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A plea for the conservation of Western Balkan peatlands – a case study from Croatia

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ABSTRACT

Peatlands are among the most threatened habitats in Europe, particularly near the southern edge of their distribution in the Western Balkans. However, baseline data on their ecological condition are lacking in many countries, including Croatia. To provide a basis for effective conservation and management of these priority habitats, this study presents a comprehensive overview of habitat characteristics, main threats, and plant and invertebrate assemblages for 80 % of the known Croatian peatlands. Furthermore, we assess the conservation status of each peatland and analyse their similarities in terms of habitat condition, threat intensity and current management. Nearly two-thirds of the investigated peatlands were found to be in highly unfavourable conditions, with transition mires being especially vulnerable to advanced vegetation succession and hydrological degradation, typically caused by artificial drainage. In some Croatian peatlands, these processes have resulted in the loss of typical peatland plant species and may lead to local extinctions of rare tyrphophilous and stenotopic invertebrates. In line with our findings, we propose general guidelines for active peatland conservation measures, including restricting vegetation succession, improving hydrological conditions and minimizing anthropogenic impacts, which can be applied to other peatlands facing similar challenges. Targeted, site-specific management efforts will be essential to secure the long-term persistence of peatland habitats in Croatia and the wider region of the Western Balkans.

1. Introduction

Peatlands are among the most widely distributed wetland ecosystems, occurring from arctic to tropical regions, and covering about 3 % of Earth's land and freshwater surface (Joosten and Clarke, 2002; Tanneberger et al., 2022). Characterized by sedentary accumulation of dead organic material (peat), the decomposition of which is suppressed by waterlogging (Montanarella et al., 2006), peatlands store as much as 30 % of the global soil carbon and provide a number of ecosystem functions, including water regulation, carbon sequestration, sediment retention and biodiversity maintenance (Harenda et al., 2018; Joosten et al., 2012). Despite their

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importance, about 10 % of peatlands are drained and exploited through cultivation, peat extraction, forestry and other destructive activities, causing declines in their extent and organic matter content (Montanarella et al., 2006), while significantly contributing to anthropogenic carbon dioxide emissions and biodiversity loss (Joosten et al., 2012; Tanneberger et al., 2022, 2021). Systematic peatland research is fundamental to the effective conservation of these ecosystems, as it not only advances our understanding of their ecological functioning, but also provides the baseline data required for the development of appropriate management strategies (Taylor et al., 2019).

Unsustainable land use and climate change are considered to be the major drivers of peatland decline in recent times (Joosten et al., 2012; Pellerin and Lavoie, 2003). Anthropogenic pressures, coupled with a rapid increase in global temperatures, higher frequency and duration of droughts, cause deterioration of hydrological conditions through reduction in water table levels (Harenda et al., 2018; Pellerin and Lavoie, 2003), the primary cause of peatland degradation (Grzybowski and Glińska-Lewczuk, 2020). Additionally, changes in grazing, mowing or burning regimes increase nutrient availability and facilitate encroachment by expansive plant species, particularly in temperate bogs (Pellerin et al., 2021). Peatland succession causes alterations in both abiotic and biotic habitat properties (Laine et al., 2021; Li et al., 2022), inducing changes in often highly specialized and localized peatland communities (Pellerin and Lavoie, 2003; Topić and Stančić, 2006). The decline or disappearance of peatland-associated species ultimately contributes to biodiversity loss at both local and regional scales (Woziwoda and Kopeć, 2014).

In Europe, peatlands cover about 10 % of the total surface area, with their occurrence and extent greatly diminishing from the north-west to the south-east of the continent, following climate gradients, i.e., higher summer temperatures and lower rainfall (Tanneberger et al., 2021, 2017). European peatlands are among the most threatened in the world owing to the many centuries of direct and indirect anthropogenic impacts (Tanneberger et al., 2021). Although peatlands are priority habitats for conservation from the global standards, e.g., the Ramsar convention, to more local policies, e.g., the EU-based Natura 2000 network (Grzybowski and Glińska-Lewczuk, 2020; Harenda et al., 2018), there is still a general lack of comprehensive and comparable baseline data on their extent and current status in most European countries (Joosten and Clarke, 2002). Such data are necessary for adequate conservation planning and restoration activities (Montanarella et al., 2006), the main goal of which is to enable the natural functioning and self-sustenance of European peatlands, thus restoring the ecosystem services they provide (Grzybowski and Glińska-Lewczuk, 2020; Joosten et al., 2012; Minayeva et al., 2009).

