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PLANT AND SOIL INVERTEBRATE DIVERSITY OF A RARE ALKALINE FEN IN CROATIA

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In Croatia, alkaline fens are rare and highly endangered ecosystems that rely on precipitation and mineral-rich ground water. They are characterized by extreme environmental conditions such as high soil moisture, low nutrients and oxygen availability. In this study we present plant (vascular plants and bryophytes) and soil invertebrate diversity (isopods, carabid beetles and ants), together with soil properties of the alkaline fen Dretulja River Valley, near the settlement Plaški, Croatia. Our objective was to discover whether plant and animal communities are specialized to this extreme habitat, the answer to which is of great value for biodiversity conservation. The unique fen conditions supported high plant diversity, including extremely rare and threatened plant species (e.g. the carnivores *Pinguicula vulgaris*, *Drosera rotundifolia* and *Utricularia minor*) and relic vegetation of dominantly Holarctic (e.g. *Carex flava*, *C. lepidocarpa*, *C. rostrata*, *Parnassia palustris*) and boreal elements (e.g. *Scorpidium revolvens* and *S. scorpioides*). Analysis of the Ellenberg-type indicator values of plant species demonstrates that the fen habitat is well-insolated, water-saturated, moderately alkaline and nutrient-poor. In contrast to plants, soil invertebrate diversity, particularly isopods and carabid beetles, was reduced due to the harsh environmental conditions. Only ants demonstrated any great capacity to tolerate extreme environmental stresses, although they were also low in abundance. Soil invertebrate communities were predominantly composed of hygrophilous to mesophilous species, typically associated with wetlands, meadows and open bogs. Notably, we recorded *Asellus aquaticus*, a freshwater isopod species, whose presence in the samples was likely due to being washed into traps during elevated water levels. Additionally, we recorded a tyrphophilous ant species *Myrmica scabrinodis* in the fen. Thus, the composition and structure of plant and invertebrate communities indicates that the fen's hydrological conditions remained well-preserved and to preserve great fen biodiversity it is essential to maintain these hydrological conditions.

Keywords: peatlands, tyrphophilous species, Isopoda, Carabidae, Formicidae

Randić, A., Šegota, V., Bujan, J., Bedek, J., Alegro, A. & Brigić, A.: Raznolikost biljaka i beskralježnjaka tla na rijetkom bazofilnom cretu u Hrvatskoj. Nat. Croat., Vol. 34, No. 1, 129-148, 2025, Zagreb.

Bazofilni cretovi su rijetki i vrlo ugroženi ekosustavi u Hrvatskoj koji ovise o oborinama i mineraliziranoj podzemnoj vodi. Karakteriziraju ih ekstremni okolišni uvjeti, poput visoke vlažnosti tla i niske dostupnosti hranjivih tvari i kisika. U ovom istraživanju predstavljamo raznolikost biljaka

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(vaskularnih biljaka i mahovina) i beskralješnjaka tla (jednakonožnih račića, trčaka i mrava), zajedno sa svojstvima tla bazofilnog creta u dolini rijeke Dretulje blizu Plaškog (Hrvatska). Zanimalo nas je postoji li specijalizacija biljnih i životinjskih zajednica u ovom ekstremnom staništu koje ima veliku vrijednost za očuvanje bioraznolikosti. Jedinstveni uvjeti creta podržavaju visoku biljnu raznolikost, uključujući izuzetno rijetke i ugrožene biljne vrste (npr. mesožderke *Pinguicula vulgaris*, *Drosera rotundifolia* i *Utricularia minor*) i reliktne biljne zajednice dominantno holarktičkih (npr. *Carex flava, C. lepidocarpa, C. rostrata, Parnassia palustris*) i borealnih elemenata (npr. *Scorpidium revolvens* i *S. scorpioides*). Analiza Ellenbergovih indikatorskih vrijednosti biljnih vrsta pokazuje dobro osunčano, vodom zasićeno, umjereno bazofilno i hranjivim tvarima siromašno stanište. Suprotno biljkama, raznolikost beskraljšnjaka tla, posebice jednakonožnih račića i trčaka, bila je smanjena uslijed nepovoljnih okolišnih uvjeta. Samo su mravi pokazali veću sposobnost podnošenja ekstremnih okolišnih prilika, iako je i njihova brojnost bila mala. Zajednice beskralješnjaka tla su se uglavnom sastojale od higrofilnih do mezofilnih vrsta, obično povezanih s vlažnim područjima, livadama i nezasjenjenim acidofilnim cretovima. Naime, zabilježili smo vrstu slatkovodnog jednakonožnog račića *Asellus aquaticus*, čije je prisustvo u uzorcima vjerojatno bilo uzrokovano time što su ih povišene vode isprale u lovne posude. Na cretu smo također zabilježili i tirfofilnu vrstu mrava *Myrmica scabrinodis*. Dakle, sastav i struktura biljnih zajednica i zajednica beskralješnjaka tla ukazuju na to da su hidrološki uvjeti creta ostali dobro očuvani. Kako bi se očuvala velika biološka raznolikost creta, neophodno je održavati ove hidrološke uvjete.

Ključne riječi: cretovi, tirfofilne vrste, Isopoda, Carabidae, Formicidae

INTRODUCTION

Peatlands are a specific type of wetland habitats that are typically classified into two main types based on their hydrology, nutrient availability, and pH: fens and bogs (Rydin & Jeglum, 2006). Fens are alkaline habitats sustained by precipitation and mineral-rich ground water, while bogs are nutrient-poor, acidic, and primarily fed by precipitation (Rydin & Jeglum, 2006; Spitzer & Danks, 2006; Vitt, 2006). Fens are often intermixed with bogs, which occur in the extensive peatlands of northern North America and Europe, as well as in many smaller seepage areas throughout the temperate zone, and in high mountain valleys (Keddy, 2024). In Croatia, both peatland types were formed during, or immediately after the last glaciation (Horvat, 1950). They were once much more widespread, but today, apart from a few larger ones, most peatlands are disconnected patches smaller than 1 ha, strongly dependent on microclimatic conditions (Alegro & Topić, 2017; Topić & Stančić, 2006). Thus, due to their size, isolation, drainage, abandonment of traditional land management practices, rapid vegetation succession coupled with climate change, they are Croatia's most threatened habitats (Alegro & Topić, 2017; Brigić *et al.*, 2017a; Minayeva *et al.*, 2009; Topić & Stančić, 2006).

