



Saproxylic beetle assemblages in floodplain forests of Kopački rit Nature Park (Croatia): A baseline for Natura 2000 monitoring

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Abstract. Saproxylic beetles are a key component of forest biodiversity and important indicators of forest naturalness, dead-wood continuity and habitat quality. Floodplain forests with old oak stands are among the most species-rich forest ecosystems in Europe, yet data on saproxylic beetle assemblages from such habitats remain scarce in south-eastern Europe. In this study, saproxylic beetles were investigated in three floodplain forest communities within Kopački rit Nature Park (eastern Croatia) using flight-intercept, pitfall and aerial attractant traps during the 2014 vegetation season. A total of 64 saproxylic beetle species from 14 families were recorded. Species richness and abundance were highest in oak-hornbeam forests, intermediate in poplar forests and lowest in willow-dominated stands, which nevertheless supported structurally distinct assemblages. Diversity indices and ordination analyses revealed a strong gradient in community structure from oak-dominated to willow-dominated floodplain forests. Flight-intercept traps were the most efficient sampling method, whereas other trap types provided complementary information on habitat-specific taxa. Several species listed on the European Red List of Saproxylic Beetles were recorded, including the Natura 2000 species *Lucanus cervus* and *Cucujus cinnaberinus*. Of particular importance was the detection of *Rhysodes sulcatus*, which triggered targeted faunistic surveys that confirmed its presence at additional Croatian localities and led to its formal inclusion in the Croatian Natura 2000 species list. Although the data were collected in 2014, they provide a valuable baseline for assessing saproxylic beetle diversity in natural floodplain forests and for the development of national Natura 2000 monitoring programmes. The results highlight the exceptional conservation value of Kopački rit as one of the best-preserved floodplain forest systems in the Continental biogeographical region.

INTRODUCTION

Saproxylic beetles are organisms that depend, during at least part of their life cycle, on dead or decaying wood, wood-inhabiting fungi or other organisms associated with wood decomposition. Through their role in the breakdown of woody biomass and nutrient cycling, they represent a key functional component of forest ecosystems and contribute substantially to overall forest biodiversity (Alexander, 2008). The diversity and structure of saproxylic beetle assemblages are closely linked to forest continuity, dead-wood availability, presence of veteran trees, and habitat complexity, as shown in European saproxylic beetle studies (Bouget et al., 2008; Bergman et al., 2012; Ulyshen et al., 2018).

Across Europe, saproxylic beetles account for a disproportionately high share of threatened forest invertebrates. Long-term habitat loss, intensive forest management, removal of old and dead trees and reduced dead-wood availability have caused severe population declines in many saproxylic species, including numerous specialists with

narrow ecological requirements (Nieto & Alexander, 2010; Cáliz et al., 2018; Seibold et al., 2019). Floodplain forests are among the most species-rich but also the most vulnerable habitats for saproxylic organisms, as they combine high structural heterogeneity with strong hydrological dynamics and increasing anthropogenic pressures (Lachat et al., 2012; Litavský et al., 2021). Consequently, these ecosystems play a crucial role in the conservation of saproxylic biodiversity, particularly within protected areas and Natura 2000 sites.

Reliable assessment of saproxylic beetle diversity strongly depends on the sampling methods applied. Different trapping techniques target different ecological guilds, life-history traits, and activity patterns, and no single method can provide a complete representation of saproxylic assemblages (Ranius & Jansson, 2002; Martikainen & Kaila, 2004; Bouget et al., 2008). Comparative evaluations of sampling efficiency and selectivity are therefore essential, especially in structurally complex forest ecosystems, where methodological choices can substantially influence

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estimates of species richness, assemblage composition, and conservation value – as supported by multiple multi-method studies of saproxylic beetle diversity (Hyvärinen et al., 2006).

In Croatia, research on saproxylic beetles has increased during the last two decades, but remains spatially fragmented and methodologically heterogeneous. Previous studies have documented saproxylic assemblages in floodplain forests, urban parks and protected areas, consistently highlighting the importance of old trees and dead wood for threatened and Natura 2000 species (Dražina & Temunović, 2011; Krčmar, 2014; Šag et al., 2016; Turić et al., 2019; Đurić, 2020; Černi, 2021). Investigations in the Kopački rit Nature Park have confirmed the presence of several red-listed and conservation-relevant saproxylic beetles, including *Lucanus cervus* (Linnaeus, 1758) and *Cucujus cinnaberinus* (Scopoli, 1763), emphasising the exceptional biodiversity value of this floodplain ecosystem. However, a systematic comparison of sampling methods across different floodplain forest community types within this Natura 2000 site has so far been lacking. These faunistic and ecological studies also laid the foundation for the development of a national monitoring framework for Natura 2000 saproxylic beetles in Croatia, initiated with the monitoring of *Lucanus cervus* and later expanded to other target species (Katušić et al., 2017).