Originating from the late glacial period, Western Balkans peatlands are relict habitats close to the southern edge of peatland distribution in Europe (Hruševar et al., 2023; Minayeva et al., 2009), typically covering small and highly fragmented areas (Topić and Stančić, 2006). The abandonment of traditional land management practices (e.g., extensive grazing or regular mowing regimes), coupled with long-term climate warming, gives rise to natural vegetation succession (Minayeva et al., 2009) as the primary agent of peatland disappearance in the Western Balkans (Alegro and Topić, 2017; Brigić et al., 2019). For instance, in the Dubravica transition mire in NW Croatia, two smaller mire areas have completely disappeared within 55 years whereas the largest mire has undergone a reduction to 37 % of its originally documented area, the water level having fallen beneath the minimum necessary values for the long-term survival of peatland vegetation (Hršak,1996). Some historically known transition mires, such as Lepenica, have almost completely disappeared in the last 20 years due to hydrological alteration caused by the construction of a reservoir (Alegro and Topić, 2017).

Croatia is listed among the European countries with the highest proportion of degraded peatland (91 %-100 %), even though more than 75 % of the national peatlands are included in protected areas (Tanneberger et al., 2021). Tanneberger et al. (2017) estimated that Croatian peatlands *sensu* Joosten et al. (2017), i.e., areas with a naturally accumulated layer of peat on the surface, cover 33.1 km² (0.06 % of the total area of the country). According to the same authors, the area covered by mires, i.e., peatlands with active peat formation (Joosten et al., 2017), amounts to only 0.3 km² (0.76 % of the total peatland area in the country). Nevertheless, these authors point out that their rough national estimates were conducted primarily using available published data, emphasizing the need for more detailed, country-wide inventories (Tanneberger et al., 2017).

The first objective of this study is to present a comprehensive overview of Croatian peatlands based on: i) habitat characteristics, ii) main threats, iii) management status, iv) plant species composition (focusing on their conservation status), and v) invertebrate assemblages (with an emphasis on peatland indicator species). This overview draws upon nearly 20 years of peatland research, integrating published studies, the authors' unpublished data, and expert knowledge. Using the collected data, we evaluate the conservation status of each peatland based on predefined criteria by Grzybowski and Glińska-Lewczuk (2020), to establish the current state as a baseline for future conservation and restoration efforts. Furthermore, we test the similarities of Croatian peatlands in terms of habitat condition, main threats and current management to identify potential peatland-specific patterns that could guide the development of more effective management practices. Overall, the data presented in this paper are intended to provide a basis not only for future scientific research on Croatian and Western Balkan peatlands, but also for conservation planning and for the establishment of appropriate monitoring and management strategies adjusted to peatland characteristics, their conservation status and the threats specific to this region.

2. Material and methods

2.1. Study area

Croatia is situated in the northern mid-latitudes of Europe, with its climate influenced by the Adriatic Sea, the unique topography of the Dinaric Alps, and the Pannonian plain (Zaninović et al., 2008). According to the EEA (European Environment Agency, 2020) the country is included in three biogeographical regions: Mediterranean, Alpine and Continental (Fig. 1), the latter two harbouring all the

known peatland habitats (Alegro and Topić, 2017). Croatian peatlands are minerotrophic, i.e. primarily fed by groundwater and additionally by rainfall, with two main types generally recognized: acidic (base-poor) mires and alkaline (base-rich) fens (Antonić et al., 2005; Topić and Stančić, 2006).

There are three main areas of peatland distribution in Croatia: 1) the western part of Hrvatsko Zagorje region, 2) Banovina (Banija) region and the surroundings of the city of Karlovac, and 3) Gorski Kotar region (Hršak, 1996), with some isolated peatland habitats found also on Velebit, Žumberak and Papuk mountains (Alegro and Topić, 2017). Peatlands are typically developed in wetland areas within the zonal sessile oak-common hornbeam forests (*Epimedio-Carpinetum betuli* (Horvat 1938) Borhidi1963) at 160–180 m a.s.l. and in extrazonal (e.g. boreal-type *Picea abies* dominated forests) vegetation types in the beech-fir forest zone (*Omphalodo-Fagetum* s. lat.) at 700–1200 m a.s.l. (Modrić Surina, 2011; Topić and Stančić, 2006). According to the most recent overview of Croatian peatlands, 21 small and scattered localities are currently known in the country, covering a total area of only 25–30 ha (Alegro and Topić, 2017).

2.2. Data collecting

We studied the 17 largest Croatian peatlands, distributed across the entire geographic range of peatland habitats in the country (see *Study area*; Fig. 1). For each peatland, we compiled all the available information on: habitat area (ha), hydrological regime, characteristic plant associations and invertebrate assemblages, threatened plant species according to the National Red List (Nikolić et al., 2025; Nikolić and Topić, 2005), plant species protected at the national level (NN 144/2013, 73/2016), plant species included in the Habitats Directive (Council Directive 92/43/EEC; NN 144/2013, 73/2016), invertebrate species that can be used as environmental indicators of peatland condition (Brigić et al., 2017), invertebrate species included in the Habitats Directive (see above), extant threats following the Natura 2000 reference list (European Environment Agency, 2020), protection category and management type. The primary data sources included Natura 2000 Standard Data Forms (Ministry of Economy and Sustainable Development, 2019), relevant