Fens, like peat bogs, are highly specialized and extreme habitats characterized by persistently high water levels, low nutrient availability, and limited oxygen supply (Rydin & Jeglum, 2006). These challenging environmental conditions create a unique ecosystem that supports specialized plant and soil invertebrate communities (Desrochers & van Duinen, 2006; Rydin & Jeglum, 2006). Thus, organisms living in fens are adapted to these extreme environmental conditions, e.g. carnivorous plants, such as *Pinguicula* and *Drosera* species, compensate for nutrient-poor conditions of phosphorous and nitrogen by capturing and digesting insects, while invertebrates have small body size, select specific microhabitats and tolerate anoxia (Rosenberg & Danks, 1987). Moreover, their life cycles are either rapid or slow, with dormant stages resistant to adverse conditions (Rydin & Jeglum, 2006).

Species that inhabit peatlands are classified into four categories: (a) tyrphobiontic -

occur exclusively in peat bogs, (b) tyrphophilous - typical of peat bogs, but not strictly confined to them, (c) tyrphoneutral - distributed across different types of habitats, and (d) tyrphoxenous - immigrants that cannot survive in peat bogs (Roubal, 1934; Peus, 1928). Tyrphobiontic species are closely associated with pristine peat bogs in the boreal, subarctic or arctic regions of Northern Europe, Siberia and North America (Spitzer & Danks, 2006). Towards the southern limits of their distribution, these species are progressively replaced by tyrphophilous species (Brigić *et al.*, 2017a; Bujan *et al.*, 2015). To a lesser extent both tyrphobiontic and tyrphophilous species can also be found in fens, but their presence is less pronounced (Bujan *et al.*, 2015; Assandri & Bazzi, 2022).

To assess the quality of these threatened habitats, we used both plant and invertebrate ecological indicators, which reflect key environmental conditions, such as water level and habitat stability. Soil invertebrates, including isopods, carabid beetles and ants, are particularly valuable indicators due to their sensitivity to microhabitat changes and their established role in monitoring ecosystem health in peatlands (Brigić *et al.*, 2019, 2017ab; Batzer *et al.*, 2016; Gerlach *et al.*, 2013). Moreover, the presence and abundance of tyrphobiontic and tyrphophilous species often reflects the quality of habitats in European peatlands (Brigić *et al.*, 2017a; Buchholz *et al.*, 2009; Bezděk *et al.*, 2006). Changes in environmental variables, e.g. vegetation composition and structure, soil moisture and microhabitat availability, drive spatio-temporal shifts in invertebrate communities across peatlands (Brigić *et al.*, 2021, 2019, 2017ab; Batzer *et al.*, 2016). While pristine peatlands support specialist species, degraded peatlands favor hygrophilous species, often with good dispersal abilities, which are prone to reacting to unstable environmental conditions (Šoštarić *et al.*, 2012; Buchholz *et al.*, 2009). Although present, fens in Croatia remain understudied, with limited data on plant and some invertebrate communities. Gaining a deeper understanding of these ecosystems is essential to understand their ecological dynamics and ensure the integrity of natural habitats, helping to prevent further degradation.

Thus, we sampled a large fen within the NATURA 2000 site, the Dretulja River Valley near Plaški. Our objectives were to: (1) assess the plant composition and vegetation diversity of the alkaline fen, while examining how soil properties (e.g. soil temperature, soil moisture, pH) govern the plant community composition; 2) determine the occurrence of key soil invertebrate indicator groups, including isopods, carabid beetles and ants; (3) analyze the community structure and life history traits of focal invertebrates; and (4) provide guidelines for future conservation and management efforts.

MATERIAL AND METHODS

Study area

The alkaline fen Dretulja River Valley, near Plaški (N 45.3515°, E 45.0756°) is located in the south of the Ogulin-Plaški Basin, northeast of the Velika and Mala Kapela mountain range, at 376 m a.s.l. (Fig. 1). This region is characterized by a temperate, humid climate with a hot summer, a mean annual temperature of 8.5 °C, and a mean annual precipitation of 1450 mm (Zaninović *et al.*, 2008). The fen covers an area of 6 ha with the karstic partially subterranean Dretulja River flowing through it. The slopes of the river valley with shallow permeable dolomites above impermeable flysch deposits direct the water from higher hills towards the base of the valley, where the uneven micro-relief creates alternating raised micro-elevations and lowered micro-depressions so that standing water accumulates in the depressions and remains in the fen. The whole area has been protected as NATURA 2000 site, the Dretulja River Valley (site code HR2000609). From a biogeographical perspective, the fen is situated within the continental biogeographical region (according to EEA, 2024).

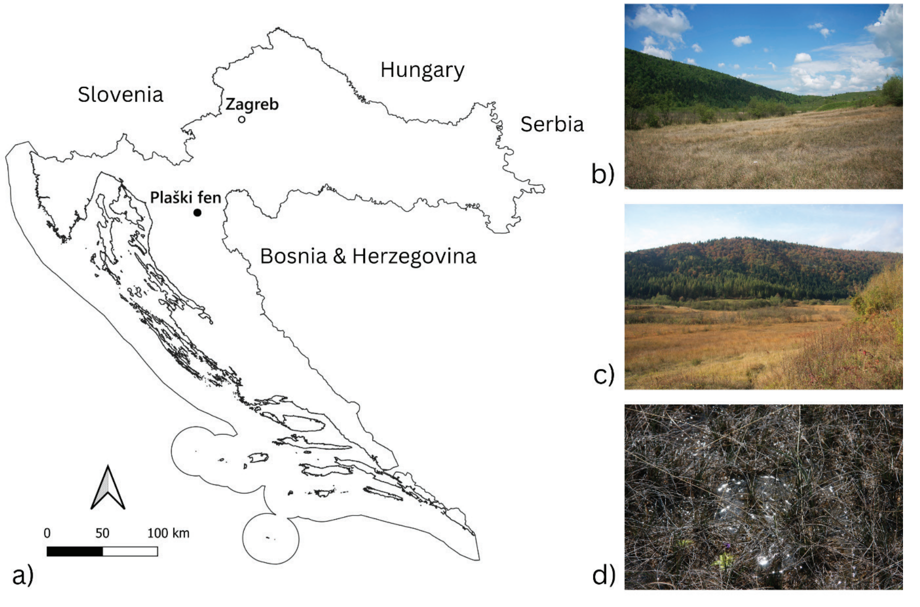

Fig. 1. a) Geographical position of the alkaline fen Dretulja River Valley, near Plaški (Croatia); b) alkaline fen in May 2008; c) alkaline fen in October 2008; d) retention of water on the fen soil surface.

