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ECOLOGY VERSUS TOPONYMY: ECOLOGICAL REASSESSMENT OF A HISTORICALLY MISNAMED LOCALITY (SUNĐER, VELEBIT MOUNTAIN)

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Peatlands are unique ecosystems that differ significantly from other wetlands in terms of landforms, hydromorphology, water chemistry, nutrient availability, and the diversity of organisms and life forms they support. They are globally important for biodiversity, carbon sequestration, and the preservation of long-term paleoenvironmental records due to their slow accumulation of organic matter. In Croatia, the four southernmost peatlands (Sunđerac, Ljubica, Rakita, and Vodice kod Petrašice) are located along the Velebit Mountain range. However, for decades, scientific literature suggested the presence of an additional peatland known as "Sunđer." This name caused confusion as it implied the existence of a separate site, distinct from Sunđerac. The misinterpretations probably stemmed from Pevalek's 1925 report, where he misnamed Sunđerac, calling it "Sunđer", and was inaccurate in his mapping of the location. The discovery of a permanent pond, Solila, close to the "Sunđer" locality, has reopened the debate and led to further ecological research. We investigated bryophytes, vascular plants and ground beetles, reliable indicators of peatland habitat quality, to test whether Solila could represent the long-misidentified "Sunđer" mire. No species characteristic of peatland ecosystems were found in any of the indicator groups. The only vascular plant species associated with mire vegetation was *Carex echinata*, which also occurs in acidic grasslands and spruce mire forests. Nevertheless, in this relatively small area, we found a surprisingly high diversity of plants and ground beetles, including riparian species, that would not be found in this area without permanent surface water. Permanent ponds such as Solila can therefore make a significant contribution to local biodiversity in karst landscapes.

Key words: Sunđer, Sunđerac, transitional mire, permanent pond

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Cretovi su jedinstveni ekosustavi koji se značajno razlikuju od ostalih močvarnih staništa u smislu reljefnih oblika, hidromorfologije, kemije vode, dostupnosti hranjivih tvari te raznolikosti organizama i životnih oblika koje podržavaju. Globalno su važni za bioraznolikost, sekvestraciju ugljika i očuvanje dugoročnih paleoekoloških zapisa uslijed sporog nakupljanja organske tvari. U Hrvatskoj se četiri najjužnija creta (Sunđerac, Ljubica, Rakita i Vodice kod Petrašice) nalaze na području Velebita. Međutim, desetljećima je znanstvena literatura sugerirala prisutnost dodatnog creta poznatog kao

„Sunđer“. Ime je izazivalo nedoumice jer je impliciralo postojanje zasebnog lokaliteta, različitog od Sunđerca. Pogrešna tumačenja vjerojatno su proizašla iz Pevalekovog izvješća iz 1925., u kojem je Sunđerac pogrešno nazvao „Sunđerom“ i pokušao netočno kartirati njegovu lokaciju. Otkriće stalne lokve Solila, u blizini lokaliteta „Sunđer“, ponovno je otvorilo raspravu i dovelo do daljnjih ekoloških istraživanja. Istražili smo mahovine, vaskularne biljke i trčke, pouzdane indikatore kvalitete staništa cretova, kako bismo ispitali jesu li Solila taj dugo pogrešno identificirani cret "Sunđer". Niti u jednoj od indikatorskih skupina nisu zabilježene vrste karakteristične za cretne ekosustave. Jedina vrsta vaskularnih biljaka povezana s cretnom vegetacijom bila je *Carex echinata*, koja se također javlja na kiselim travnjacima i u smrekovim cretnim šumama. Ipak, na ovom relativno malom području pronašli smo iznenađujuće veliku raznolikost biljaka i trčaka, uključujući riparijske vrste, koje ne bi bile prisutne na ovom području bez stalnog vodenog tijela. Stalne lokve, poput Solila, stoga mogu značajno doprinijeti lokalnoj bioraznolikosti u krškom krajoliku.

Ključne riječi: Sunđer, Sunđerac, prijelazni cret, stalna lokva

INTRODUCTION

Peatlands, a specific type of wetland habitats with accumulations of organic matter, are characterised by high soil moisture and acidity, and extremely low oxygen levels and nutrient availability (Rydin & Jeglum, 2006; Spitzer & Danks, 2006). They are widespread in northern, western and central Europe, while in Croatia they represent small and isolated habitat patches embedded mainly in forest matrix types (Topić & Stančić, 2006; Alegro & Topić, 2017). Species inhabiting peatlands are typically highly specialized and exhibit a strong ecological dependence on these environments (Rydin & Jeglum, 2006; Spitzer & Danks, 2006). A typical example includes *Sphagnum* mosses and tyrphobiontic insect species, strictly confined to peat bog ecosystems (Spitzer *et al.*, 1999; Bucholz *et al.*, 2009). The four southernmost peatlands in Croatia — Sunđerac, Ljubica, Rakita and Vodice kod Petrašice (the latter referred to as Klepina Duliba and/or Štirovača bog in the older literature), are located along the Velebit Mountain range, a boundary between the Mediterranean and Alpine biogeographical regions (Rebrina *et al.*, 2025; regions according to EEA, 2025). Nevertheless, the presence of a fifth peatland on the Velebit Mountain — Sunđer, has remained a mystery for almost a century (Alegro & Šegota, 2009).

Sunđer transitional mire was described about a century ago by Pevalek (1925). According to his description, the site is located on Velebit Mountain at an altitude of 1,196 metres above sea level. It is found about 8 kilometres south of Štirovača, between the peaks of Šatorina (1,624 m), Laktin Vrh (1,504 m) and Pašinac (1,408 m). The transitional mire was described as a clearing about 200–300 metres long and 30 metres wide, mostly covered with peat moss (*Sphagnum subsecundum* Nees, *S. recurvum* nom. dub., and *S. capillifolium* (Ehrh.) Hedw.) and scattered spruce and fir trees (Pevalek, 1925). Next to *Sphagnum* sp. mosses, characteristic indicator plants (e.g. *Rhynchospora alba* (L.) Vahl, *Potentilla erecta* (L.) Raeusch., and *Parnassia palustris* L.) were recorded in the mire. It should be emphasised that Pevalek (1925) also referred to another closely related toponym, known as Sunđerac, an area with similar ecological characteristics, located on the route from Pazarište to Štirovača. However, he states that he did not visit the latter locality personally.