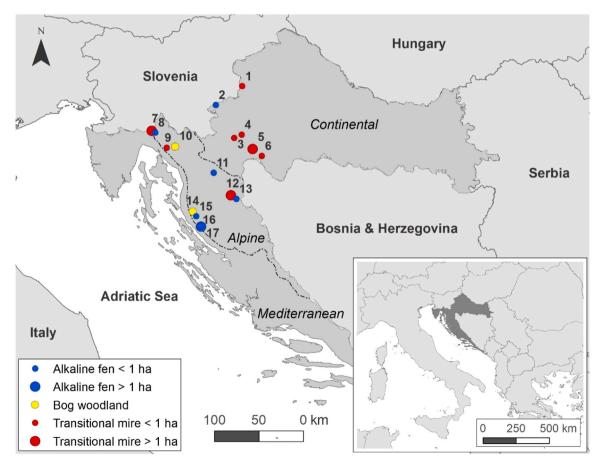


Fig. 1. Distribution of the Croatian peatlands included in this study. Legend: 1 - Dubravica, 2 - Jarak, 3 - Vukmanić, 4 - Banski Moravci, 5 - Đon močvar (Blatuša), 6 - Šaševa, 7 - Trstenik, 8 - Rečice (Ričice), 9 - Lepenica, 10 - Sungerski lug, 11 - Dretulja River Valley (Plaški), 12 - Ljeskovačke bare, 13 - Kapela Korenička – bare, 14 - Vodice kod Petrašice (Klepina Duliba, Štirovača), 15 - Sunđerac, 16 - Rakita (Raketa), 17 - Ljubica. Peatland area (smaller or larger than 1 ha) is represented by circles of different sizes, while the separate colours differentiate peatland types (alkaline fen, bog woodland, transition mire).

scientific literature, expert reports on Croatian peatlands, and the authors' unpublished field observations. Ecological classification of invertebrate species inhabiting peatlands follows Peus (1932) and Roubal (1934): i) tyrphobiont – habitat specialists confined to peatlands, ii) tyrphophilous – showing a preference for peatland habitats but not confined to them, iii) tyrphoneutral – occurring in peatlands but showing no preference for peatland habitats, iv) tyrphoxenous species – vagrants from the surrounding habitats that do not inhabit peatlands.

We assessed the conservation status of each peatland using a protocol adapted from Grzybowski and Glińska-Lewczuk (2020), adopting the three-level scale assessment method used by the European Commission. We assigned one of the three levels: FV (favourable), U1 (unfavourable-inadequate) or U2 (unfavourable-bad status, to each peatland with respect to five parameters: i) the number of typical plant species, ii) *Sphagnum* sp./moss cover, iii) expansive herbaceous plant cover, iv) shrub/tree cover and v) drainage. The overall conservation status of each peatland was determined by the parameter assigned the worst status (Grzybowski and Glińska-Lewczuk, 2020). For detailed assessment guidelines used in the current study, please see Table S1.

2.3. Statistical analyses

To assess the similarities of Croatian peatlands based on their condition, main threats and management, we adopted clustering analysis in PRIMER 6 (Clarke and Gorley, 2006). We used the following metrics: i) the occurrence of typical plant species and ii) *Sphagnum* sp./moss cover (1 = high, 2 = medium, 3 = low), iii) drainage, iv) vegetation succession and v) other threats (threat intensity 1 = none, 2 = low, 3 = medium, 4 = high), and vi) management (1 = regular, 2 = occasional, 3 = incidental, 4 = none), according to Natura 2000 Standard Data Forms (Ministry of Economy and Sustainable Development, 2019) and other available data, including our own observations (for additional information see *Data collecting*). For all metrics, the lowest value represents the most favourable status and the highest value the least favourable one.

Using original, non-standardized data, a resemblance matrix was built with Gower distance as a resemblance measure most appropriate for categorical data clustering (dos Santos and Zárate, 2015). Hierarchical cluster analysis (HCA) on the resemblance matrix with average linkage cluster mode was then performed, using similarity profile analysis (SIMPROF) with 999 permutations to identify peatlands that fall into clusters based on the similarity in condition, threats and management, and to test whether these clusters are statistically supported (Clarke and Gorley, 2006). One-way analysis of similarities (ANOSIM) with 999 permutations was then adopted to test for differences among the clusters identified by SIMPROF as having statistical support. Prior to the ANOSIM, it was necessary to standardise data to relative composition and a resemblance matrix was then built using Gower distance as a resemblance measure (Clarke and Gorley, 2006) For further visualization of the relationships between peatland clusters and main threats, condition and management, we built a heat map based on two-way cluster analysis (TW-HCA) with Gower distance using the *pheatmap* package in RStudio, R ver. 4.1.2 (RStudio Team, 2020).

Differences in the number of threatened, nationally protected, and Habitats Directive-listed plant species among the main peatland types (alkaline fen, bog woodland, transition mire) were tested using Kruskal-Wallis H test in SPSS Statistics ver. 27.0 (IBM Corp., 2020). Pairwise multiple comparisons were performed *post hoc* using Dunn's test with Bonferroni correction.