Vegetation and flora sampling and analyses

Fen vegetation was sampled in 2008 using phytosociological relevés following standard Central European methodology (Braun-Blanquet, 1964; Dierschke, 1994) with the abundance ranks: + = up to 5 individuals; 1 = up to 50 individuals; 2m = more than 50 individuals; 2a = coverage between 5 and 15%; 2b = coverage between 15 and 25%; 3 = coverage between 25 and 50%; 4 = coverage between 50 and 75% and 5 = coverage over 75% (Barkman *et al.*, 1964). Additionally, flora of the wider area of the fen was investigated. The nomenclature of vascular plants follows Euro + Med PlantBase (Euro+Med, 2006-onwards), while the nomenclature of the bryophytes follows Hodgetts & Lockhart (2020).

We assigned chorotypes of vascular plants following Lauber *et al.* (2024), and the life-form spectrum of the vascular flora was assigned according to Raunkiaer (1934). As for bryophytes, we used Hill & Preston (1998), Hill *et al.* (2007) and Van Zuijlen *et al.* (2023) for the chorological analysis, Mägdefrau (1982), Hill *et al.* (2007) and Van Zuijlen *et al.* (2023) for the analysis of life-form spectra, while the life strategies we assigned according to During (1992), Dierssen (2001) and Van Zuijlen *et al.* (2023). Life-form spectra are classified as follows: phanerophytes – tall, woody or herbaceous perennials with resting buds more than 25 cm above soil level (e.g. trees and shrubs), chamaephytes – plants with perennating buds or shoot apices borne very close to the ground, or small, woody herbaceous plants having resting buds not more than 25 cm above soil level, hemicryptophytes – plants with resting buds at or near the level of the soil, geophytes – plants with resting buds lying beneath the surface of the ground as rhizomes, bulbs, corms, etc., therophytes – plants whose shoots and roots die after seed production and which complete their whole life cycle within one year. 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 key environmental factors such as EIV for light, moisture, nutrients, temperature and pH reaction for vascular plants (Tichý *et al.*, 2023) and bryophytes (Van Zuijlen *et al.*, 2023; Hill *et al.*, 2007). IUCN Red List categories for vascular plants were assigned according to Nikolić & Topić (2006) and for bryophytes according to Hodgetts *et al.* (2019).

Soil properties

We measured soil temperature at a depth of 7 cm using a P300 Dostmann electronic thermometer, once from May to December near each pitfall trap. Soil moisture and pH values were measured from the collected soil samples (d = 10 cm, h = 2 cm). We determined water content using the gravimetric method (Reynolds, 1970) and measured pH values in a 1: 2.5 mixture of soil: water using a WTW pH 330i meter.

Invertebrate sampling and analyses

We sampled soil invertebrates using pitfall traps (polythene cups, V = 300 mL) at two sites. Each site contained 5 pitfall traps placed 5 m apart in a linear transect. The transects were positioned perpendicularly to the Dretulja River, with one located on a micro-elevation on higher, better-drained ground and the other in the micro-depression. The traps were partially filled with a saturated salt solution with a drop of neutrally smelling detergent to reduce surface tension. A Styrofoam roof was placed above each trap to protect it from rain (Woodcock, 2005). We collected the samples monthly from May to December 2008.

Soil invertebrates were identified as follows: terrestrial isopods according to Schmölzer (1965), aquatic isopods according to Verovnik *et al.* (2009), with nomenclature following Boyko *et al.* (2024); carabid beetles according to Müller-Motzfeld (2006) and Turin *et al.* (2003), with nomenclature following Löbl & Löbl (2017); ants according to Seifert (2007), Czechowski *et al.* (2002), Kutter (1977), Collingwood (1979) and Agosti & Collingwood (1987), with nomenclature following (Bolton, 2024). Specimens are deposited in the Department of Biology, Faculty of Science, Zagreb and Croatian Myrmecological Society, Zagreb.

For each soil invertebrate species dominance and frequency were calculated (c.f. in Brigić, 2012). Soil invertebrates were assigned life history trait categories using morpho-ecological features which potentially affect the occurrence patterns of these groups (e.g. Bračko, 2023; Ribera *et al.*, 2001; Schmalfuss, 1984). Life history traits were extracted from the literature, e.g. for terrestrial isopods according to Lafuente *et al.* (2021) and Ferenţi *et al.* (2013), for carabid beetles according to Turin *et al.* (2003), Hůrka (1996), Lindroth *et al.* (1992), for ants according to Bračko (2023) and Seifert (2018). The following traits were analyzed: for isopods, groups (aquatic *vs.* terrestrial) and habitat preference; for carabid beetles, habitat, moisture preference, and wing development; and for ants, habitat and thermal preferences. IUCN categories for carabid beetles were assigned according to Croatian Red List - threatened carabid beetles (Vujčić-Karlo *et al.*, 2007).

RESULTS

Vegetation and floristic features

In total 43 taxa of vascular flora and 10 taxa of bryophytes were recorded within the investigated habitat (Tab. 1). Among vascular plants the majority of species are hemicryptophytes (58%) and geophytes (37%) (Fig. 2a). Almost two thirds of the bryophytes are turfs (Fig. 2d) and exhibit competitive perennial strategies (Fig. 2e). The most numerous chorotypes of vascular plants were Circum-Holarctic and Eurasian (Fig. 2b) and of bryophytes boreo-temperate (34%), boreo-arctic montane (22%) and wide-temperate (22%) (Fig. 2f).