The aim of this study was therefore to compare the efficiency and selectivity of three commonly used sampling methods for saproxylic beetles – window flight-intercept traps, pitfall traps and aerial attractant traps – across three floodplain forest communities in Kopački rit Nature Park (eastern Croatia). Special emphasis was placed on threatened and Natura 2000 species, with the objective of providing both methodological and ecological insights into saproxylic beetle assemblages along a floodplain forest gradient in the Continental biogeographical region. Despite their recognised conservation importance, floodplain saproxylic beetle assemblages in south-eastern Europe remain poorly quantified using standardised multi-method designs. In Croatia in particular, no previous study has evaluated how different trapping methods perform across floodplain forest types within a Natura 2000 site. By combining a multi-method sampling design with community-level diversity metrics across a natural floodplain forest gradient, this study addresses both methodological bias and habitat-driven structuring of saproxylic beetle assemblages in one of the last near-natural floodplain systems of the Pannonian Basin.

MATERIAL AND METHODS

Study area

The study was conducted in the Kopački rit Nature Park, located in northeastern Croatia, one of the largest and best-preserved floodplain ecosystems in Europe. The area is shaped by seasonal flooding of the Danube River and, to a lesser extent, the Drava River, resulting in pronounced hydrological dynamics and high habitat heterogeneity (Bonacci et al., 2002). Owing to its ecological importance, Kopački rit is protected as a Nature Park, with

the most valuable core area designated as a Special Zoological Reserve, and is listed as a Ramsar site (No. 3HR002).

Three study sites representing different floodplain forest communities were selected (Fig. 1). The first site (A) comprised an oak-hornbeam forest (*Carpino betuli-Quercetum roboris*), representing a terrestrial habitat largely outside the regular flooding pulse. The second site (B) was characterised by white and black poplar stands (*Populetum nigro-albae*), where flooding occurs for shorter periods. The third site (C) consisted of an open forest community of white and fragile willow with blackberry (*Salicetum albo-fragilis*), characterised by low canopy cover and pronounced exposure to sunlight and wind. These sites represent a gradient of forest structure, flooding intensity, and microhabitat availability typical of the floodplain forest mosaic in Kopački rit.

Sampling methods

Saproxylic beetles were sampled using four trapping methods commonly applied in studies of forest-dwelling Coleoptera: (1) cross-vanes window flight-intercept traps (CWFT), (2) single-plane window flight-intercept traps (SWFT), (3) pitfall traps (PFT), and (4) aerial traps with attractant (AT).

Window flight-intercept traps were used in two designs following Bouget et al. (2008). Cross-vanes window flight-intercept traps consisted of two transparent plexiglass panels (490 × 170 mm) mounted crosswise and fixed above a collecting container (Fig. 2A). Single-plane window flight-intercept traps were constructed from a mosquito net (460 × 400 mm) stretched vertically above a collecting container (Fig. 2B). Both trap types were suspended at approximately 1.5 m above ground level and fixed to a wooden support near standing trees. The collecting containers were filled with a preservative solution consisting of ethanol diluted with water (1 : 1) and a small amount of detergent to reduce surface tension.

Pitfall traps were constructed from 2 L plastic bottles cut in half and equipped with a roof made of yellow plastic plates to reduce rain and debris input (Fig. 2C). Traps were buried flush with the soil surface near tree trunks, stumps, or tree cavities. A preservative mixture of water, red wine, vinegar, and ethanol in a ratio of 1 : 1 : 1 : 1 was used, following Durbešić et al. (1994) and Rukavina et al. (2010).

Aerial traps with attractant were modified after Horwitz (2011). These traps consisted of 2 L plastic bottles with lateral openings, suspended from surrounding trees at a height of approximately 1.5 m (Fig. 2D). Red wine was used as an attractant.

Sampling design and specimen processing

Sampling was conducted from April to October 2014, covering the main activity period of adult saproxylic beetles in temperate Europe (Buse et al., 2008). At each study site, six sampling locations were established along a linear transect. At each location, two traps were deployed, resulting in a total of 12 traps per site and 36 traps across all study sites. Traps were checked regularly throughout the sampling period.