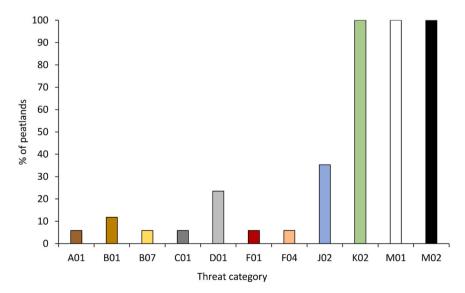


Fig. 2. Main threats to the 17 studied peatland habitats; threat codes and names according to Natura 2000 reference list (European Environment Agency, 2020). Legend: A01 Cultivation; B01 Forest planting on open ground; B07 Other forestry activities; C01 Mining and quarrying; D01 Roads, paths and railroads; F01 Hunting and collection of wild animals (terrestrial); F04 Taking / Removal of terrestrial plants, general; J02 Human induced changes in hydraulic conditions; K02 Biocenotic evolution, succession; M01 Changes in abiotic conditions; M02 Changes in biotic conditions.

3. Results

3.1. Peatland characteristics and main threats

The majority of the investigated peatlands are located in the Continental biogeographical region of Croatia (64.7 %), with the rest situated in the Alpine biogeographical region (Dinaric Alps; 37.5 %). Only five peatlands (29.4 %) cover areas larger than 1 ha, the largest being the Don močvar mire (about 4.5 ha), followed by Trstenik and Ljeskovačke bare mires (both about 2 ha) and Ljubica fen (1.6 ha) (Fig. 1; Table S2). Transition mires and alkaline fens are similarly represented (47.1 % vs. 41.2 %), with three peatlands harbouring plant associations characteristic of both habitat types, although either transition mire (Ljeskovačke bare, Trstenik) or alkaline fen (Sunderac) predominates (Fig. 1; Table S2). Only two transition mires exhibit elements of ombrotrophy (Don močvar and Trstenik; Table S2). Finally, two of the investigated peatlands (Sungerski lug and Vodice kod Petrašice) belong to the bog woodland habitat type (Fig. 1; Table S2). The most common plant association in transition mires is *Drosero-Caricetum stellulatae*, although in some mires (e.g. Banski Moravci, Dubravica and Lepenica) only impoverished remnants are present. On the other hand, alkaline fens are mainly characterised by the association *Eriophoro-Caricetum paniceae*, often in mosaics with other wetland communities (Table S2).

The primary threat to all the Croatian peatlands studied is vegetation succession (encroachment by expansive plant species) and the resulting changes in abiotic and biotic conditions (Fig. 2; Table S2). This is followed by human-induced hydrological changes (detected in six peatlands) and threats related to adjacent road infrastructure (four peatlands; Fig. 2; Table S2). Other threats are of a more local significance, depending on the prevailing human activities in a given area (Fig. 2; Table S2).

3.2. Peatland protection and management

Among the peatlands included in this study, more than half (58.8 %) are situated within areas protected at the national or local level; four peatlands (Banski Moravci, Dubravica, Đon močvar, Jarak; 23.5 %) are protected as Special Botanical Reserves, whereas seven (41.2 %) are situated within national or nature parks (Table S2). Furthermore, all of the investigated peatlands (except Banski Moravci mire) are included in the Natura 2000 network (Table S2). Nevertheless, regular management activities are conducted in only two peatlands (Dubravica and Ljeskovačke bare; 11.8 %), while four of them (23.5 %) are occasionally and three (17.7 %) incidentally managed (Table S2). Almost half of the investigated peatlands are not covered by any management activities (Table S2).

3.3. Peatland similarity based on habitat condition, threats and management

Hierarchical cluster analysis of Croatian peatlands, based on habitat condition, prevailing threats and management status, identified two statistically supported clusters with 46.2 % similarity (Fig. 3). One cluster was composed of Banski Moravci, Dubravica, Lepenica and Trstenik mires, while the other cluster encompassed all the other peatlands (Fig. 3). The difference between the clusters was statistically significant (ANOSIM, R-statistic = 0.299, p = 0.037). The results of the TW-HCA indicated a close association between the level of vegetation succession and peatland management, as well as between moss cover and the occurrence of characteristic plant species (Fig. 4). Moreover, peatlands affected by drainage were also more frequently exposed to other threats, primarily related to increased human activity (Fig. 2; Fig. 4).

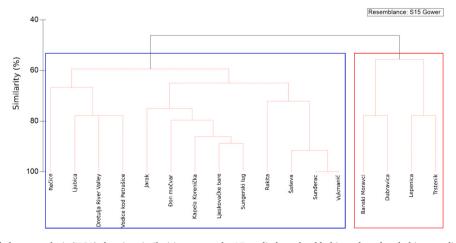


Fig. 3. Hierarchical cluster analysis (HCA) showing similarities among the 17 studied peatland habitats, based on habitat condition (the occurrence of characteristic plant species, Sphagnum sp./other moss cover), threats (drainage, vegetation succession, other threats) and management. Statistically supported clusters are marked by rectangles of different colours (ANOSIM, p < 0.050).