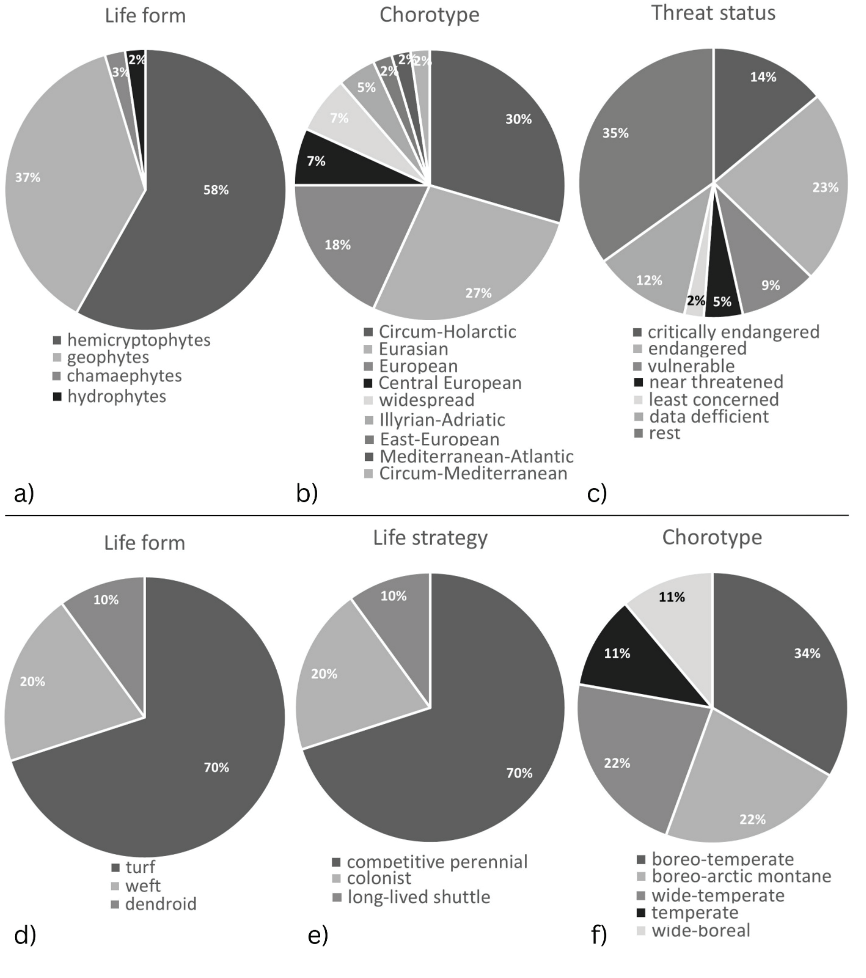

Fig. 2. Frequency of vascular flora: a) life-forms; b) chorotypes; and c) threat categories; bryophytes: d) life-forms; e) life strategies f) chorotypes in the alkaline fen Dretulja River Valley, near Plaški (Croatia).

Tab. 1. Vascular plants and bryophytes recorded in the alkaline fen Dretulja River Valley, near Plaški and IUCN categories of vascular plants according to Nikolić & Topić (2005) (Croatia). Species that do not have a threat category are not included in the Red Book of Vascular Flora of Croatia (Nikolić & Topić, 2005).

Species name	**IUCN category**
Vascular plants	
Allium tuberosum Rottler ex Spreng.	EN
Anacamptis palustris (Jacq.) R. M. Bateman, Pridgeon & M. W. Chase	DD
Angelica palustris (Besser) Hoffm.	DD
Carex davalliana Sm.	EN
Carex demissa Hornem.	
Carex echinata Murray	EN
Carex flava L.	EN
Carex hostiana DC.	EN
Carex lepidocarpa Tausch	EN
Carex pallescens L.	
Carex panicea L.	VU
Carex pulicaris L.	CR
Carex punctata Gaudin	
Carex rostrata Stokes	VU
Carex vesicaria L.	VU
Carex viridula Michx.	EN
Cladium mariscus (L.) Pohl	
Dactylorhiza incarnata (L.) Soó	EN
Drosera rotundifolia L.	CR
Epipactis palustris (L.) Crantz.	
Equisetum palustre L.	
Eriophorum latifolium Hoppe	EN
Euphorbia illirica Lam. (= *Euphorbia villosa* Waldst. et Kit. ex Willd.)	
Gymnadenia conopsea (L.) R. Br.	
Hydrocotyle vulgaris L.	CR
Menyanthes trifoliata L.	EN
Molinia caerulea (L.) Moench	
Neotinea ustulata (L.) R. M. Bateman, Pridgeon & M. W. Chase	VU
Parnassia palustris L.	
Peucedanum coriaceum Rchb. (ssp. *pospichalii* (Thellung) Horvatić)	DD
Phragmites australis (Cav.) Steud.	
Pinguicula vulgaris L.	CR
Potentilla erecta (L.) Räusch.	
Sanguisorba officinalis L.	DD
Schoenus nigricans L.	
Scilla litardierei Breistr.	NT

Species name	IUCN category
Vascular plants	
Scirpoides holoschoenus (L.) Soják	NT
Serratula tinctoria L.	LC
Spiranthes aestivalis (Poir.) Rich.	DD
Succisa pratensis Moench	
Tofieldia calyculata (L.) Wahlenb.	CR
Triglochin palustris L.	CR
Utricularia minor L.	
Bryophytes	
Barbula unguiculata Hedw.	
Calliergonella cuspidata (Hedw.) Loeske	
Campylium stellatum (Hedw.) Lange & C.E.O.Jensen	
Climacium dendroides (Hedw.) F. Weber et D. Mohr	
Cratoneuron filicinum (Hedw.) Spruce	
Fissidens adianthoides Hedw.	
Palustriella falcata (Brid.) Hedenäs	
Philonotis calcarea (Bruch & Schimp.) Schimp.	
Scorpidium revolvens (Sw. ex anon.) Rubers	
Scorpidium scorpioides (Hedw.) Limpr.	

Ellenberg-type indicator values (EIVs) for recorded species for light, moisture and reaction were high (mean ± SE, L = 7.8 ± 0.1; M = 7.9 ± 0.2 and R = 6.2 ± 0.2, respectively), for temperature intermediate (T = 4.8 ± 0.2), and for nutrients low (N = 3.0 ± 0.2) (Fig. 3).

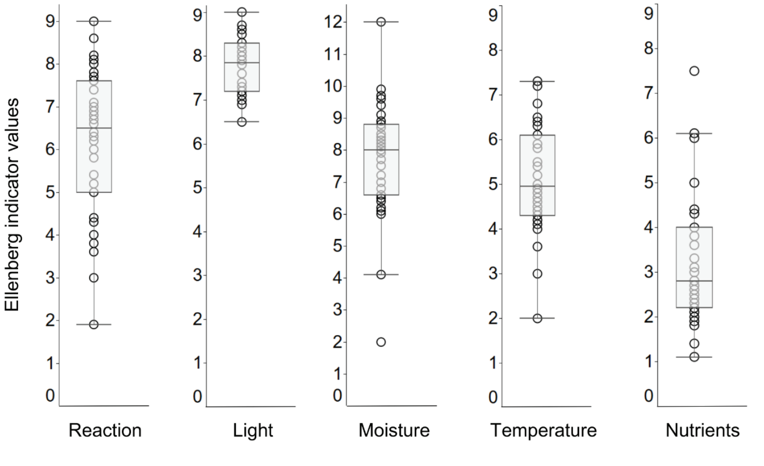

Fig. 3. Box-plot graphs of Ellenberg's indicator values (EIVs) for reaction (R), light (L), moisture (F), temperature (T) and nutrients (N) for vascular plants and bryophytes in the alkaline fen Dretulja River Valley, near Plaški.

