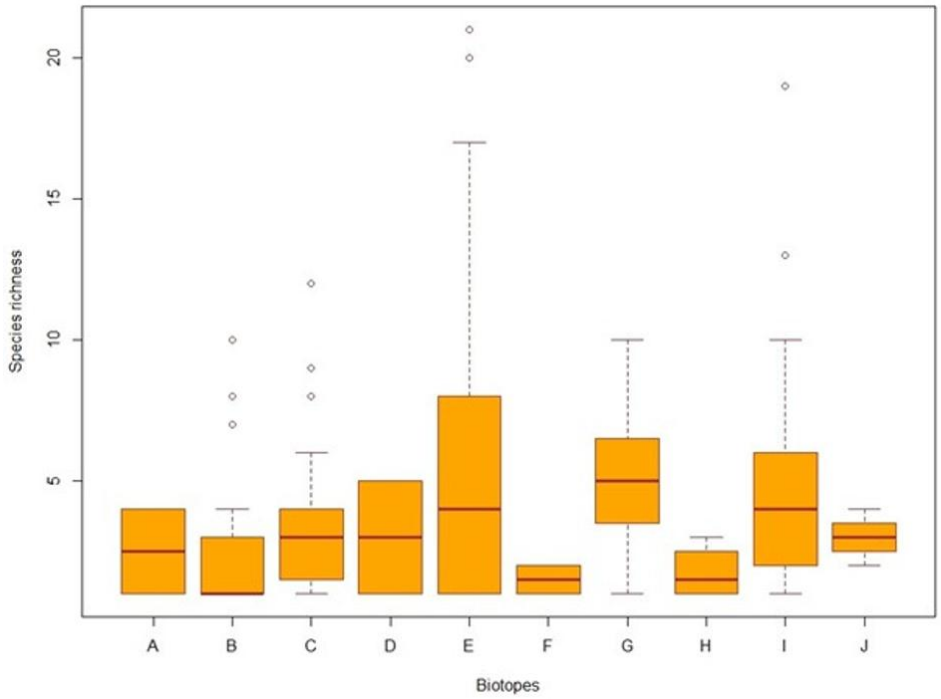


Fig. 5 Differences in the number of species richness among biotopes. Explanations: A = Fishpond, B = Foothill brook, C = Foothill river, D = Mountain streams, E = Non-peat-forming swamp, F = Peatland swamp, G = Pond, H = Springs, I = Temporary pools, J = Wetland.

The rarefaction analysis revealed highest species richness in agricultural land use, intermediate for natural and lowest species richness for urban land use (Fig. 6).

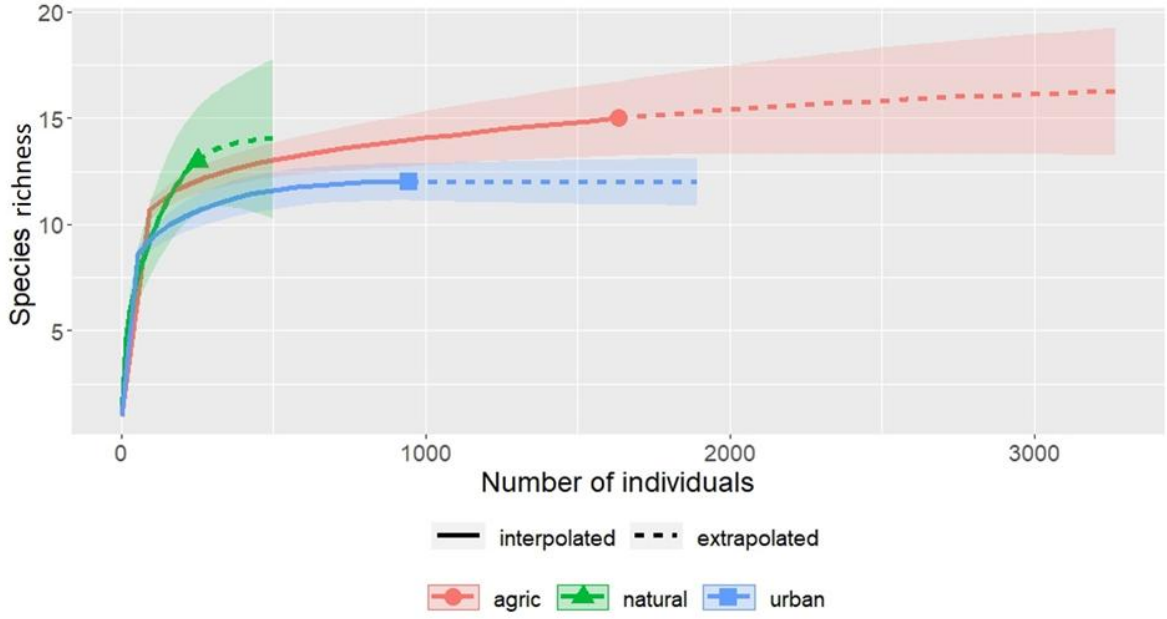


Fig. 6 Extrapolation curves (dashed lines) of total species richness in each habitat type.