After a thorough review of old literature (Pevalek, 1925; Pichler, 1928; Horvat, 1932, 1962; Pavletić, 1955), an examination of topographic maps, and a comprehensive field study in 2009, it was confirmed that only a single mire exists in the area — Sunđerac (Alegro & Šegota, 2009). Upon visiting the Sunđer site as marked on the topographic maps, it became evident that the site did not correspond to a mire as described by Pevalek (1925). It was a large, deep sinkhole, with slopes covered by grassland of Bosnian fescue (*Festuca bosniaca* Kumm. & Sendtn.) and, to a lesser extent, with spruce (*Picea abies* (L.) H. Karst.) stands. At the bottom of the sinkhole, there was a small patch of grassland belonging to a community of *Deschampsia caespitosa* (L.) P. Beauv. which thrives in areas receiving snowmelt. There was no evidence of permanently wet habitats in the sinkhole, due to the porous karst substrate, which makes the formation of mires impossible (Alegro & Šegota, 2009). Thus, Pevalek (1925) clearly visited Sunđerac and misnamed it Sunđer, and later tried to pinpoint it on a map, referring to the peaks of Šatorina, Laktin Vrh, and Pašinac. This conclusion is further supported by the observation that none of the biologists or hikers familiar with the mires of the Velebit have ever visited both sites; all have visited a single site and have only heard of the other. From further discussions about the access road and the location, it appears that all explorers actually visited only the Sunđerac mire.

However, just as the case seemed resolved, in 2023, employees of the Velebit Nature Park directed the authors of this paper to an area near the Sunđer sinkhole known as Solila, featuring a permanent pond. As the area is generally characterised by limited water resources (Pevalek, 1925), it became clear that the 'dinosaur' could, in fact, still be 'alive'. The presence of permanent standing water and the proximity of the area to the Sunđer toponym, presented a new opportunity to identify mire indicator taxa that may still be undetected in the region. To address the existing ambiguity, we selected plant and insect taxa (ground beetles) known to effectively indicate peatland habitat quality and ecosystem stability (Brigić *et al.*, 2017; Randić *et al.*, 2025), and conducted a field study aiming to verify our original conclusion that the Sunđer mire did not exist.

In particular, our objectives were to: 1) conduct hydrogeological reconnaissance of the Solila pond in the Velebit Mountain by identifying general regional and specific local hydrogeological characteristics of the area; 2) assess the composition and diversity of two indicator groups — plants (bryophytes and vascular plants) and ground beetles — within and around the pond; 3) evaluate the influence of the pond on plant species composition (using Ellenberg-type indicator values) and ground beetle assemblages (by analysing selected life history traits). For selected indicator groups, we aimed to evaluate the occurrence of peatland-associated species (*for details see* Brigić *et al.*, 2017; Rebrina *et al.*, 2025), as their occurrence could inform future conservation strategies and habitat management in the area.

MATERIAL AND METHODS

Study area

This study was conducted near the permanent pond Solila, southeast of the Klepina Duliba, Štirovača, within Velebit Nature Park (WGS coordinates 44° 38′ 13″ N, 15° 05′ 12″ E). The pond, located at an elevation of 1,170 meters above sea level, is relatively small, approximately 30 m^2 in area and designated as a spring on topographic maps (Bioportal, 2025). It is surrounded by an old spruce forest (L. *aserpitio krapfii-Piceetum* Vukelić, Alegro et Šegota 2010), which partially shades the water surface (Fig. 1ab). The pond margin is subject to trampling by wild animals and feral horses utilizing the pond as a water source. While this disturbance is mostly beneficial, as it prevents the pond from becoming overgrown, some nitrogen input is nevertheless plausible.

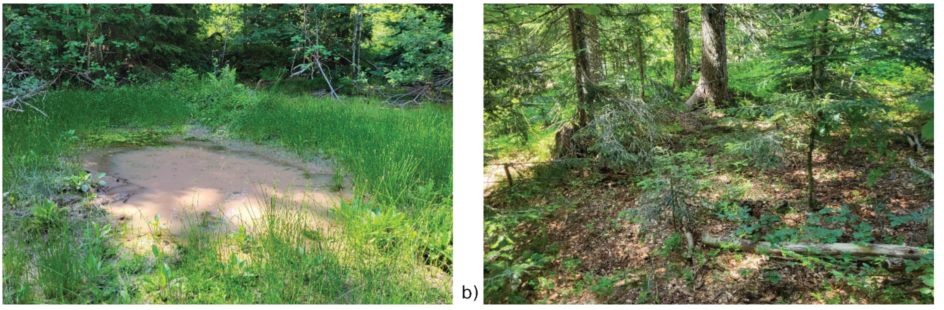
a) b)

Fig. 1. Investigated habitat types: a) permanent pond Solila (Velebit Mountain, Croatia); b) spruce forest surrounding the pond.

Hydrogeological reconnaissance and mapping

A hydrogeological evaluation of the geological structure and features of the wider area surrounding the study site was conducted. The surroundings of the permanent pond Solila were then surveyed and mapped in detail to identify hydrogeological features that facilitate surface water retention and contribute to the pond's formation. Surface rock types, their hydrogeological properties, as well as their contacts and spatial distribution, were characterized within the area potentially influencing the pond. Hydrogeological characterization was conducted according to established methods for hydrogeological mapping (UNESCO, 1970; Chamine *et al.*, 2015).