The vegetation of the investigated area belongs to ass. *Junco subnodulosi-Schoenetum nigricantis* Allorge 1921 (syn. *Orchidi-Schoenetum nigricantis* Oberd. 1957) (NATURA 2000 habitat type 7230 Alkaline fens) represented by the following reléve (with abundances in parenthesis after species names) – vascular plants: *Schoenus nigricans* L. (5), *Molinia caerulea* (L.) *Moench* (3), *Cladium mariscus* (L.) *Pohl* (2b), *Drosera rotundifolia* L. (1), *Parnassia palustris* L. (1), *Pinguicula vulgaris* L. (1), *Scirpoides holoschoenus* (L.) *Soják* (1), *Anacamptis palustris* (Jacq.) R. M. Bateman, Pridgeon & M. W. Chase (+), *Phragmites australis* (Cav.) Steud. (+), *Potentilla erecta* (L.) Räusch. (+), *Tofieldia calyculata* (L.) Wahlenb. (+), *Utricularia minor* L. (+); bryophytes: *Campylium stellatum* (Hedw.) Lange & C.E.O.Jensen (4), *Palustriella falcata* (Brid.) Hedenäs (1), *Calliergonella cuspidata* (Hedw.) Loeske (+), *Cratoneuron filicinum* (Hedw.) Spruce (+), *Scorpidium revolvens* (Sw. ex anon.) Rubers (+), *Fissidens adianthoides* Hedw. (+), *Phylonotis calcarea* (Bruch & Schimp.) Schimp. (+), *Scorpidium scorpioides* (Hedw.) Limpr. (+) and cyanobacteria: *Nostoc* sp. (1), *Lyngbya versicolor* (1).

Soil properties

Soil temperature increased from May to August (mean ± SD; 13.86 ± 6.43, Fig. 4a), ranging from 3 °C measured in December to 27 °C in August. The soil was saturated with water (66.84% ± 10.25%), with a maximum value of 83.55% measured in December and a minimum value of 52.71% recorded in June (Fig. 4a). The soil was slightly alkaline (7.30 ± 0.15), and the pH values ranged from 7.06 to 7.42. (Fig. 4b).

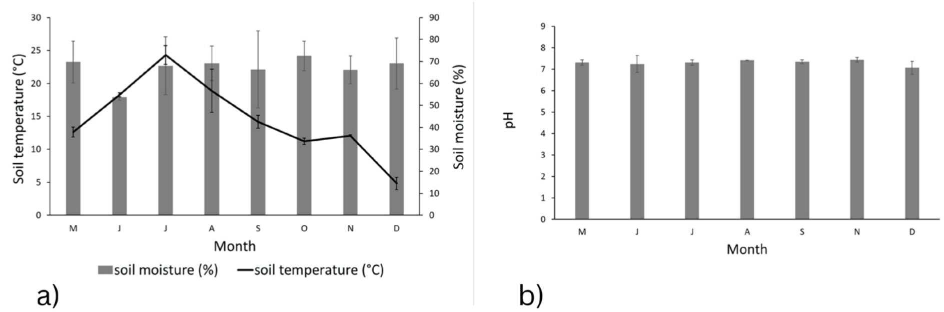

Fig. 4. Soil physico-chemical properties measured during the growing season in the alkaline fen Dretulja River Valley, near Plaški (Croatia): a) soil temperature (°C, mean) represented by the line and soil moisture (%, mean) presented with bars (± SD); b) soil pH (mean ± SD).

Invertebrate fen assemblages with life history traits

In total, three isopod species and 26 individuals were collected (Fig. 5, Tab. 2), and the most abundant isopod species was *Trachelipus rathkii* (50%). *Asellus aquaticus* belongs to the aquatic isopods of suborder Asellota, while the species *Ligidium germanicum* and *T. rathkii* belong to terrestrial isopods of the suborder Oniscidea. Isopod assemblages were composed of both aquatic and terrestrial species, adapted to freshwater habitats and high soil moisture (Fig. 6ab).

The lowest number of individuals compared to the other invertebrate taxa sampled was found in carabid beetles, with a total of 12 individuals belonging to five species sampled (Fig. 5, Tab. 3). The most abundant species was *Oodes helopiodes* (Tab. 3). Most carabid beetles recorded in the studied area preferred open habitats and were able to fly, and all carabid beetles were either hygrophilous or mesophilous (Fig. 6cdf).

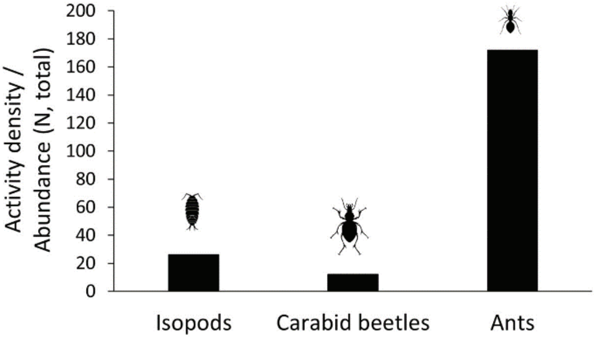

Fig. 5. Activity density (total) of multiple invertebrate taxa recorded at the alkaline fen Dretulja River Valley, near Plaški (Croatia).

Tab. 2. Isopod species and their abundances recorded in the alkaline fen Dretulja River Valley, near Plaški, Croatia.

Species name	Activity density (N)	Dominance (%)	Frequency (%)
Ligidium germanicum Verhoeff, 1901	6	23.08	55.56
Trachelipus rathkii (Brand, 1833)	13	50.00	66.67
Asellus aquaticus (Linnaeus, 1758)	7	26.92	22.22
Species richness (S)	**3**		
Activity density (N, total)	**26**		

Tab. 3. Carabid beetle species and their abundances recorded in the alkaline fen Dretulja River Valley, near Plaški.