Collected specimens were preserved in 70% ethanol, subsequently dried, pinned, and identified to species level. Identification was based on standard taxonomic keys and monographs (Mikšić, 1965, 1970; Freude et al., 1969, 1971; Mikšić et al., 1971, 1973, 1985; Bell & Bell, 1978, 1979, 2002, 2009; Baraud, 1992; Bense, 1995; Sláma, 2006; Ballerio et al., 2010; Bonacci et al., 2012; Novák, 2014). All specimens were labelled and deposited in the entomological collection of the Department of Biology, Josip Juraj Strossmayer University of Osijek.

For the purpose of this study, saproxylic beetles were defined in a broad ecological sense (saproxylic *sensu lato*), including species that depend on dead or decaying wood, wood-inhabiting

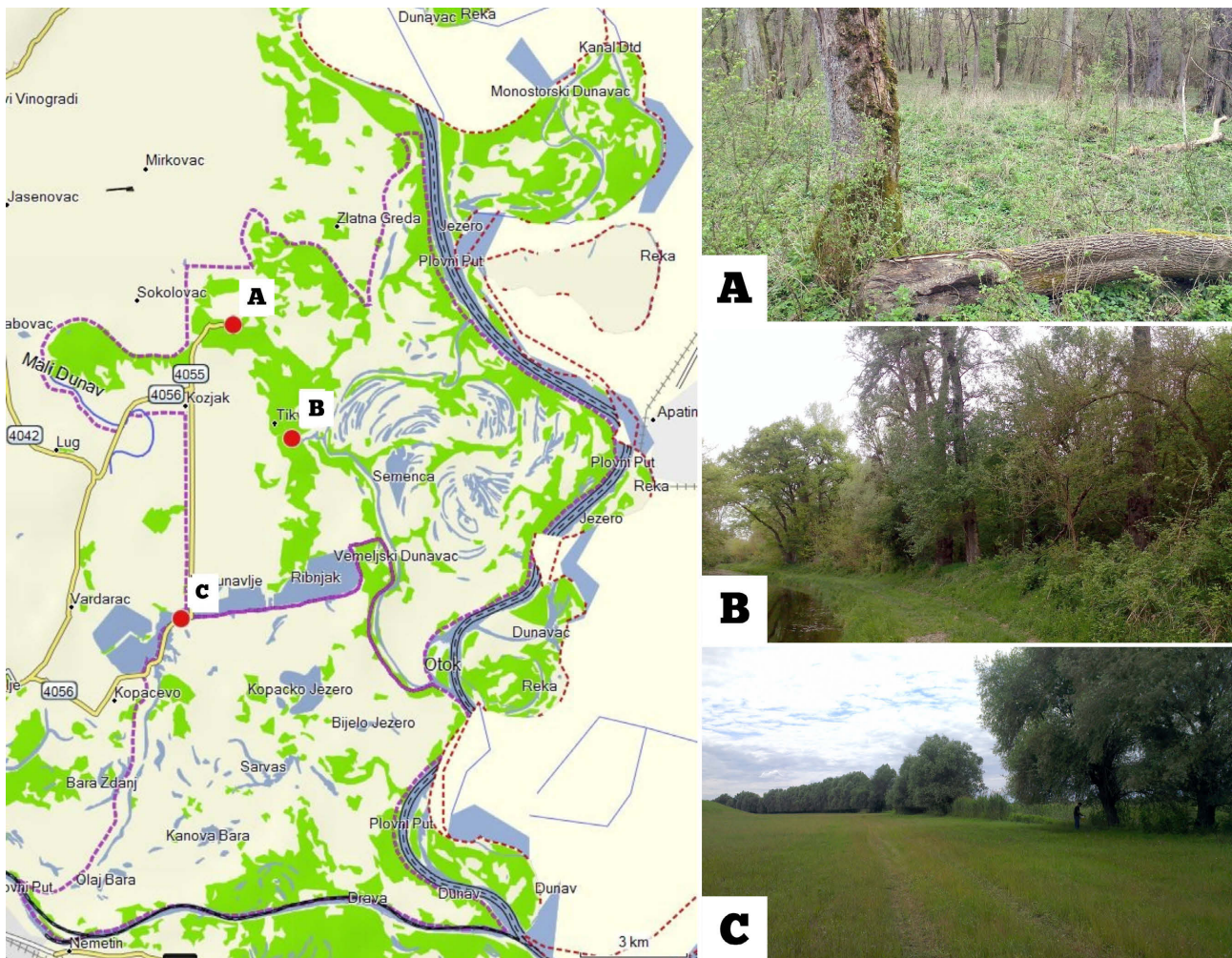


Fig. 1. Map of researched area with marked study sites (A, B, and C). (Photo: M. Šag, N. Turić.)