Microclimatic and edaphic conditions

During each sampling visit, the following environmental variables were measured in the vicinity of each pitfall trap: air temperature (°C) and air relative humidity (%) using a digital thermo-hygrometer (TROTEC T200); soil temperature (°C) at 7 cm depth using a digital probe thermometer (TFA-Dostmann) and soil moisture (%), using a probe hygrometer (FieldScout TDR100). Four replicate measurements were taken for each site in August and September 2023 and then averaged to obtain a site-level value. Vegetation height (mean, m) near each pitfall trap was used as a proxy for vegetation structure and/or productivity. To compare the differences among environmental variables and vegetation among the habitats, the Mann–Whitney U test was used. The tests were run in the Statistica 14.0.0. software package (TIBCO Software Inc., 2020).

Flora sampling and analyses

For flora sampling, performed in late July and late October, we used a Braun-Blanquet scale (Braun-Blanquet, 1964) to estimate the coverage of macrophytes and helophytes (1 = < 5%, 2 = 5–25%, 3 = 25–50%; 4 = 50–75%; 5 = over 75%). Macrophytes and helophytes were identified in the field, while bryophytes were sampled, dried and identified in the laboratory according to Paton (1999), Frahm & Frey (2004), Smith (2004), Frey *et al.* (2006), Hallingbäck *et al.* (2008), Atherton *et al.* (2010), Lüth (2019) and Erzberger (2021). The nomenclature of vascular plants follows Euro+ Med PlantBase (Euro+med PlantBase, 2006-onwards), while the nomenclature of the bryophytes follows Hodgetts *et al.* (2020). The bryophyte material is stored at the Herbarium Croaticum (ZA), the Department of Biology, Faculty of Science, Zagreb and all records have been added to the Flora Croatica Database (Alegro & Šegota, 2025).

Ellenberg-type indicator values (EIVs), a set of ecological indicator values assigned to plant species based on their environmental preferences, were applied to assess habitat conditions. Namely, we used EIVs for key environmental factors (light, moisture, nutrients, temperature and pH reaction) for vascular plants (Tichý *et al.*, 2023) and bryophytes (Hill *et al.*, 2007; Van Zuijlen *et al.*, 2023). All EIVs range from 1 to 9, with the exception of moisture for vascular plants, which ranges from 1 to 12. EIVs were weighted according to the species' abundances. We assigned chorotypes to the vascular plants following Lauber *et al.* (2024), and to the bryophytes following Hill & Preston (1998), Hill *et al.* (2007) and Van Zuijlen *et al.* (2023). The species' vegetation affiliations were taken from Chytrý *et al.* (2022) for vascular plants and Dierssen (2001) for bryophytes.

Ground beetle sampling and analyses

We sampled ground beetles using pitfall traps (polyethylene cups, V = 300 mL) in two habitat types — the pond margin and the forest edge. Due to the small size of the pond (30 m^2), two sampling sites were selected along its margin as far apart as possible, and in parallel to these, two corresponding sites were selected at the forest edge. Within each site, four pitfall traps were placed five meters apart in a linear transect (2 habitat types × 2 sites × 4 pitfall traps = 16 traps in total). The traps were partially filled with a mixture of antifreeze and water in a 3:2 ratio, with a drop of neutrally smelling detergent to reduce the liquid surface tension. A dark bitumen roof was placed above the traps to protect them from litter and rain (Woodcock, 2005). The pitfall traps were set in July and samples were collected once a month in August and September 2023. All samples were preserved in 75% ethanol.

Ground beetles were identified to species level using a Zeiss Stemi 508 stereomicroscope, following standard taxonomic procedures according to Mlynář (1977), Trautner & Geigenmüller (1987), Turin *et al.* (2003) and Müller-Motzfeld (2006), with nomenclature following Löbl & Löbl (2017). *Pterostichus nigrita* was identified based on morphological characteristics of female and male genitalia (c.f. in Brigić *et al.*, 2014). Specimens are deposited at the Department of Biology, Faculty of Science, Zagreb.

Activity density data from the two sampling visits were pooled by habitat type. Dominance was expressed as the proportion of each ground beetle species within the assemblage. The categories were used according to Tietze (1973): dominant (>5%), subdominant (1–4.99%), recendent (0.5–0.99%), and subrecendent species (0.01–0.49%).

In order to detect peatland-associated species, ground beetles were classified into four categories: tyrphobiontic, tyrphophilous, tyrphoneutral and tyrphoxenous (Peus, 1928; Roubal, 1934; for details see Brigić *et al.*, 2017). Tyrphophilous species constitute essential indicator taxa for peat bogs of the Western Balkans, as their presence and composition reliably reflect the ecological integrity and conservation status of these unique and vulnerable habitats (Brigić *et al.*, 2017).

Rank-abundance curves, derived from relative activity density of each species within the assemblage, were generated separately for each habitat type to characterize community structure and species dominance patterns. Functional trait values were assigned to ground beetle species according to relevant literature (Lindroth, 1992; Wachmann *et al.*, 1995; Hůrka, 1996; Turin *et al.*, 2003; Homburg *et al.*, 2014) and expert knowledge. Each species was assigned to one of the categories for the following functional traits: habitat preference — open habitat species, generalist or forest specialist; flight ability — brachypterous, dimorphic or macropterous; and moisture preference — hygrophilous, mesophilous, or xerophilous. Hierarchical cluster analysis based on the Bray–Curtis similarity matrix (group average linking) was used to assess similarities in the composition of ground beetle assemblages between the pond margin and forest edge. Prior to the analysis, singletons were removed from the dataset, and activity density data were presence/absence transformed. The analyses were conducted in the Primer 6.0 software package (Clarke & Gorley, 2006).

RESULTS

Hydrogeological properties

In the wider area around the permanent pond Solila, Triassic and Jurassic carbonate rocks (limestones and dolomites) dominate (Sokač *et al.*, 1974; Velić *et al.*, 1974). These rocks, especially limestones, are prone to karstification, making the terrain permeable and allowing rainwater to quickly infiltrate underground, preventing surface water accumulation. However, within the Triassic sequence, impermeable Upper Triassic clastic deposits occur. These terrestrial sediments rest on karstified bedrock and transition into Upper Triassic dolomites and Jurassic carbonates. Water flow on clastic deposits is mainly surface runoff, with minor subsurface flow through the weathered zone.