Agricultural land use had the highest conservation value followed by natural and urban land use types (Fig. 7).

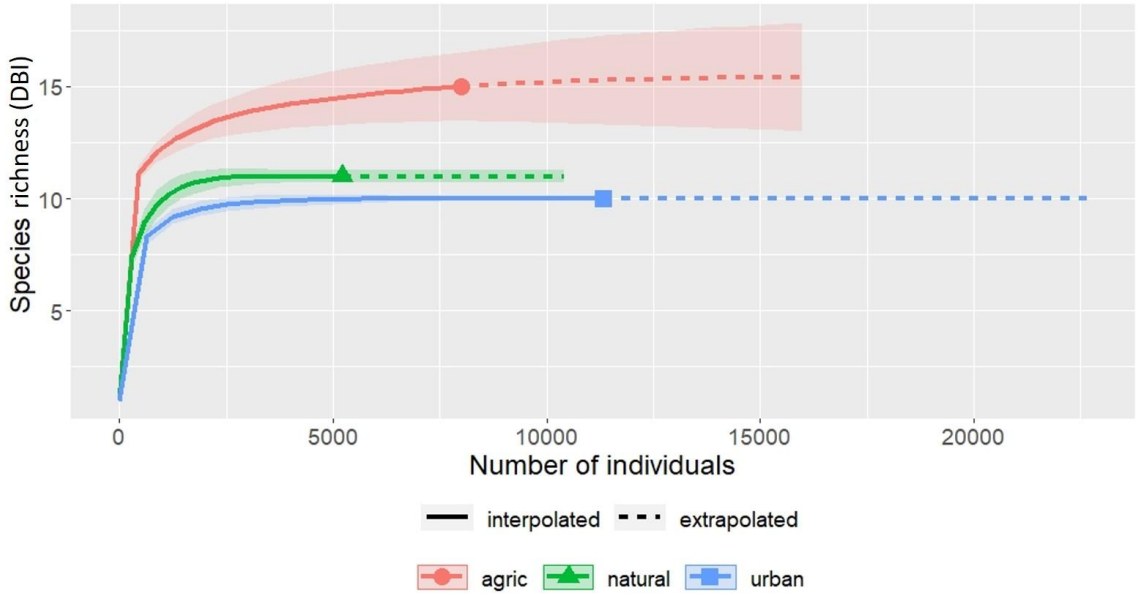


Fig. 7 Extrapolation curves (dashed lines) of species richness limited to species with DBI > 0 in each land use type.

Dragonfly communities across land use types

Dragonfly communities differed significantly among the different habitat types (CCA (SD= 5.4): pseudo-F = 2.0, $p < 0.001$, adjusted explained variance = 9.2%). We confirmed a statistically significant effect on the spatial dispersion of dragonflies in agricultural ($p = 0.034$), urban ($p = 0.011$) and natural ($p = 0.018$) environment. Odonate communities were separated on the first axis according to the studied land use types. The variability of dragonflies explained by land use (agricultural, natural, urban) was 67.9% on the first axis and 89.56% on the second cumulative axis. However, some generalist species did not show any clear land use preferences and were found across most localities (especially *Anax imperator, Libellula depressa, or Aeshna cyanea*), other species were associated with one of the land use types (Fig. 8).