fungi, or associated microhabitats during at least part of their life cycle, as well as species regularly occurring in dead-wood-related habitats. Taxonomic and ecological classification of species followed current European literature (e.g. Alexander, 2008; Bouget et al., 2008; Seibold et al., 2015). Strictly non-saproxyllic species were excluded where appropriate; however, some taxa with broader ecological niches (e.g. certain Scarabaeidae and Geotrupidae) were retained when regularly associated with forest microhabitats such as tree bases, cavities or decomposing organic matter. The applied trapping methods primarily target actively dispersing adult beetles and may underrepresent taxa associated with concealed microhabitats (e.g. under bark, within wood, or fungi), which should be considered when interpreting assemblage composition.

Data analysis

Saproxyllic beetle assemblages were analysed in terms of species richness, abundance, dominance (Bick, 1989), and constancy (Tischler, 1949). Faunal similarity among study sites was assessed using the Sørensen similarity index (Krebs, 1999). Differences in assemblage composition among forest communities were analysed using non-metric Multidimensional Scaling (nMDS) based on abundance data (Clarke & Warwick, 2001; Legendre & Legendre, 2012).

Species accumulation curves were constructed to evaluate sampling completeness and to estimate total species richness. Observed species richness (Sobs) was compared with commonly

used non-parametric estimators, including Chao1, Chao2, Jackknife1, Jackknife2, and Bootstrap, which have been shown to perform well in biodiversity surveys of invertebrates (Krebs, 1998; Walther & Martin, 2001).

RESULTS

During the sampling period from April to October 2014, a total of 10,347 Coleoptera specimens were collected using four trapping methods. Among these, 1,088 individuals were identified as saproxyllic beetles, representing 64 species belonging to 14 families (Table S1). In addition to obligate saproxyllic species, a few taxa with broader ecological preferences were recorded. The most specimen-rich families were Cerambycidae, Cetoniidae and Lucanidae, accounting together for more than 80.23% of all recorded Coleoptera specimens.

Of the recorded species, 20 are listed on the European Red List of Saproxyllic Beetles. Fourteen species were categorised as Least Concern (LC), three as Near Threatened (NT), and three as Data Deficient (DD). Two recorded species (*L. cervus* and *C. cinnaberinus*) are listed under the Natura 2000 network.

Saproxyllic beetle assemblages differed markedly among the three studied forest communities. The highest number