The bedrock of carbonate and clastic rocks is partly covered by unconsolidated Quaternary sediments of various types: deluvial (slope), proluvial and alluvial (torrent and stream), and glacial and glacio-fluvial deposits. These sediments are mostly low-permeability due to their typically high clay content and poor sorting, resulting in surface runoff where they are thick and infiltration into karstified bedrock where they thin out. Thicker sediment accumulations predominantly develop in karst depressions downstream of clastic rock exposures due to their erosion, thereby facilitating the formation of permanent ponds.

This hydrogeological situation was confirmed by detailed mapping of the permanent pond Solila area: clastic rocks form elevated terrain west of the pond, while the depression in the Triassic dolomites where the pond is situated is covered by alluvial-proluvial deposits transported by torrential flows from the clastic terrain (Fig. 2). Suffosion depressions appear at several locations within these deposits, causing surface runoff to vanish well before reaching the eastern part of the valley where the pond lies. Consequently, the permanent pond Solila is fed solely by surface drainage from the immediately surrounding slopes, with water retained on the surface due to the barrier effect of the deposits overlying the dolomites. The groundwater level in the dolomite bedrock lies considerably deeper, as indicated by the absence of surface water in the bottoms of much deeper karst depressions nearby.

Soil analyses

Soil moisture was always higher at the pond margin than at the forest edge, with values six times higher in the former habitat (Tab. 1). Moreover, the pond margin was characterised by significantly higher air temperature, and lower air humidity and vegetation height than the forest edge (Tab. 1). Soil temperature did not differ between the studied habitat types (Tab. 1).

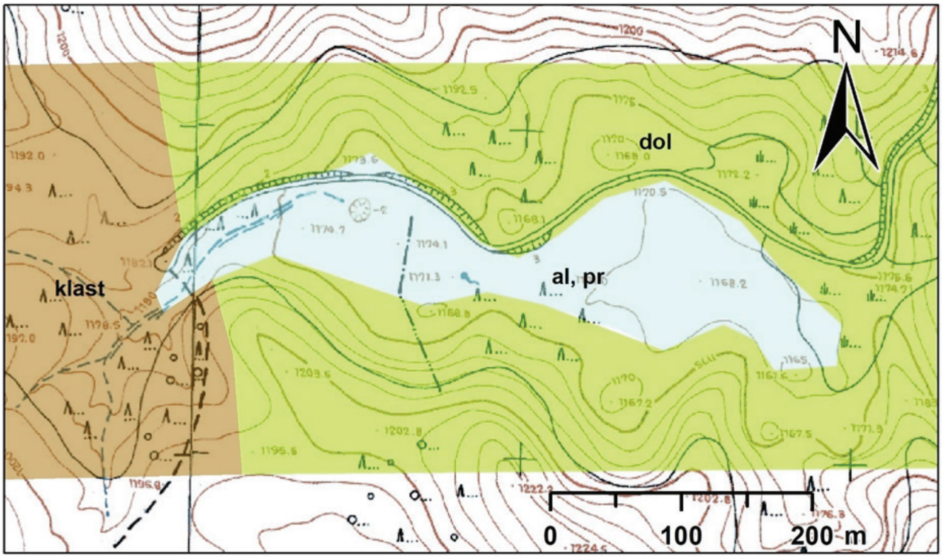

Fig. 2. Hydrogeological map of the area surrounding the permanent pond Solila (dol [green] — dolomites; klast [brown] — volcaniclastic rocks; al, pr [light blue] — unconsolidated alluvial-proluvial deposits). The permanent pond is located in the eastern part of a depression covered by alluvial-proluvial deposits.

Tab. 1. Physical properties of the air and soil measured at the pond margin and the forest edge of the permanent pond Solila (Velebit Mountain, Croatia). Values are means (SD) for two sites at each habitat type. Significance ($p < 0.001$) was determined using the Mann–Whitney U test.

Environmental variables	Pond margin		Forest edge				
	mean ± SD	min	max	mean ± SD	min	max	p
Air temperature (°C)	24.76 ± 2.97	21.30	30.90	20.36 ± 1.18	17.40	23.30	***
Air humidity (%)	63.57 ± 19.08	40.40	99.90	68.86 ± 13.55	51.00	94.40	*
Soil temperature (°C)	14.91 ± 2.70	10.50	21.00	12.95 ± 1.28	10.80	15.10	ns
Soil moisture (%)	33.80 ± 9.51	9.60	53.00	5.76 ± 3.54	1.30	16.20	***
Vegetation height (m)	0.60 ± 1.42	0.05	7.00	17.25 ± 7.46	1.00	30.00	***

Flora

The pond surface was covered with two hydrophytic floating plants, *Lemna minor* and *Callitriche* sp. Along the muddy edges of the pond, helophytic species were present, including *Alisma plantago-aquatica*, *Eleocharis palustris*, *Juncus effusus*, *Carex leporina* and *C. echinata*. Bryophyte flora was twice as rich as vascular flora, comprising 15 species, including 14 mosses and one liverwort (Tab. 2).

EIVs for recorded vascular plant species for light and moisture were high (mean ± SE, L = 7.5 ± 0.1; M = 9.2 ± 0.3), while for temperature, pH reaction and nutrients they were intermediate (T = 5.3 ± 0.3, R = 4.9 ± 0.3, N = 4.3 ± 0.5; Fig. 3a). A similar pattern with high light and moisture EIVs, (L = 6.1 ± 0.5; M = 6.1 ± 0.3) was observed for bryophyte species, however, values for temperature, pH reaction and nutrients (T = 2.9 ± 0.1, R = 3.9 ± 0.4, N = 4.2 ± 0.3; Fig. 3b) were lower than that for vascular plants.

The most prevalent chorotype of vascular plants was cosmopolitan (50%) (Fig. 4a), while for bryophytes it was boreo-temperate (66.7%) (Fig. 4b).