Species name	Activity density (N)	Dominance (%)	Frequency (%)
Carabus coriaceus Linnaeus, 1758	1	8.33	11.11
Chlaenius nigricornis Fabricius, 1787	1	8.33	11.11
Chlaenius tristis (Schaller, 1783)	2	16.67	11.11
Cylindera germanica (Linnaeus, 1758)	3	25.00	33.33
Oodes helopioides (Fabricius, 1792)	5	41.67	55.56
Species richness (S)	**5**		
Activity density (N, total)	**12**		

Ants were the dominant group among fen soil invertebrates, with a total of 172 individuals representing 11 species recorded (Tab. 4). Three ant species had the highest occurrence on the fen: *Myrmica rubra* (33%), tyrpophilous *M. scabrinodis* (33%), and *Tapinoma erraticum* (11%). Over half of the recorded species show a preference for mesophilous habitats (Fig. 6). Most of the sampled ants are species that prefer open or woodland habitats (%), as well as meadows and open bogs (Fig. 6f). Four species of

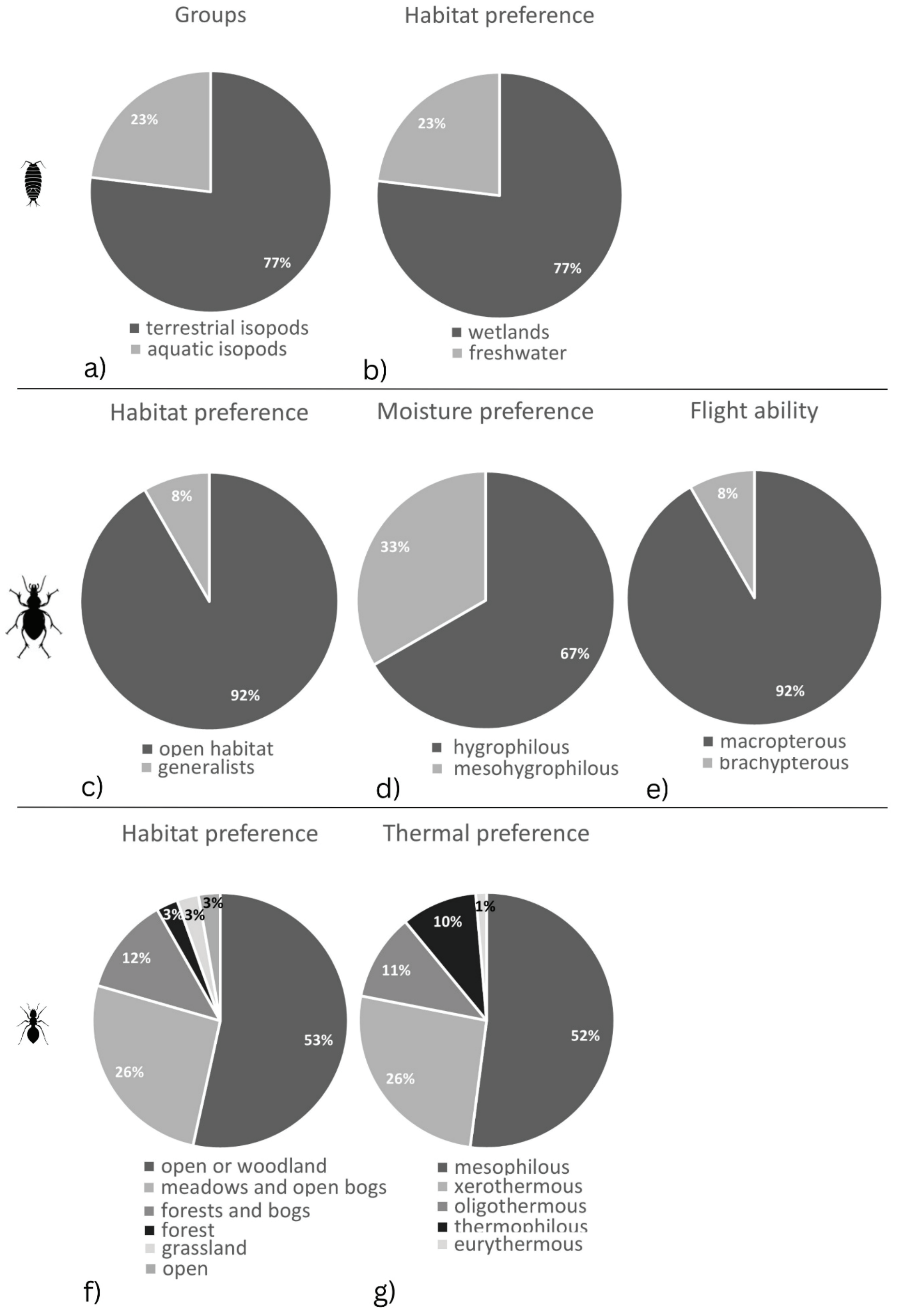

Fig. 6. The numbers of individuals recorded in the studied area according to life history traits for: (a) isopods - groups, habitat preference; (b) carabid beetles - habitat preference, moisture preference, flight ability; (c) ants – habitat preference and thermal preference.

Lasius were only recorded as queens: *L. distinguendus*, *L. fuliginosus*, *L. niger* and *L. sabularum*. Since we did not record a single worker of these species during eight months of sampling, these species probably do not have established colonies at the fen and were not included in the habitat preference analysis.

Tab. 4. Ant species and their abundances recorded in the alkaline fen Dretulja River Valley, near Plaški (Croatia, n sites = 2).

Species name	Occurrence (N)	Dominance (%)	Frequency (%)
Formica cunicularia (Latreille, 1798)	2	1.16	10.00
Formica fusca (Linnaeus, 1758)	1	0.58	10.00
Lasius brunneus (Latreille, 1798)	3	1.74	20.00
Lasius paralienus (Seifert, 1992)	2	1.16	20.00
Lasius platythorax (Seifert, 1991)	15	8.72	50.00
Myrmica rubra (Linnaeus, 1758)	57	33.14	90.00
Myrmica scabrinodis (Nylander, 1846)	57	33.14	100.00
Ponera coarctata (Latreille, 1802)	2	1.16	10.00
Tapinoma subboreale (Seifert, 2012)	1	0.58	10.00
Tapinoma erraticum (Latreille, 1798)	18	10.47	80.00
Tetramorium cf. caespitum (Linnaeus, 1758)	8	4.65	40.00
Species richness (S)	**11**		

Threatened taxa

Almost half of the recorded vascular flora of the investigated area is considered threatened out of which 14% of taxa are critically endangered (*Carex pulicaris*, *Drosera rotundifolia*, *Hydrocotyle vulgaris*, *Pinguicula vulgaris*, *Tofieldia calyculata*, *Triglochin palustris*), 23% endangered and 9% vulnerable (Tab. 1, Fig. 2c). On the other hand, two bryophyte species are near threatened, while all the rest are least-concern species. Floristic peculiarities of the investigated fen are three insectivorous plants (*Pinguicula vulgaris*, *Drosera rotundifolia* and *Utricularia minor*). In addition, a number of strictly protected orchid species were found (*Anacamptis palustris*, *Dactylorhiza incarnata*, *Epipactis palustris*, *Gymnadenia conopsea*, *Neotinea ustulata* and *Spiranthes aestivalis*), latter being nationally rare and data deficient (DD).