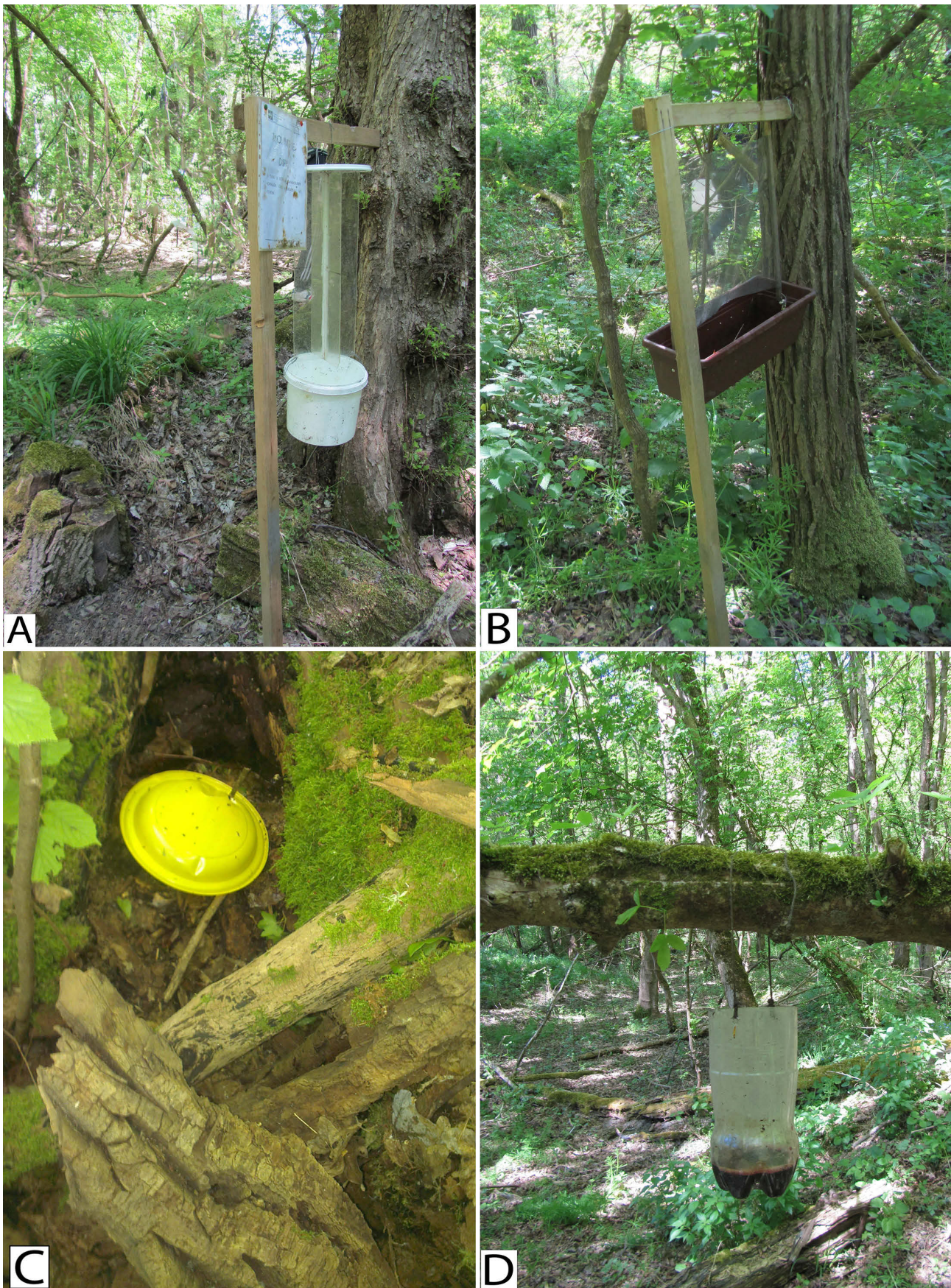


Fig. 2. Methods for sampling saproxylic beetles. A – cross-vanes window flight trap (CWFT); B – single-plane window flight trap (SWFT); C – pitfall trap (PFT); D – air trap with attractant (AT). Pitfall trap placed at the base of a tree; the trap is buried flush with the soil surface and not directly visible. The yellow plate indicates the trap location. (Photo: M. Šag, N. Turić.)

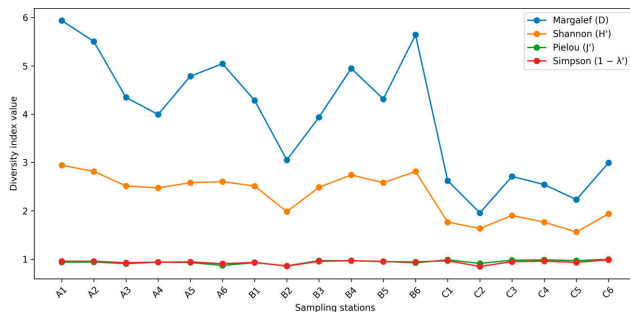


Fig. 3. Diversity indices of saproxylic beetle assemblages across sampling stations (A1–C6) in Kopački rit Nature Park. Shown are Margalef’s species richness index (D), Shannon-Weaver diversity index (H’), Pielou’s evenness index (J’) and Simpson’s diversity index (1 – λ’). Stations A1–A6 represent oak-hornbeam forest, B1–B6 poplar forest and C1–C6 willow-dominated forest.

of individuals was recorded at study site A (oak-hornbeam forest), where 620 individuals were sampled, accounting for 56.99% of all saproxylic beetles collected. Study site B (white and black poplar forest) yielded 386 individuals (35.48%), while study site C (white willow forest with blackberry) had the lowest abundance, with 82 individuals (7.54%) of the total catch. Species richness followed the same pattern, being highest at sites A and B, and lowest at site C.