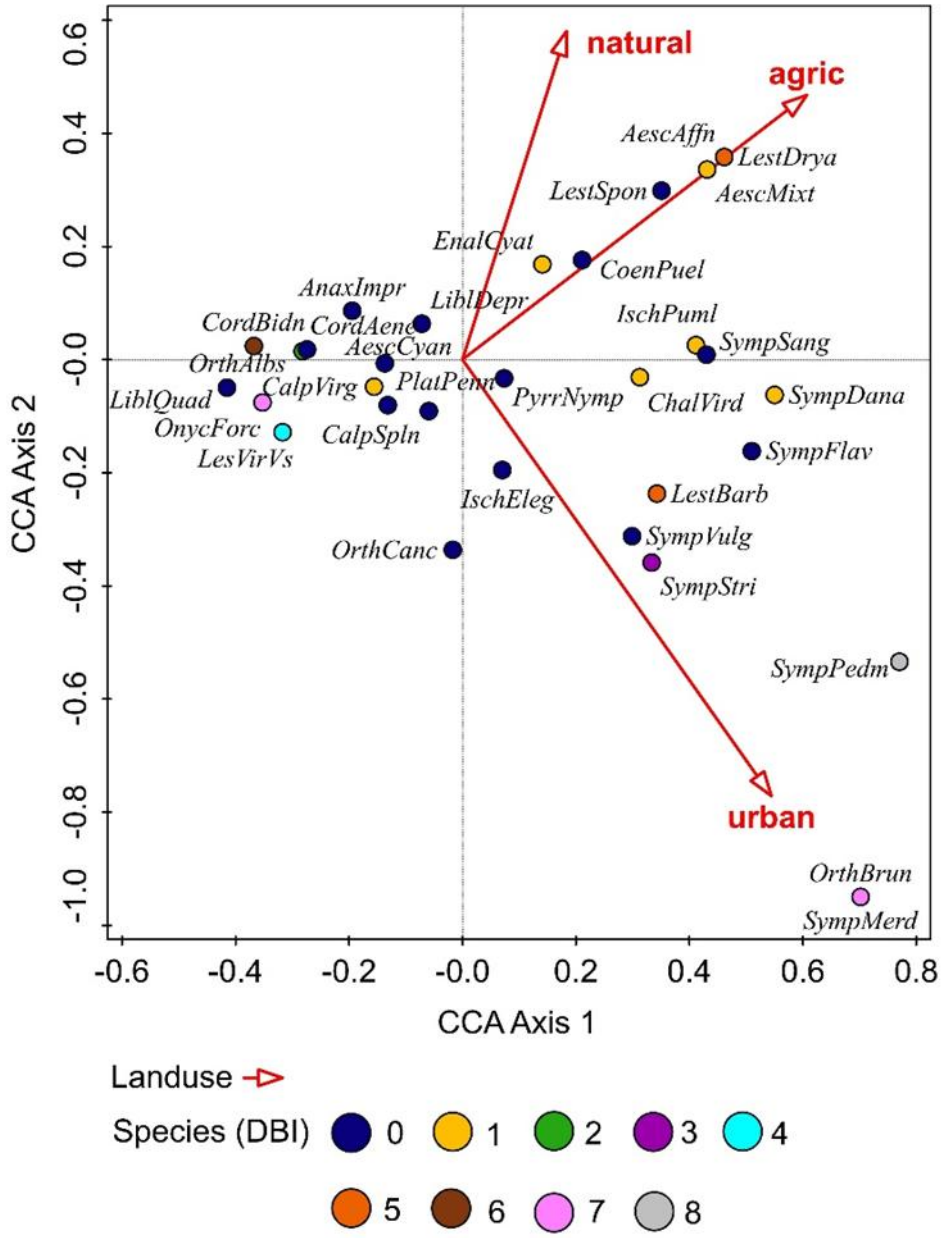


Fig. 8 Ordination plot showing the relationship between odonate species and land use type Circles with different colours refer to the DBI value of each species. Abbreviations used: AescAffn – *Aeshna affinis*, AescCyan – *Aeshna cyaena*, AescMixt – *Aeshna mixta*, AnaxImpr – *Anax imperator*, CalpSpln – *Calopteryx splendens*, CalpVirg – *Calopteryx virgo*, CoenPuel – *Coenagrion puella*, CordAene – *Cordulia aenea*, CordBidn – *Cordulegaster bidentata*, EnalCyat – *Enallagma cyathigerum*, ChalVird – *Chalcolestes viridis*, IschEleg – *Ischnura elegans*, IschPuml – *Ischnura pumilio*, LestBarb – *Lestes barbarus*, LestDrya – *Lestes dryas*, LestSpon – *Lestes sponsa*, LestVirVs – *Lestes virens vestalis*, LiblDepr – *Libellula depressa*, LiblQuad – *Libellula quadrimaculata*, OnycForc – *Onychogomphus forcipatus*, OrthAlbs – *Orthetrum albistylum*, OrthBrun – *Othetrum brunneum*, OrthCanc – *Orthetrum cancellatum*, PlatPenn – *Platycnemis pennipes*, PyrrNymp – *Pyrrhosoma nymphula*, SymDana – *Sympetrum danae*, SympFlav – *Sympetrum flaveolum*, SympMerd – *Sympetrum meridionale*, SympPede – *Sympetrum pedemontanum*, SympSang – *Sympetrum sanguineum*, SympStri – *Sympetrum striolatum*, SympVulg – *Sympetrum vulgatum*.