Two out of five recorded carabid beetle species are listed in the Croatian Red List of Threatened Carabid Beetle Species: *Chlaenius tristis* (Schaller, 1783) as endangered and *Oodes helopioides* (Fabricius, 1792) as near threatened (Vujčić-Karlo *et al.*, 2007).

DISCUSSION

The present study reveals that (1) the unique fen conditions support high plant diversity and threatened flora; (2) vascular flora and bryophytes are rich in Holarctic and boreal elements; (3) the fen is an extreme habitat for soil invertebrates due to high soil moisture; (4) the composition and structure of plant and invertebrate communities indicates that the fen's hydrological conditions remain well-preserved; (5) maintaining these hydrological conditions is essential for the long-term conservation of fen biodiversity.

Fen vegetation and soil properties

Vegetation of the studied association *Junco subnodulosi-Schoenetum nigricantis* Allorge 1921 in the Dretulja River Valley represents the relic postglacial fen community that remained preserved in specific ecological conditions (Gaži-Baskova, 1973; Horvatić, 1963, 1930). The Dretulja River Valley is, to the best of our knowledge, a unique site with this vegetation type in Croatia. In Europe, this fen community is found in warmer lowland areas, mainly close to the Alps and Carpathians and contains many species that occur mainly in the south of Central Europe (Leuschner & Ellenberg, 2017), thus this Croatian site lies on the very border of its distribution. The studied fen community belongs to the class *Scheuchzerio palustris-Caricetea fuscae* Tx. 1937 characterized by the dominance of sedges and mosses. Congruently, the flora of investigated alkaline fen is particularly rich in members of the sedge family (13 *Carex* species, *Schoenus nigricans*, *Eriophorum latifolium* and *Cladium mariscus*). *Schoenus nigricans* dominated communities are very rare in inland Croatia, and besides the studied fen community in Dretulja River Valley, they have been also recorded in three periodically inundated karst fields (Lapačko Polje in Lika and Vrličko Polje and Paško Polje in the Dalmatian Hinterland) (Gaži & Trinajstić, 1970; Gaži-Baskova, 1963), however within humid grasslands of class *Molinio-Arrhenatheretea* Tx. 1937 that do not belong in fen vegetation.

The studied alkaline fen is more or less permanently saturated with water along the sloping terrain (seepage) due to the numerous small springs feeding the shallow soil above the dolomites (Gaži-Baskova, 1973). Ecological analyses of the Ellenberg-type indicator values (EIVs) of recorded vascular and bryophyte flora clearly reveal a well-insolated, water-saturated (moist to damp) habitat with low nutrient availability. Calculated moderate alkaline conditions are in line with the slightly alkaline measured soil reaction, expected for this type of habitat.

Flora and life history traits

Central European fens support around 200 species of vascular plants, of which the majority are found in base-rich and calcareous fens (Succow & Joosten, 2001). Consistently with this, the flora of alkaline fen in Dretulja River Valley is very rich in vascular plants, containing 43 species. The vascular flora of the fen does not reflect the typical, south-east European biogeographical pattern of the surrounding vegetation, revealing the relic origin of dominantly Holarctic plant species common in wet fen habitats (*Carex echinata*, *C. flava*, *C. lepidocarpa*, *C. rostrata*, *C. vesicaria*, *Drosera rotundifolia*, *Equisetum palustre*, *Menyanthes trifoliata*, *Parnassia palustris*, *Pinguicula vulgaris*, *Triglochin palustris* and *Utricularia minor*) (Fig. 2). Among bryophytes, the boreal element is even more pronounced (66%) with the boreo-arctic *Scorpidium revolvens* and *S. scorpioides*, wide boreal *Climacium dendroides* and boreo-temperate *Fissidens adianthoides*, *Palustriella falcata* and *Philonotis calcarea*. In fact, these are all so-called brown mosses, a systematically heterogenous group of bryophytes, typical for alkaline fens, where they are engaged in peat formation. Two distinct Illyrian-Adriatic endemic vascular plants (*Scilla litardierei* and *Peucedanum coriaceum*) arrived in the fen from adjacent wet meadows, giving this vegetation a specific phytogeographical characteristic.

As expected, the dominant life-form found in the fen were hemicryptophytes – plants with resting buds at or near the level of the soil. The flora of continental temperate Europe is largely composed of hemicryptophytes with perennating buds at the ground surface (Leuschner & Ellenberg, 2017). It is the most widespread life form in the floras of humid temperate climates, but its prevalence decreases with increasing vapour pressure deficit. Conversely, more stable systems with higher moisture become more favourable for hemicryptophytes (Midolo *et al.*, 2024). Surprisingly, geophytes (plants with resting buds lying beneath the surface of the ground as rhizomes, bulbss, corm, etc.) comprise more than one third of vascular flora, which might be explained by the fact that geophytes in Europe are confined to higher latitudes (Midolo *et al.*, 2024), as are alkaline fens. The complete absence of therophytes, phanerophytes, and the negligible number of chamaephytes was to be expected for this type of habitat because of the high moisture.

Turfs, the dominant bryophyte life-form, feature many loosely or closely packed vertical stems with limited branching (Hill *et al.*, 2007; Bates, 1998), colonizing microhabitats usually subjected to seasonal floods, however, they are not very hydrodynamic-resistant, either to desiccation or to water abrasion (Vieira *et al.*, 2012; Vitt & Glime, 1984). Most of the fen bryophytes exhibited competitive perennial strategies (70%), e.g. species with long life span, rapid growth and dominant sexual and low or nearly absent asexual reproduction (Glime, 2020). This life strategy has often been recorded in the Mediterranean temporary streams of Croatia (Rimac *et al.*, 2022), demonstrating a similar variability in water availability. This is to a certain extent in line with the measured soil moisture of the investigated fen, indicating the decline in soil moisture during some summer months.