Based on abundance data, standard diversity indices were calculated to characterise differences in community structure among sampling stations (Fig. 3). Margalef’s species richness index (D), Pielou’s evenness index (J’), Shannon-Weaver diversity index (H’) and Simpson’s diversity index (1 – λ’) all showed consistent trends across the forest types. Shannon-Weaver diversity (H’) ranged from 1.561 at station C5 to a maximum of 2.943 at station A1, indicating substantially higher diversity in oak-hornbeam forests compared to willow-dominated stands. The lowest Simpson diversity value (1 – λ’) was recorded at C2 (0.848), whereas the highest value occurred at C6 (0.9877), reflecting very high evenness and low dominance at this site. Pielou’s evenness (J’) was lowest at B2 (0.8614) and highest at C6 (0.9956), showing that although willow stands sup-

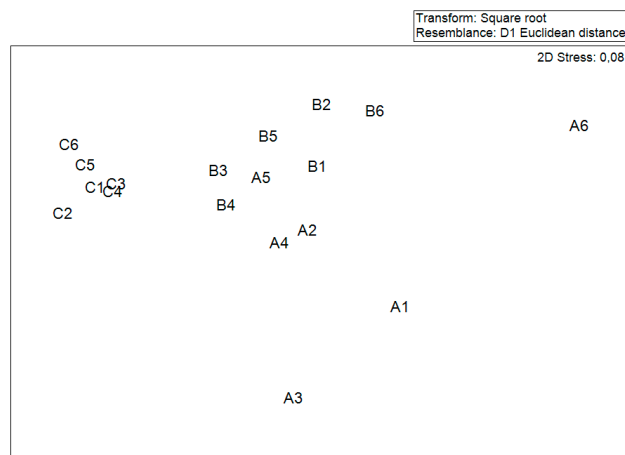


Fig. 4. Non-metric multidimensional scaling (nMDS) ordination of saproxylic beetle assemblages based on species abundance data. Each point represents a sampling station (A1–C6).

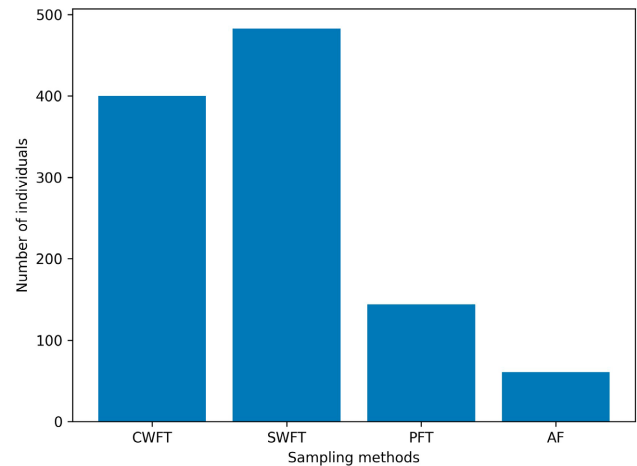


Fig. 5. Efficiency of three trapping methods used for sampling saproxylic beetles in Kopački rit Nature Park. Shown are the total numbers of individuals captured by single-plane window flight-intercept traps (SWFT), cross-vanes window flight-intercept traps (CWFT), pitfall traps (PFT) and aerial attractant traps (AF).

ported fewer species, their assemblages were highly even in structure. Margalef’s index (D) varied from 1.958 at C2 to 5.938 at A1, confirming a strong gradient in species richness from willow stands to oak-hornbeam forests.

Faunal similarity among forest communities, expressed by the Sørensen similarity index, was highest between sites A and B (67.44%), while similarity between A and C was 32.78% (10 shared species). The lowest similarity was observed between B and C (27.11%), indicating pronounced differences in species composition between the poplar and willow floodplain forests.

Non-metric multidimensional scaling (nMDS) based on species abundance data showed a clear separation of saproxylic beetle assemblages among forest community types (Fig. 4). Assemblages from willow-dominated stands (site C) formed a distinct cluster, reflecting both lower abundance and a different species composition. In contrast, assemblages from oak-hornbeam (A) and poplar forests (B) showed considerable overlap, indicating higher faunal similarity, consistent with Sørensen similarity values. Interpretation of ordination patterns followed standard community ecology principles (McCune & Grace, 2002). This indicates that forest type explains a substantial proportion of community variation beyond differences in local species richness alone.