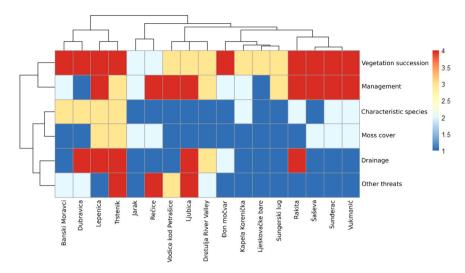


Fig. 4. Heat map visualization of two-way hierarchical cluster analysis (TW-HCA) showing the relationships between peatland clusters and habitat condition, threats and management. Colour gradient indicates the strength of the associations between each of the investigated peatlands and individual metrics, from minimum association (most favourable status; dark blue) to maximum association (least favourable status; dark red).

3.4. Conservation status assessment

Our assessments showed that all the Croatian peatlands studied were in an unfavourable condition (Table 1). Most of the peatlands had an unfavourable-bad (U2) conservation status (64.7 %), with the remaining peatlands (35.3 %) having an unfavourable-inadequate (U1) status (Table 1). In general, transition mires were in a worse condition than alkaline fens (100 % vs. 28.6 % assessed as U2; Table 1). The factor that primarily contributed to the unfavourable conservation status of Croatian peatlands was vegetation succession, through the increase in expansive herb species cover (assessed as U2 in 58.8 % and as U1 in 41.2 % of peatlands) and/or the increase in shrub or tree cover (assessed as U2 in 29.4 % and as U1 in 41.2 % peatlands; Table 1). It was followed by the poor state of hydration and a corresponding decline in the occurrence of typical peatland plants (both factors assessed as either U2 or U1 in 47.1 % of peatlands), and a decrease in *Sphagnum* sp. or other moss species cover (assessed as either U2 or U1 in 41.2 % of peatlands; Table 1).

3.5. Plant and invertebrate species composition

Three peatlands particularly stood out in terms of the number of threatened and nationally protected plant species: Dretulja River Valley and Ljubica fens, and Đon močvar mire (Fig. 5; Table S3). These were followed by the alkaline fens Jarak, Rakita and Rečice, and

Table 1
Conservation status assessment for the 17 studied peatland habitats; for each peatland, habitat condition was assessed independently with respect to each of the five assessment criteria and overall; Legend: FV – favourable, U1 – unfavourable inadequate, U2 – unfavourable bad.

Peatland	Characteristic plant species	Sphagnum sp. / other moss cover	Expansive herb species	Expansive shrub / tree species	Hydration	Overall condition
Banski Moravci	U2	FV	U2	U2	U1	U2
Dretulja River Valley (Plaški)	FV	FV	U1	FV	U1	U1
Dubravica	U2	FV	U2	FV	U2	U2
Đon močvar (Blatuša)	FV	FV	U2	U2	U1	U2
Jarak	FV	U1	U1	FV	FV	U1
Kapela Korenička – bare	U1	FV	U2	FV	FV	U2
Lepenica	U2	U2	U2	U2	U2	U2
Ljeskovačke bare	FV	FV	U2	U1	FV	U2
Ljubica	FV	FV	U1	U1	U2	U2
Rakita (Raketa)	U1	FV	U1	U1	U1	U1
Rečice (Ričice)	FV	U1	U1	FV	FV	U1
Sunđerac	U1	U1	U1	U1	FV	U1
Sungerski lug	FV	FV	U2	U1	FV	U2
Šaševa	FV	U1	U2	U2	FV	U2
Trstenik	U2	U2	U2	U1	U2	U2
Vodice kod Petrašice (Klepina Duliba, Štirovača)	FV	FV	U1	U1	FV	U1
Vukmanić	U1	U1	U2	U2	FV	U2

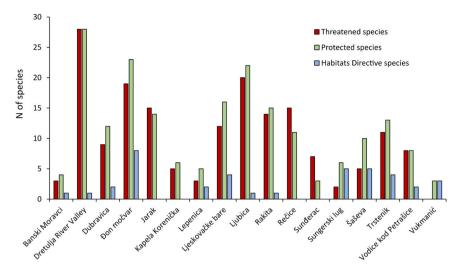


Fig. 5. Total numbers of threatened, nationally protected, and Habitats Directive-listed plant species recorded from the 17 studied peatland habitats.

by the Ljeskovačke bare transition mire (Fig. 5; Table S3). No statistically significant differences among peatland types were found in the number of threatened (Kruskal-Wallis H test, H = 4.755, d.f. = 2, p = 0.093) or nationally protected plant species (H = 1.256, d.f. = 2, p = 0.534). Nevertheless, the number of plant species included in the Habitats Directive differed significantly among peatland types (H = 11.056, d.f. = 2, p = 0.004); in particular, transition mires harboured a larger number of such species than alkaline fens (Dunn's test with Bonferroni correction, Z = 3.125, p = 0.005). As many as eight Habitats Directive-listed *Sphagnum* species were found in the largest Croatian mire, Don močvar, alone, followed by the bog woodland Sungerski lug and the transition mires Šaševa, Ljeskovačke bare and Trstenik (Fig. 5; Table S3). At least five Croatian peatlands (Dubravica, Don močvar, Lepenica, Sunderac, Vukmanić) have probably lost one or more threatened and/or protected plant species in recent years (Table S3; species marked with an asterisk).