Tab. 2. Vascular plants and bryophytes recorded at the permanent pond Solila (Velebit Mountain, Croatia). Abundances: 1 = < 5%, 2 = 5–25%, 3 = 25–50%; 4 = 50–75%; 5 = over 75%.

Species	Abundance
Vascular plants	
Callitriche sp.	4
Lemna minor L.	3
*Alisma plantago-aquatic*a L.	3
Eleocharis palustris (L.) R. Br.	4
Juncus effusus L.	2
Carex leporina L.	2
Carex echinata Murray	3
Bryophytes	
Aulacomnium palustre (Hedw.) Schwägr.	2
Brachythecium glareosum (Bruch ex Spruce) Schimp.	1
Brachythecium rivulare Schimp.	2
Drepanocladus aduncus (Hedw.) Warnst.	2
Herzogiella seligeri (Brid.) Z. Iwats.	2
Hylocomiadelphus triquetrus (Hedw.) Ochyra & Stebel	2
Leptodictyum riparium (Hedw.) Warnst.	2
Plagiothecium laetum Schimp.	1
Polytrichum commune Hedw.	2
Polytrichum formosum Hedw.	2
Rhizomnium punctatum (Hedw.) T. J. Kop.	1
Rhytidiadelphus loreus (Hedw.) Warnst.	2
Sanionia uncinata (Hedw.) Loeske	2
Sarmentypnum exannulatum (Schimp.) Hedenäs	2
Scapania irrigua (Nees) Nees	1

Ground beetle assemblages

Altogether 522 ground beetle specimens belonging to 30 species were collected (Tab. 3); 14 species with 85 specimens were recorded at the pond margin and 20 species with 437 specimens at the forest edge (Tab. 3). Both habitat types harboured a high number of exclusive species, with 10 such species recorded in the pond margin and 16 along the forest edge. Accordingly, species overlap between the two habitats was minimal and encompassed the following species: *Calathus fuscipes*, *Carabus violaceus azurescens*, *Nebria dahlii velebitica*, and *Pterostichus burmeisteri* (Tab. 3). With the exception of *C. fuscipes*, these taxa prevailed in terms of abundance at the forest edge, with only a few individuals collected at the pond margin. Tyrphophilous species were absent from both habitat types. All collected species were classified as tyrphoneutral.

Rank-abundance curves show that four species dominated the total catch: *Nebria dahlii velebitica*, *Carabus violaceus azurescens*, *Cychrus attenuatus* and *Agonum viduum*, accounting for 76.04% of the catch. At the pond margin, four species prevailed in terms

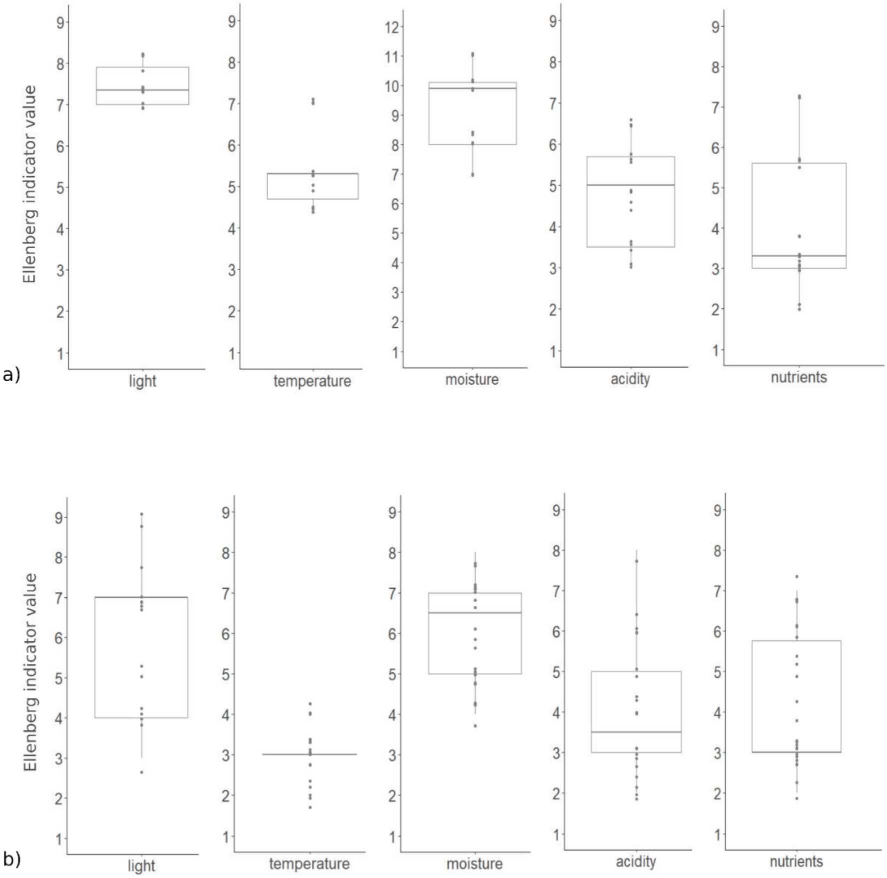

Fig. 3. Box-plot graphs of Ellenberg's indicator values (EIVs) for light (L), temperature (T), moisture (M), reaction (R), and nutrients (N) for: a) vascular plants; b) bryophytes at the permanent pond Solila (Velebit Mountain, Croatia).