Adult activity of saproxylic beetles was recorded throughout the sampling period, showing pronounced seasonal variation. The highest total abundance occurred between April and August, with a clear peak in May, when 359 individuals were collected. Beetle activity gradually declined during the summer months and was lowest towards the end of the sampling season.

At the family level, Cerambycidae showed a distinct activity peak in May, while Cetoniidae also exhibited highest activity in late spring. Lucanidae displayed a bimodal pattern, with a major peak in June and a second, lower peak in August.

Sampling efficiency differed markedly among the four trapping methods. Window flight-intercept traps were the most effective, yielding the highest numbers of both individuals and species. The single-plane window flight-intercept trap (SWFT) captured the largest number of saproxylic beetles (483 individuals), followed by the cross-panes window flight-intercept trap (CWFT) (Fig. 5).

Pitfall traps (PFT) collected 286 individuals, showing lower efficiency compared to flight-intercept traps, while aerial traps with attractant (AF) captured the smallest proportion of saproxylic beetles, accounting for 11.21% of the total catch. The two flight-intercept trap designs (SWFT and CWFT) showed consistently higher capture rates than pitfall and aerial attractant traps, indicating their higher efficiency for sampling saproxylic beetle assemblages in floodplain forests. Sampling completeness was evaluated using species accumulation curves and non-parametric richness estimators (Fig. S1). Both approaches indicated that the sampling effort did not fully capture the total saproxylic beetle diversity in the study area. In particular, Chao1 and Jackknife2 estimators suggested a potential richness of approximately 90 species, compared to the 64 species recorded in this survey.

DISCUSSION

Distinct differences in saproxylic beetle assemblages were observed among floodplain forest communities of the Kopački rit Nature Park, reflecting both habitat structure and sampling method effects. Pronounced differences were detected in the efficiency and selectivity of the applied sampling methods, with flight-intercept traps (FIT) yielding the highest species richness and abundance of saproxylic beetles. This pattern is consistent with previous studies from European deciduous and floodplain forests, where FIT have repeatedly been shown to capture a broad spectrum of saproxylic taxa (Ranius & Jansson, 2002; Hyvärinen et al., 2006; Bouget et al., 2008). The high efficiency of FIT reflects their ability to intercept actively dispersing adults associated with standing dead wood, veteran trees and canopy-level microhabitats, including species whose larval development sites are spatially separated from adult activity areas.

It is important to note that the composition of the recorded assemblages partly reflects the methodological approach used in this study. As in other multi-method surveys of saproxylic beetles, taxa associated with concealed or highly specialised microhabitats may be underrepresented, while actively dispersing species are more effectively sampled. Therefore, the presented assemblages should be interpreted as a representative subset of the saproxylic community detectable by standardised trapping methods, rather than a complete inventory of all saproxylic taxa present.

Multi-method comparisons further demonstrate that FIT were particularly effective for forest-dwelling Coleoptera because they intercept adults moving between breeding substrates and feeding or mating sites (Hyvärinen et al., 2006). This is especially relevant for saproxylic beetles, whose larval habitats are often concealed within dead

wood while adults disperse widely within the forest matrix. Recent syntheses emphasise that no single trapping method can capture the full saproxylic community and that combining complementary methods across microhabitats and vertical forest strata is essential for reliable biodiversity assessment (Seibold et al., 2015, 2019).

Comparable methodological patterns have been reported from Central European floodplain forests, where FIT consistently outperformed ground-based methods in both abundance and species richness (Schlaghamerský et al., 2008; Lachat et al., 2012). Although pitfall and attractant-based traps were less efficient in terms of total catch, they contributed complementary information by targeting taxa associated with soil surface activity, tree bases, cavities and bait-responsive guilds. The clear separation between FIT-based and ground-based traps in both abundance and species composition indicates that sampling method strongly influences the perceived structure of saproxylic beetle assemblages, particularly in heterogeneous floodplain forests characterised by pronounced vertical stratification and microhabitat diversity. These results support the use of combined sampling approaches in long-term monitoring schemes.

Saproxylic beetle assemblages differed markedly among the studied forest community types. Oak-hornbeam forests supported the highest abundance and species richness, followed by poplar-dominated forests, while willow-dominated stands hosted distinct but less abundant assemblages. Such patterns are well documented across Europe and reflect the close relationship between forest structure, dead-wood availability and saproxylic beetle diversity (Ranius & Jansson, 2000; Buse et al., 2008; Vodka et al., 2009; Gossner et al., 2013).