We also tested via CCA the affinity of species on biotope types and autecological traits as 'cwm'. The explained variability of dragonflies on the first axis was 34.58 % and on the second cumulative axis 49.30%. The variability of dragonflies explained by traits was 46.48% on the first axis and 66,28% on the second cumulative axis (Figure 9).

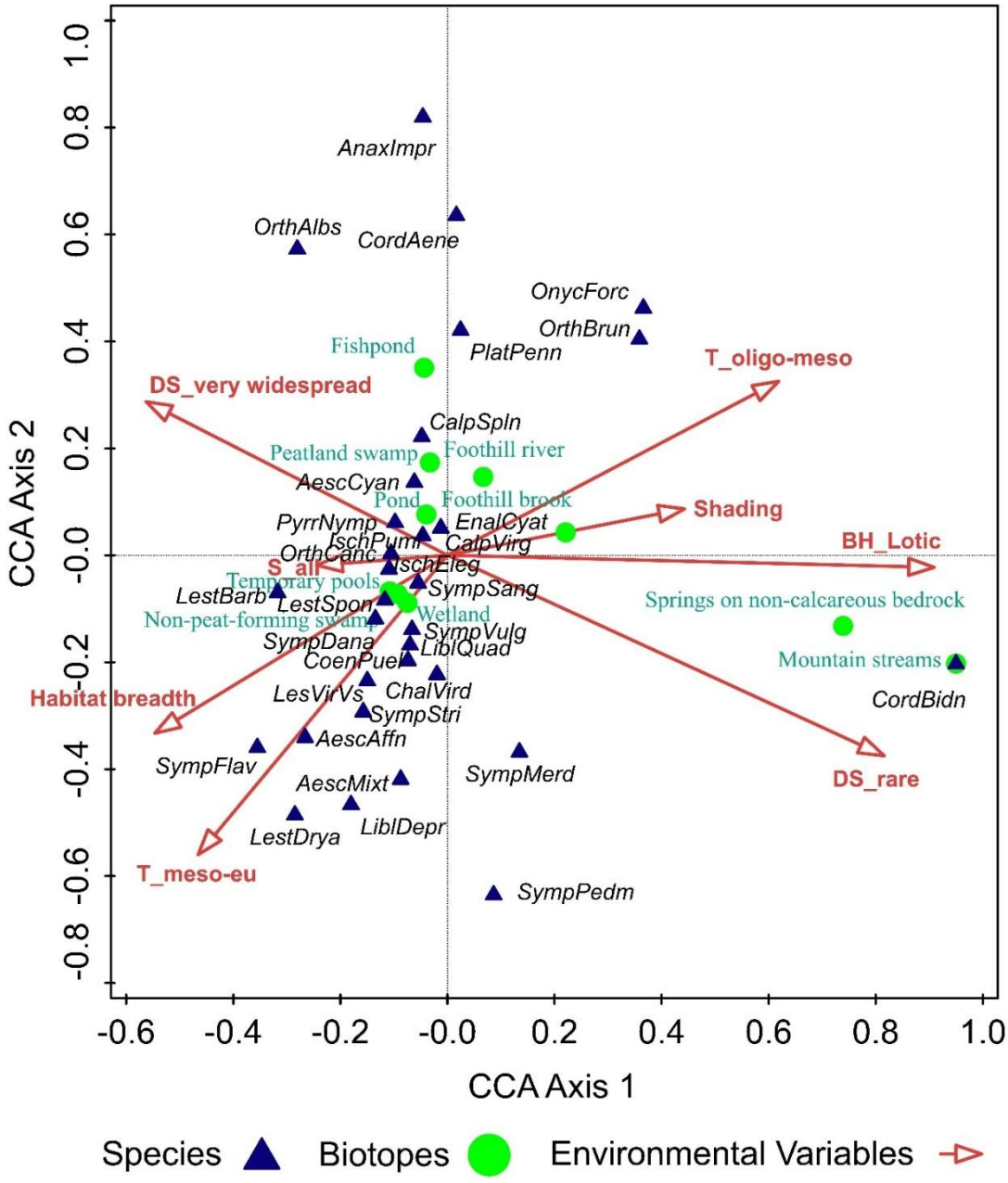


Fig. 9 Ordination plot showing the relationship between odonate species and occupied biotope types with passively projected autecological traits of each species. Abbreviations used: AescAffn – *Aeshna affinis*, AescCyan – *Aeshna cyaena*, AescMixt – *Aeshna mixta*, AnaxImpr – *Anax imperator*, CalpSpln – *Calopteryx splendens*, CalpVirg – *Calopteryx virgo*, CoenPuel – *Coenagrion puella*, CordAene – *Cordulia aenea*, CordBidn – *Cordulegaster bidentata*, EnalCyat – *Enallagma cyathigerum*, ChalVird – *Chalcolestes viridis*, IschEleg – *Ischnura elegans*, IschPuml – *Ischnura pumilio*, LestBarb – *Lestes barbarus*, LestDrya – *Lestes dryas*, LestSpon – *Lestes sponsa*,

LestVirVs – *Lestes virens vestalis*, LiblDepr – *Libellula depressa*, LiblQuad – *Libellula quadrimaculata*, OnycForc – *Onychogomphus forcipatus*, OrthAlbs – *Orthetrum albistylum*, OrthBrun – *Othetrum brunneum*, OrthCanc – *Orthetrum cancellatum*, PlatPenn – *Platycnemis pennipes*, PyrrNymp – *Pyrrhosoma nymphula*, SymDana – *Sympetrum danae*, SympFlav – *Sympetrum flaveolum*, SympMerd – *Sympetrum meridionale*, SympPede – *Sympetrum pedemontanum*, SympSang – *Sympetrum sanguineum*, SympStri – *Sympetrum striolatum*, SympVulg – *Sympetrum vulgatum*.

Discussion

Our study revealed substantial differences in species richness across the studied land use and biotope types. We demonstrated that agricultural and urban land use sites were characterised by Odonata assemblages that differed from those in natural land use. The hypothesis that agricultural or urban areas will host only a subset of species from the natural land use was not confirmed. Urban, but more prominently agricultural land use provided for the establishment of richer assemblage of widespread, generalist species, while urban land use also indicated species of high conservation importance. Natural land use showed reduced species richness, on the other hand, it hosted specialised and uncommon species. The highest species richness was observed at a site of agricultural land use, followed by urban and natural land use sites. The relatively low DBI score (i.e., conservation value) for natural land use may be due to the limited number of suitable sites for lentic species and the fact that natural areas were predominantly represented by less diverse lotic habitats. Agricultural areas, on the other hand, are typical to form a connected pondscape that are utilised as "stepping stones" for many threatened odonate species with high conservation value (Briggs et al. 2019).

Local land use type and DBI score