Invertebrates were studied at ten Croatian peatlands, with a primary focus on arthropod taxa (Table S4). The largest among them, Don močvar mire, harboured the highest number of peatland indicator species, followed by Dubravica and Trstenik mires (Fig. 6; Table S4). The most common tyrphophilous species was the ground beetle *Pterostichus diligens*, recorded in five Croatian peatlands, followed by *Pterostichus rhaeticus* and the ant *Myrmica scabrinodis*, both of which are known from four peatlands (Table S4). Particularly noteworthy is the occurrence of the ground beetle *Carabus* (*variolosus*) *nodulosus*, listed under the Habitats Directive, in three Croatian peatlands, with the largest known population in the country inhabiting Don močvar mire (Table S4). In addition, three tyrphophilous spiders, *Piratula hygrophila*, *P. uliginosa* and *Trochosa spinipalpis* (Nentwig et al., 2025; Scott et al., 2006), have been recorded at the Dubravica mire (Table S4).

Don močvar mire is also notable for its permanent water bodies of several types (Brigić et al., 2021), supporting at least four tyrphophilous species of aquatic insects (Previšić et al., 2013) and species-rich oligochaete assemblages (Table S4). No tyrphobiont

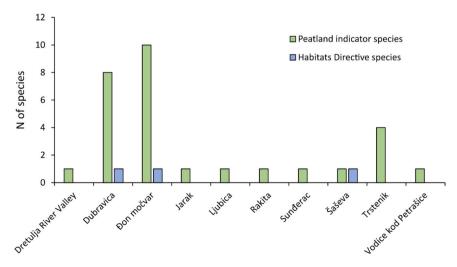


Fig. 6. Total numbers of peatland indicator and Habitats Directive-listed invertebrate species recorded from the 10 studied peatland habitats.

invertebrates have been recorded from any of the Croatian peatlands so far. Conversely, the occurrence of succession indicator species of terrestrial isopods has been observed in several peatlands (Antonović et al., 2012), notably Dubravica, Đon močvar and Trstenik mires (Table S4).

4. Discussion

4.1. Major threats to Western Balkan peatlands: insights from Croatia

Vegetation succession was identified as the principal threat to Croatian peatlands, affecting all of the investigated peatlands to a certain degree (Antonović et al., 2012; Brigić et al., 2019; Ministry of Economy and Sustainable Development, 2019). Successional changes are closely linked to degradation in hydrological conditions, primarily caused by artificial drainage, the second most important threat to these habitats, including the largest and most valuable (Đon močvar, Trstenik). In at least four mires (Banski Moravci, Dubravica, Lepenica and Trstenik), advanced vegetation succession, coupled with severe hydrological degradation due to drainage in three of them, has already resulted in a substantial loss of typical peatland vegetation. Similarly, the combined effects of human-induced hydrological degradation and local successional processes have led to the loss of key habitat features and reduced connectivity in Polish peatlands (Grzybowski and Glińska-Lewczuk, 2020). Nevertheless, some Croatian peatlands (e.g., Sunderac, Vukmanić), although unaffected by drainage or other anthropogenic disturbances, still exhibit considerable vegetation decline, likely due to successional changes and the accompanying shifts in nutrient availability and/or water table levels (Pellerin et al., 2021).

Water availability and balance are fundamental in determining the structure and function of peatland ecosystems (Harenda et al., 2018). Indeed, our findings suggest that the deterioration in hydrological conditions is typically associated with a reduction in moss cover (including *Sphagnum* species, where present) and a corresponding decline of specialized peatland flora. This occurs because any disturbance that lowers the water table shifts the balance in favour of encroaching plant species, creating a positive feedback loop that further dries the habitat (Payne et al., 2016; Pellerin et al., 2021). The long-term persistence of peatlands in Croatia, and the Western Balkans more broadly, will therefore primarily depend on the restoration of their hydrological conditions, a prerequisite for all subsequent restoration efforts, including vegetation management (Mälson et al., 2010; Monteverde et al., 2022).