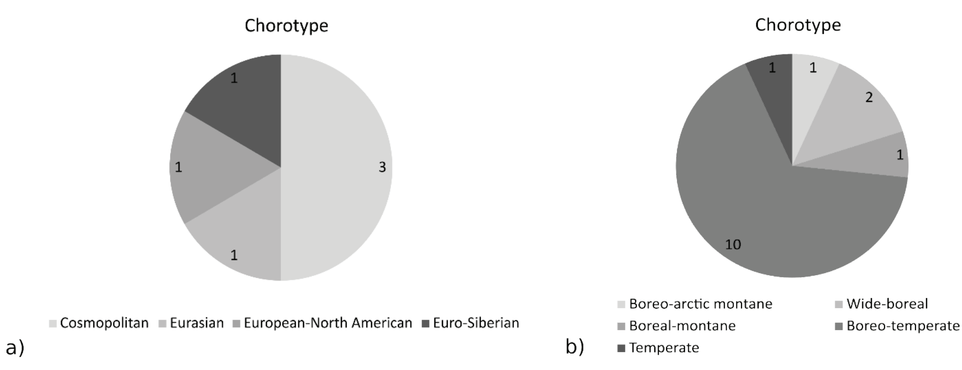

Fig. 4. Frequency of chorotypes for: a) vascular flora; b) bryophytes at the permanent pond Solila (Velebit Mountain, Croatia).

of abundance: *A. viduum, Bembidion lampros, N. dahlii velebitica,* and *Pterostichus nigrita,* while five species: *N. dahlii velebitica, C. violaceus azurescens, C. attenuatus, Calathus micropterus*, and *P. burmeisteri*, prevailed at the forest edge (Fig. 5a, Tab. 3). All other species recorded at the pond margin were subdominant. At the forest edge, three species were subdominant, followed by four recendent species and eight subrecendent (sporadic) species (Tab. 3).

Tab. 3. Ground beetle species and their activity density recorded at the pond margin and the forest edge, of the permanent pond Solila (Velebit Mountain, Croatia). Dominant ground beetle species are represented in bold. Legend: N — activity density, % — percentage.

Species	Pond margin		Forest edge		Total	
	N	%	N	%	N	%
Abax ovalis (Duftschmid, 1812)			5	1.14	5	0.96
Acupalpus flavicollis (Sturm, 1825)	1	1.18			1	0.19
***Agonum viduum* (Panzer, 1796)**	**41**	**48.24**			**41**	**7.85**
Amara ovata (Fabricius, 1792)	1	1.18			1	0.19
Bembidion guttula (Fabricius, 1792)	3	3.53			3	0.57
***Bembidion lampros* (Herbst, 1784)**	**13**	**15.29**			13	2.49
Calathus fuscipes (Goeze, 1777)	2	2.35	1	0.23	3	0.57
Calathus melanocephalus (Linnaeus, 1758)			1	0.23	1	0.19
***Calathus micropterus* (Duftschmid, 1812)**			**26**	**5.95**	26	4.98
Carabus convexus Fabricius, 1775			3	0.69	3	0.57
Carabus croaticus Dejean, 1826			4	0.92	4	0.77
Carabus hortensis Linnaeus, 1758			2	0.46	2	0.38
Carabus parreyssi Palliardi, 1825			1	0.23	1	0.19
***Carabus violaceus azurescens* Dejean, 1826**	3	3.53	**113**	**25.86**	**116**	**22.22**
***Cychrus attenuatus* (Fabricius, 1792)**			**59**	**13.50**	**59**	**11.30**
Harpalus rufipes (De Geer, 1774)	3	3.53			3	0.57
Leistus piceus Frölich, 1799			2	0.46	2	0.38
Leistus spinibarbis Chaudoir, 1843			1	0.23	1	0.19
Licinus hoffmannseggii (Panzer, 1802)			1	0.23	1	0.19
Loricera pilicornis (Fabricius, 1775)	4	4.70			4	0.77
Microlestes minutulus (Goeze, 1777)	1	1.18			1	0.19
***Nebria dahlii velebitica* Heyden, 1884**	**5**	**5.88**	**176**	**40.27**	**181**	**34.67**
Notiophilus biguttatus (Fabricius, 1779)			5	1.14	5	0.96
Paratachys bistriatus (Duftschmid, 1812)			1	0.23	1	0.19
Platynus scrobiculatus (Fabricius, 1801)	1	1.18			1	0.19
Pterostichus brevis (Duftschmid, 1812)			4	0.91	4	0.77
***Pterostichus burmeisteri* Heer, 1838**	2	2.35	**24**	**5.49**	26	4.98
***Pterostichus nigrita* (Paykull, 1790)**	**5**	**5.88**			5	0.96
Pterostichus oblongopunctatus (Fabricius, 1787)			3	0.69	3	0.57
Synuchus vivalis (Illiger, 1798)			5	1.14	5	0.96
Species richness (S)	**14**		**20**		**30**	
Abundance (N)	**85**		**437**		**522**	

The results of the hierarchical cluster analysis revealed a generally low similarity in ground beetle assemblages between the studied habitat types, at less than 18% (Fig. 5b), i.e. each habitat harbours a unique ground beetle assemblage. At 63% similarity, forest edge samples grouped closely together, suggesting a common assemblage structure characteristic of that habitat type, while pond margin assemblages had lower similarity (around 40%; Fig. 5b).