Soil invertebrate assemblages at the fen

We found low species richness and activity density of isopods and carabid beetles, while ants showed a greater capacity to tolerate and adapt to extreme environmental stresses, corroborating previous findings (Brigić *et al.*, 2021; Bujan *et al.*, 2015). Extreme environmental conditions, particularly high soil moisture which sometimes exceeds 80% during the growing season most likely reduced suitable shelter sites and food availability for soil invertebrates (Brigić *et al.*, 2019, 2017b; Tomescu *et al.*, 2015; Plum, 2005). Our results indicate that fens with a well-preserved hydrological regime and a high-water table are less prone to colonization by isopods and carabid beetles. Conversely, peat bogs in Croatia, e.g. Đon Močvar bog and Dubravica bog, undergoing specific successional stages experience increased colonization pressure (Brigić *et al.*, 2019, 2017ab; Antonović *et al.*, 2012).

The isopod assemblages in fens are generally composed of both aquatic and terrestrial species, which are adapted to high soil moisture as frequent inhabitants of wetlands (e.g. Ferenți *et al.*, 2013; Farkas, 1998). The aquatic isopod *Asellus aquaticus* favored such conditions, as part of the benthic macroinvertebrate community very common in ponds or slow-moving streams (Mellanby, 1963) and was probably surviving the unfavorable conditions in interstitial spaces (Peeters *et al.*, 2002). It was likely washed into pitfall traps by high water levels. Moreover, this species has been recorded in northern European peat bogs (e.g. Anderson *et al.*, 2017; Druvietis *et al.*, 2010), but has not been found in Croatian peatlands so far (Brigić *et al.*, 2019, 2017ab; Antonović *et al.*, 2012). At the fen, we recorded two terrestrial isopod species: *Ligidium germanicum*¸ known from both peat bogs (Brigić *et al.*, 2017b; Tomescu *et al.*, 2015) and alkaline fens (Brigić *et al.*, 2019; Sterzyńska *et al.*, 2015), and *Trachelipus rathkii*, which, although the most abundant species in two Croatian peat bogs (Brigić *et al.*, 2017b; Antonović *et al.*, 2012), also appears to establish a stable population in the fen. Similarly to the isopod assemblage, the impoverished carabid beetle assemblage in the fen is composed of highly hygrophilous species that inhabit riparian habitats, wetlands and peat bogs (Buchholz *et al.*, 2009; Hůrka, 1996; Lindroth, 1992). Moreover, *O. helopioides* exhibits partially subaquatic lifestyle, seeking refuge among submerged plants when threatened (Lindroth, 1992). With the exception of *Carabus coriaceus*, all recorded carabid beetle species have good flight abilities and can easily escape and colonize drier parts of the fen when groundwater level is too high (Lindroth, 1992; Hůrka, 1996). Thus, our findings indicate that groundwater level in the studied fen is high enough to support highly hygrophilous species and to suppress colonization of terrestrial invertebrates from adjacent meadow and forest habitats.

Ant species richness and activity were high compared to the other invertebrates we studied. However, although ants outnumbered other invertebrates in this study, their richness and abundance were low. We expected the number of species to be higher here than in a six times smaller fen in Croatia, where we found 16 ant species (Bujan *et al.*, 2015). Yet, here we recorded only 11 ant species, most of which were rare, with <10 individuals recorded over eight months of sampling. High water level and regular stream flow in combination with vegetation without *Sphagnum* spp. mats reduce adequate nesting sites and food availability at the fen (Bujan *et al.*, 2015). This prevents most ant species from forming colonies in fen habitats. Two dominant ant species *Myrmica rubra* and *M. scabrinodis* are mesophilous species which prefer wet habitats and have been recorded in other European bogs lacking specialist ants (Markó *et al.*, 2004; Maes *et al.*, 2003) including the ones in Croatia (Brigić *et al.*, 2017a). The tyrphophilous species *M. scabrinodis* can often be found in peatland habitats due to their high moisture preference and tolerance (Seifert, 1988). *Myrmica rubra* and *M. scabrinodis* together with *M. ruginodis* were suggested to be characteristic of South European marshland ant communities (Markó *et al.*, 2004). These species can tolerate long inundations (Boomsma & Isaaks, 1982) and quickly re-colonize once inundated areas (Maes *et al.*, 2003). Surprisingly we have not found any *M. rugiodis*, although this species was among dominant species in other Croatian peatlands (Brigić *et al.*, 2017a; Bujan *et al.*, 2015). *Lasius platythorax*, a common species in Croatian peatlands, was only the fourth most frequent species in our study (9%) which was surprising, as it was one of the most dominant ants in the Jarak fen (Bujan *et al.*, 2015) and in the Đon močvar peat bog (Brigić *et al.*, 2017a). Perhaps the lack of adequate nesting sites prevents this oligothermous species from establishing a strong population at this site. Among the most frequent species was the xerothermous *Tapinoma erraticum*, which was recorded for the first time in Croatian peatlands, and this could be due to the vicinity of the forest.

Conservation implication

The alkaline fen in the Dretulja River Valley near Plaški is an exceptionally rare habitat in Croatia, especially considering the fact that most temperate zone fens are restricted to higher altitudes. With almost half of the recorded vascular plant species being IUCN red-listed, this habitat is of high conservation value. Furthermore, it holds populations of several of the rarest species in the country, e.g. *Drosera rotundifolia*, *Utricularia minor*, *Spiranthes aestivalis*, *Carex pulicaris*, *C. punctata*, *Angelica palustris* and *Pinguicula vulgaris* being botanically unique in the North West Balkans. Moreover, the soil invertebrate community is composed of species of conservation interest, such as threatened carabid beetles *Chlaenius tristis* and *Oodes helopioides* and the indicator tyrphophilous ant *Myrmica scabrinodis* (Bujan *et al.*, 2015; Vujčić-Karlo *et al.*, 2007). The latter species is also one of the host species of the threatened large blue butterflies *Phengaris* (*Maculinea*), and accordingly the presence of the ant is important for the conservation of the butterfly (Jansen *et al.*, 2012).

The alkaline fen in the Dretulja River Valley near Plaški is, however, in rather good condition in comparison to other Croatian peatlands. The shallow, nutrient-poor and constantly saturated substrate disables severe and rapid encroachment on the fen by shrubs and trees. However, there have been some attempts to control neighbouring willow thickets using prescribed burns in recent times. There is no evidence that the habitat is affected by any grazing activities of wild or domesticated animals. Since water saturation is the principal ecological factor shaping the habitat, any hydrological modification would cause soil desiccation and habitat destruction. A quarry is located in close proximity to the fen, and has the potential to negatively impact the hydrological conditions of the site. Thus, mitigation measures should be implemented in order to preserve the integrity of the fen.

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