4.2. Current status of peatland management and protection in Croatia

All of the peatlands in our study are either included within nationally designated protected areas (national or nature parks, special reserves) categorized under the Nature Protection Act (NN 80/13, 15/18, 14/19, 127/19, 155/23), or are covered by the Natura 2000 network (NN 124/13, 105/15, 80/19, 119/23), thus confirming that more than 75 % of Croatian peatlands are included in protected areas (Tanneberger et al., 2021). Unfortunately, nearly two-thirds of the investigated peatlands are currently not included in any management activities or are subject to incidental management at best. This is particularly concerning as we found that peatlands lacking proper management are generally more vulnerable to vegetation succession. Indeed, *in situ* research has demonstrated that with increasing time since peatland restoration efforts, shrub and herb cover tend to increase, whereas moss cover will typically decline, especially in minerotrophic peatlands (Purre et al., 2021).

The situation could improve in the future, as management plans have recently been developed for each Natura 2000 site in Croatia, outlining the objectives and measures for active conservation of threatened habitat types (EU Operational Programme Competitiveness and Cohesion 2014–2020, project K.K.06.5.2.03.0001). However, the relationship between peatland management and vegetation succession remains ambiguous. A few unmanaged Croatian peatlands (e.g., Rečice, Vodice kod Petrašice) are only moderately impacted by encroachment, presumably owing to hydrological conditions still sufficiently favourable to give peatland vegetation a competitive advantage over expansive plant species (Pellerin et al., 2021). This confirms the observation that the effects of vegetation succession on peatland moss cover are influenced by site-specific conditions (Limpens et al., 2003; Purre et al., 2021).

4.3. Croatian peatlands as declining biodiversity hotspots

The critical condition of Croatian peatlands, and transition mires in particular, is especially concerning from the conservation perspective, as these habitats represent the last refuge to some critically endangered and Habitats Directive-listed plant species in the country, including Hamatocaulis vernicosus (Ljeskovačke bare), Calla palustris (Sungerski lug), Osmunda regalis and Sphagnum compactum (Šaševa), Eriophorum vaginatum, Sphagnum papillosum and S. tenellum (Trstenik) (Alegro and Topić, 2017). The importance of transition mires for the conservation of plant species listed under the Habitats Directive, particularly Sphagnum mosses, stands in marked contrast to the degree of their current ecological degradation (see above). Alarmingly, some valuable plant species have already been lost from individual peatlands in recent years, including Hamatocaulis vernicosus from Dubravica, Lycopodiella indundata from Don močvar, Drosera rotundifolia from Lepenica, and Rhychospora alba and all five Sphagnum species from Sunderac. In a particularly extreme case, three previously recorded threatened plant species (i.e., Drosera rotundifolia, Osmunda regalis and Rhychospora alba) have most probably disappeared from the severely degraded Vukmanić mire.

The peatlands investigated also harbour tyrphophilous and rare stenotopic invertebrates, including both terrestrial (e.g., the carabids *Pterostichus diligens* and *P. rhaeticus*, the ant *Myrmica scabrinodis*, the spider *Araneus alsine*) and aquatic species (e.g., caddisflies *Hagenella clathrata* and *Rhadicoleptus alpestris*), some of which are also included in the Habitats Directive (*Carabus (variolosus) nod-ulosus*). Many of these species face a high risk of local extinction, since the investigated sites constitute the majority, if not the entirety, of their known distribution in the country (Brigić et al., 2017, 2014; Previšić et al., 2013). However, most of the studied peatland

assemblages are characterized by a low activity density of tyrphophilous species in relation to northern European peatlands (Brigić et al., 2014) and a species composition more broadly representative of wetland habitats; for instance, orthopteran assemblages include the tyrphophilous *Metrioptera brachyptera* (Krištín et al., 2012; Peus, 1932) only at a single site (Trstenik mire). This may be attributed to the restricted size and high degree of peatland habitat fragmentation in Croatia (Alegro and Topić, 2017), as the associated invertebrate communities generally display low resilience to environmental disturbances and have limited recolonization potential (Batzer et al., 2016).

Notably, no true tyrphobionts have been recorded in Croatian peatlands to date. Peatland specialists with narrow ecological niches such as the carabids *Agonum ericeti* and *Carabus menetriesi* or the ants Formica picea and Formica uralensis, often used as peatland indicators in northern Europe (Vepsäläinen et al., 2000), either do not reach southern Europe (Pawłowski, 2005) or are present only at high elevations (above 800 m) in this region (Brigić et al., 2017). In addition to these biogeographical limitations, Croatian peatlands possibly do not provide the conditions necessary to sustain viable populations of tyrphobiont species; for instance, there are no true ombrotrophic bogs capable of supporting specialists such as *A. ericeti* (Främbs, 1994). Accordingly, in the Western Balkans, the southern limit of peatland distribution in Europe (Minayeva et al., 2009), tyrphophilous invertebrates can be used as reliable indicators of peatland habitat condition (Brigić et al., 2017; Spitzer and Danks, 2006). Overall, the absence of tyrphobionts and the low activity densities of tyrphophilous species, coupled with the presence of succession indicator species at some peatland sites, suggest advanced successional and hydrological changes in Croatian peatlands (Antonović et al., 2012; Lehmitz et al., 2020), further emphasizing their severe degradation.