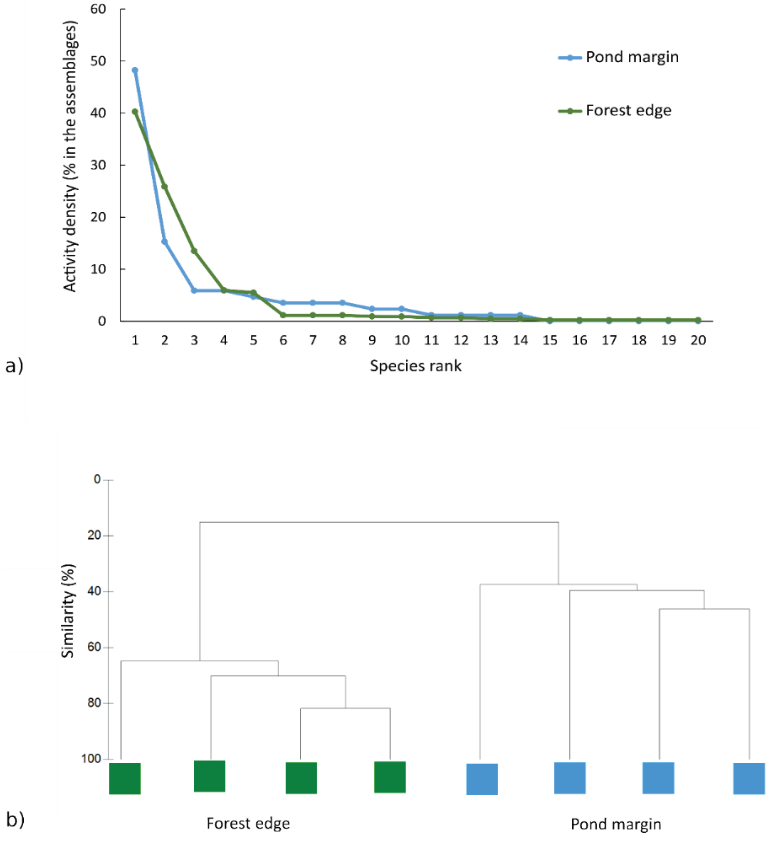

Fig. 5. Ground beetle assemblages: a) rank abundance curves for pond margin (blue) and forest edge (green); b) hierarchical cluster analysis based on the Bray–Curtis similarity index (*group average linking*) and species' presence/absence at the permanent pond Solila (Velebit Mountain, Croatia).

In terms of functional traits, activity densities of hygrophilous (pond margin: 73%; forest edge: 64%) and mesophilous (26%; 35.5%) ground beetles were high in both habitat types (Fig. 6ab). However, an asymmetrical wing development pattern was observed between the habitats, with macropterous individuals predominating at the pond margin (79%; 2%), and brachypterous forms at the forest edge (13%; 96%; Fig. 6cd).

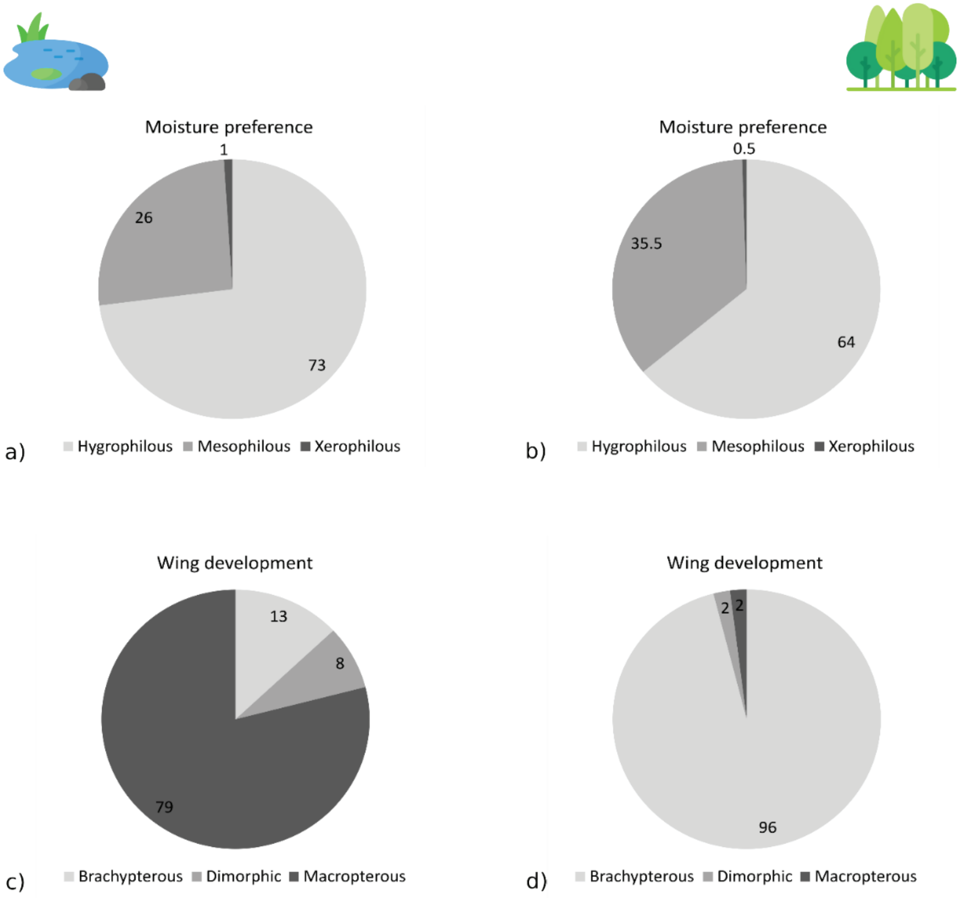

Fig. 6. Frequency of ground beetle activity density per functional trait group in two habitat types: pond margin and forest edge at the permanent pond Solila (Velebit Mountain, Croatia): a), b) moisture preferences; and c), d) wing development.

DISCUSSION

Is the 'dinosaur' still 'alive'?

Our study clearly shows that the permanent pond Solila cannot be regarded as the 'mysterious' peatland area described by Pevalek (1925) as Sunđer. Species typical of peatland ecosystems were not found in either of the indicator groups: bryophyte and vascular plant flora, and ground beetles. The only vascular plant species associated with mire vegetation was *Carex echinata*, which is a constant species in blanket bogs and a diagnostic species of both poor fens and very nutrient-rich moss-sedge fens (Chytrý *et al.*, 2022). However, this species is also common in acidic grasslands and spruce mire forests (Chytrý *et al.*, 2022). With respect to bryophyte taxa composition, *Sphagnum* mosses — typical peatland plants — were not recorded. While the bryophyte taxa recorded are primarily acidophilous, they are not solely associated with peatland vegetation. Species such as *Scapania irrigua*, *Sarmentypnum exannulatum*, and *Aulacomnium palustre*, though observed in peatland habitats (Chytrý *et al*., 2022), predominantly thrive along the moist, seasonally exposed banks of ponds, lakes, streams, gravel pits, and quarries (Dierssen, 2001). In contrast, *Polytrichum commune*, *Plagiothecium laetum*, *Rhytidiadelphus loreus*, *Hylocomiadelphus triquetrus*, and *Polytrichum formosum* are more frequently found in wet, acidic coniferous woodlands (Dierssen, 2001). With respect to ground beetle assemblages, no tyrphophilous species known as indicators of the Western Balkans peatlands were found in either of the habitat types — the pond margin or the forest edge surrounding the Solila pond (Brigić *et al*., 2017). All this leads to the conclusion that the 'dinosaur' is not 'alive' after all.