We did not detect any significant differences in the conservation value among the three land-use types. This suggests that urban and agricultural areas may support species of high conservation value similarly to natural areas. Similarly, (Briggs et al. 2019) also did not find differences in DBI scores across various pond types across a protected area-sugarcane-forestry mosaic suggesting that transformed areas might be important contributors to regional conservation. These findings contradict those of Kietzka et al. (2018), who reported significantly higher DBI scores for natural land use types compared to agricultural or urban ones in the Western Cape Province, South Africa. They reported consistently lower DBI scores at artificial land use types-interpreting this as evidence of a shift from habitat specialists to more widespread, eurytopic species. The discrepancy could stem from differences in species pools, land use intensity and also habitat heterogeneity between the regions. The extrapolated DBI score revealed the highest DBI score for agricultural land use sites, followed by natural and urban sites. This implies a relatively suitable environmental conditions for wetland situated in agricultural landscape. However, the species pool within the natural land use sites, predominantly characterised by springs and mountain streams, is relatively poor compared to the wide array of standing water habitats present in the studied region. Increased habitat availability, habitat heterogeneity and resource availability may account for higher species richness and DBI scores compared to natural sites (McKinney 2002).

Species connection to land use

The Canonical Correspondence Analysis (CCA) ordination plot illustrates the relationship between Odonata species distribution and three major land use types: natural, agricultural, and urban. Notably, urban land use forms a distinct vector that separates associated species along the first canonical axis (CCA Axis 1). Thermophilous

species such as *Sympetrum meridionale* and *Orthetrum brunneum* are positioned furthest along this vector, suggesting a higher affinity for urbanized environments. This is in line with Goertzen and Suhling (2019) who showed that urban areas possess distinct species assemblage with opportunistic species supported by warm climate. Moreover, the conservation value of such species may be also relatively high compared to species that showed no connection to any land use types, which suggests that urban habitats may provide breeding habitats for these species (Goertzen and Suhling 2013). The most discriminating species in our CCA analysis for urban land use, *Sympetrum meridionale* and *Orthetrum brunneum*, in recent decades increased their abundances in Central Europe (Kalkman et al. 2015), and are a prominent species of urban assemblages. In contrast, species confined to shallow waters and habitats that may drought out during the year (e.g., *Aeshna affinis*, *Lestes dryas*) clustered near the 'agricultural' vector appear to be more associated with wetlands situated in agricultural landscape.