4.4. Site-specific approach to peatland management

The current overview of habitat characteristics, threats and conservation status for 80 % of the known Croatian peatlands unambiguously shows that the overall condition of peatland ecosystems is unsustainable at the national level. Active conservation measures should encompass all investigated peatlands, with a particular focus on transition mires, most of which are on the verge of disappearance due to advanced vegetation succession and hydrological degradation. Effective conservation of these habitats in Croatia and the Western Balkans can only be achieved through long-term management efforts. Here we suggest the following activities:

- 1) improving hydrological conditions by blocking drainage channels and maintaining water table levels through controlled flooding and/or appropriate restoration measures aimed at enhancing water retention (e.g., dam construction), thereby creating the necessary conditions for peatland vegetation regrowth or reintroduction/repopulation (Joosten et al., 2012; Mälson et al., 2010); at the same time, water retention measures will help not only maintain but also increase the extent of open water bodies as valuable peatland microhabitats (Brigić et al., 2021), which require frequent monitoring activities due to high spatio-temporal dynamics (Schultz et al., 2023);
- 2) restricting vegetation succession through regular grazing regimes, mowing or cutting of expansive woody and/or herbaceous species, complemented by mechanical clearing where necessary to create space for moss regrowth (Mälson et al., 2010), all of which must be performed carefully to prevent disrupting habitat integrity; mid-season (late June/early August) mowing (Doležal et al., 2019; Ross et al., 2019) should be most intensive (e.g., annual) during the initial years following hydrological restoration (see above), with particular emphasis on the removal of dead plant material (e.g., through *Molinia* haymaking) to reduce excess nutrients (Mälson et al., 2010);
- 3) minimising anthropogenic impacts by limiting or strictly regulating construction, forestry and other human activities in the proximity of peatland habitats, and by engaging local communities and stakeholders in their conservation through educational activities and public awareness campaigns.

Considering the highly heterogenous set of peatlands, we highlight the necessity for a site-specific approach when planning and implementing management measures at the local level. Management plans should be tailored to the unique habitat characteristics, current ecological status, prevailing threats, and specific conservation objectives for each individual peatland. For instance, the current conservation practices at the Dubravica transition mire should be maintained; they include selective mowing twice annually, manual biomass removal and the elimination of woody plants along the mire's perimeter. Additionally, measures to boost the mire's water supply should be implemented, such as constructing supply channels and elevating the groundwater level through the installation of a barrier in a nearby stream.

At the transition mires of Đon močvar and Ljeskovačke bare, it is essential to extend the mowing efforts beyond the test plots to cover as much of the mire as possible and to clear away most of the woody vegetation from its centre. However, since woody vegetation provides an essential habitat for some tyrphophilous and endangered invertebrates, it should be preserved along the mire edges and in several patches within the mire to serve as stepping stones (Brigić et al., 2017). For the Trstenik transition mire, it is important both to eliminate drainage channels that lead to water loss and to manage the biomass of the invasive grass *Molinia caerulea*. In the case of the three small, nearly depleted transition mires (Vukmanić, Lepenica, and Banski Moravci), comprehensive revitalization efforts are required. This primarily involves strategically removing trees and shrubs that create shade, thereby hindering the persistence of this heliophilous habitat.

5. Conclusions

This study is the first to quantify peatland condition in the Western Balkans using predefined criteria, and it reveals that all the

Croatian peatlands studied are in an unfavourable habitat condition. In fact, almost two-thirds of the investigated peatlands have a highly unfavourable conservation status, with more than 90 % of them being subject to advanced encroachment by expansive plant species. Our results demonstrate that transition mires in Croatia face a higher risk of habitat degradation and loss than alkaline fens, reinforcing concerns raised by previous studies (Alegro and Topić, 2017; Topić and Stančić, 2006). Alarmingly, all of the studied transition mires exhibit a highly unfavourable conservation status (with the exception of Sunderac, where alkaline fen vegetation predominates), as opposed to roughly a third of the investigated alkaline fens assigned this status. The prevalence of an alkaline, limestone substrate in the country and the more recent origin of alkaline fens enable their persistence in waterlogged, carbonate-rich areas (Topić and Stančić, 2006). Croatian transition mires, by contrast, are fragmented remnants of once more widespread habitats, now facing largely unfavourable climatic conditions and human-mediated degradation (Topić and Stančić, 2006). The rapid decrease of most mire areas in recent years, compounded by the local disappearance of associated plant species, indicates that targeted, site-specific interventions are urgently needed to ensure their continued persistence in the country.

CRediT authorship contribution statement

Andreja Brigić: Writing – review & editing, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. Jelena Bujan: Writing – review & editing, Investigation, Data curation. Antun Alegro: Writing – review & editing, Validation, Supervision, Project administration, Investigation, Funding acquisition, Data curation. Vedran Segota: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation. Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation.

Declaration of Competing Interest

We have no competing interests to declare.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2025.e03921.

Data Availability

Data will be made available on request.

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