Availability of permanent surface water enhances local diversity in a karst environment

A favourable geological setting enables the formation of a permanent water pond, despite being surrounded predominantly by karst terrain typically characterized by the scarcity of surface water. The permanent pond hosts notable plant diversity, comprising two nationally rare bryophyte species: *Scapania irrigua*, which represents the second known population in Croatia, and *Sarmentypnum exannulatum*, identified as the second recently known population (Alegro *et al*., 2014). Additionally, it is home to *Carex echinata*, a relatively uncommon species in the national context (Nikolić *et al.*, 2025).

In terms of the species' geographic origins (i.e., chorotypes), the bryophyte community reflects the more boreal aspect of the pond's flora, with two-thirds of the species belonging to boreo-temperate types, alongside one boreo-arctic montane species (*Sanionia uncinata*). Additionally, there are two wide-boreal species (*Aulacomnium palustre* and *Polytrichum commune*) and one boreal-montane species (*Plagiothecium laetum*). Vascular flora surrounding and within the pond primarily consists of cosmopolitan generalist species, including *Calitriche* sp., *Lemna minor*, *Alisma plantago-aquatica*, and *Eleocharis palustris*, displaying no connection to boreal or mire-associated habitats.

Within the relatively small landscape area of 400 m^2 encompassing the forest edge and the pond margin, we recorded a notably high diversity of ground beetle species (30 species in total). Ground beetle assemblages exhibited clear compositional differences between the two habitat types. Remarkably, approximately one-third of the species were found exclusively at the pond margin, highlighting its distinct ecological role within the karstic landscape, where surface water is scarce. The pond margin was inhabited by riparian species, such as *Acupalpus flavicollis*, *Agonum viduum* and *Pterostichus nigrita*, that are common on banks of standing and/or flowing water bodies (Lindroth, 1992; Anderson *et al*., 2000). These species have also been recorded in Croatian peatlands; however, they are not mire-associated, but rather belong to the group of tyrphoneutral species (Brigić *et al*., 2014, 2017). Other riparian species, such as *Bembidion lampros* and *Loricera pilicornis*, were recorded in riparian habitats of Croatia (Stančić *et al*., 2010; Brigić *et al*., 2024). The pond margin clearly contributes to local diversity, as it supports riparian species that would otherwise be absent from the area.

Ground beetle assemblages of the spruce forest edge were mainly composed of forest specialists, e.g. *Carabus croaticus*, *Platynus scrobiculatus* and *Nebria dahlii velebitica*, and generalists, such as *Abax ovalis*, *Cychrus attenuatus* and *Pterostichus burmeisteri*

(Brigić *et al.*, 2014). Forest specialists prefer lower temperatures, moist soils, and shaded habitats typically found in the forest interior and embedded edges (Brigić, 2012; Brigić *et al.*, 2014). In contrast, forest generalists are not restricted to forested habitats and maintain stable populations even in montane meadows (Brigić *et al.*, 2014). Many forest species maintain large populations in Dinaric beech-fir forests (Vujčić-Karlo, 1999; Brigić, 2012).

Ecological conditions reflected in life-history patterns

The evaluation of habitat conditions through Ellenberg-type indicator values revealed that the indicator values for vascular plants have a lower potential for explaining the floristic composition of the pond than those for bryophytes. Although both groups similarly characterize the vegetation in terms of light and moisture, reflecting conditions typical of a pond site with insulated standing water, bryophytes suggest a cooler, more acidic, and nutrient-poor environment than vascular plants.

Superficially, the moisture preferences of ground beetles do not appear to differ between the habitat types studied. In both habitats — pond margin and forest edge — hygrophilous ground beetle species dominated, which is consistent with previous studies in the Lika and Gorski Kotar regions (Brigić, 2012; Brigić *et al.*, 2014). These regions are characterized by shaded and humid forest environments that typically support such species (Vujčić-Karlo, 1999; Brigić *et al.*, 2014). However, the high frequency of hygrophilous species is inconsistent with the results of soil moisture measurements at the forest edge, where we recorded a rather low soil moisture. This could be due to soil structure, mainly composed of spruce and fir needles, resembling a sponge. Such soil structure has a lot of air trapped among soil particles, which could influence the measurement results (Vorobevskii *et al.*, 2024).

Although the moisture preferences of ground beetles in the two habitat types appeared to be similar, clear differences became evident when wing development — an important life-history trait — was considered. In our study, an asymmetric response in wing morphology was observed, particularly in the spatial distribution of brachypterous and macropterous species. The pond margin was predominantly inhabited by macropterous species, which are capable of flight and can respond quickly to fluctuations in water level (Bonn, 2000). In contrast, the forest edge was mainly occupied by brachypterous species that generally favour large, continuous, and stable forest habitats (Brandmayr, 1981).

In conclusion, the general appearance of the Solila permanent pond, the vegetation physiognomy, and the associated plant and ground beetle assemblages do not indicate that the studied site has peatland characteristics. While several plant species display acidophilic tendencies, they are not peatland specialists and are commonly found in other acidic environments, such as coniferous forests, acidic grasslands or seasonally exposed pond banks. Situated at the edge of a spruce forest in a region with substantial rainfall, the acidic substrate of the pond is to be anticipated. Species composition and life history traits within both indicator groups clearly reflect the ecological characteristics of riparian and forest habitats. Thus, this ecological reassessment provided key insights that contributed to resolving the long-standing 'mystery' of the alleged Sunđer peat bog.

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