Species composition of biotopes

The most numerous species of agricultural land use was *Lestes sponsa*, a widespread species throughout Europe. According to CCA, this species with other generalists were connected to temporary pools and swamps, i.e. to a habitat types that are often present in agricultural landscape. Such species may occur at newly created shallow wetlands with high vegetation (Boudot and Kalkman 2015). The presence of a combination of generalist species with higher dispersal abilities (i.e. trait labelled as 'very widespread') and not limited to the type of substrate ('all' types of substrates) may indicate degraded types of habitats (Rocha-Ortega et al. 2019). Additionally, very common species confined usually to low-altitude standing waters were linked to fishpond type biotope. Fishponds are usually rich in nutrients such as phytoplankton that allows increased fish production. High phytoplankton biomass may cause biodiversity decline of fishponds (Pálffy et al. 2013). Our ordination plot indicated large bodied anisopteran species (such as *Anax imperator*), excellent colonizers of habitats created by disturbance, which may be considered as a proxy indicators of transformed and/or non-natural areas (Kadoya et al. 2004; Rocha-Ortega et al. 2019). However, the ubiquitous damselfly, *Platycnemis pennipes* was also linked to fishpond habitat. It is one of the most common within its range in Europe and it is common at most types of standing waters. In contrast, specialist species were positioned on the opposite side of the ordination plot. This species group requires lotic waters, such as springs, mountain streams, foothill brooks and rivers. The ecological demands of such species (*Calopteryx virgo*, *Onychogomphus forcipatus* and *Cordulegaster bidentata*) are limited to meso- or even oligotrophic conditions, high shading and because of that they are also more uncommon species (in the plot, labelled as 'rare'). *Cordulegaster bidentata* was the most numerous species at natural sites. Based on CCA, the species was well-delineated to habitats, where this specialist primarily occur, i.e. at springs and subsequently at mountain streams. *Cordulegaster bidentata* as a stenothermic species has a strong affinity to woodlands in the mountains of Central Europe (Boudot and Holuša 2015). Lastly, several species were connected to 'habitat breadth' and 'meso-to-eutrophic' traits. Those are species such as *Lestes dryas*, *Libellula depressa*, *Sympetrum flaveolum* and other, that occupy a wide array of lentic habitats overgrown by dense macrophytes.

Conclusion for future biology

Odonate conservation entails protecting and restoring freshwater habitats, which, in turn, supports a wide range of aquatic and terrestrial biodiversity. The sensitivity of Odonata to environmental changes, particularly in relation to water quality, habitat integrity, and climate fluctuations, makes them valuable subjects for conservation efforts. The implications of Odonata conservation extend beyond species preservation, influencing broader ecological

stability and biodiversity management strategies. This is particularly relevant in Central Europe, where a diverse network of freshwater habitats, including lentic and lotic ecosystems may support various Odonata assemblages. Specifically in Slovakia, conservation efforts should focus on maintaining and restoring riparian vegetation, preventing habitat fragmentation, and mitigating the impacts of land use changes. Implementing habitat protection measures, such as buffer zones and sustainable land-use practices, can enhance the resilience of these ecosystems. High number of aquatic habitats in Slovakia are of anthropogenic origin. We found that the high number of different land use classes in the area increases overall habitat heterogeneity and man-made freshwater biotopes in agriculture land could serve as important secondary habitats for odonate communities because of high species richness at these localities. Conservation strategies should incorporate climate-adaptive measures, such as maintaining habitat connectivity to facilitate species dispersal and migration.

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Author contributions

KP initiated the study, coordinated the odonate sampling, selected the sampling sites and wrote major parts of the manuscript. AB thoroughly reviewed, wrote important parts and edited the manuscript. VL performed statistical analysis and was responsible for visualisation. PB reviewed the manuscript and supervised the writing process. SD provided certain odonate data.

Data availability

The data that made the findings of this research are available from the first author upon request.

Competing interests The authors declare no competing interests.

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