Oak-dominated floodplain forests with long habitat continuity and a high proportion of old and veteran trees are repeatedly identified as hotspots of saproxylic biodiversity, as these features provide a wide range of microhabitats required by specialist species (Seibold et al., 2015). The patterns observed in Kopački rit closely mirror gradients described from floodplain forests along the Danube and Mura rivers, where saproxylic assemblages respond to both forest continuity and hydrological dynamics (Vrezec, 2008; Vrezec et al., 2012).

Large-diameter dead wood, tree cavities and a full spectrum of decay stages create a diverse set of ecological niches for saproxylic beetles. In contrast, the lower abundance and distinct assemblage composition recorded in willow forests likely reflect reduced dead-wood continuity, higher disturbance frequency and greater exposure to microclimatic extremes. Similar patterns have been reported from other dynamic softwood floodplain forests in Central Europe (Lachat et al., 2012; Litavský et al., 2021). Ordination analyses and diversity profiles in the present study further indicate that willow-dominated stands are not simply species-poor variants of oak and poplar forests, but host structurally distinct saproxylic assemblages shaped by hydrological dynamics and microclimatic conditions.

Several species listed on the European Red List of Saproxyllic Beetles were recorded, confirming the high conservation value of the floodplain forests of Kopački rit. Their presence indicates the availability of suitable microhabitats associated with old trees, decaying wood, and long-term habitat continuity. In addition to strictly saproxyllic species, a small number of taxa traditionally classified as non-saproxyllic, such as dung-associated Geotrupidae (e.g. *Geotrupes spiniger*, *Bolboceras armiger*) or root-feeding Scarabaeidae (e.g. *Anomala dubia*), were also recorded. Their presence is most likely related to their use of forest microhabitats closely associated with saproxyllic processes, including tree bases, decomposing organic matter, and cavities where organic material accumulates. Similarly, some representatives of Aphodiinae, although primarily coprophagous, are known to occur in forest environments where they may exploit decomposing organic substrates associated with dead-wood microhabitats. These taxa were therefore retained in the dataset as part of a broader saproxyllic assemblage *sensu lato*, following approaches commonly applied in European studies, where ecological associations with dead-wood environments are considered alongside strict trophic classification (Seibold et al., 2015; Ulyshen et al., 2018).

Particularly noteworthy is the record of *Rhysodes sulcatus* (Fabricius, 1787), a species previously considered of uncertain status in Croatia. Its detection in Kopački rit led to its designation as a “scientific reserve” species within the EU Natura 2000 biogeographical process and prompted targeted surveys that subsequently confirmed its presence at additional Croatian localities, ultimately resulting in its formal inclusion in the Croatian Natura 2000 species list. This record thus represents an important national baseline, providing clear evidence of suitable habitat conditions and supporting the need for targeted verification and conservation measures. The subsequent confirmation of the species at other sites indicates that the Kopački rit population was not an isolated occurrence, but part of a broader, previously under-detected distribution. In this context, the occurrence of *R. sulcatus* in a naturally structured floodplain forest highlights the importance of hydrologically dynamic systems with low-intensity management for the persistence of highly specialised saproxyllic beetles.

Prior to the present study, information on saproxyllic beetles from Kopački rit Nature Park was largely limited to faunistic and checklist-based contributions. The most comprehensive overview of insect fauna from the area was provided by Krčmar (2014), who compiled available literature data and records for Kopački rit, including several saproxyllic beetle species. However, this contribution did not involve standardised field sampling or community-level analyses and therefore did not allow assessment of assemblage structure, habitat-related patterns or sampling-method performance.

In Croatia, research on saproxyllic beetles has predominantly focused on threatened and Natura 2000 target species, most notably *L. cervus*, through the development of monitoring frameworks and species-specific surveys

(Katušić et al., 2017). Additional studies have addressed the distribution, habitat suitability and conservation status of selected rare saproxyllic species, such as *C. cinnaberinus* and *Bolbelasmus unicornis* (Schrank, 1789), at the national scale (Koren, 2017; Rukavina et al., 2018). However, comparable data on saproxyllic beetle assemblages across different floodplain forest types are still scarce, particularly in large and near-natural floodplain systems. For this reason, the results obtained in Kopački rit Nature Park are best interpreted in comparison with studies from neighbouring parts of the Pannonian Basin and Central Europe, where saproxyllic beetle assemblages in floodplain forests have been studied.

Comparable conclusions have been drawn from floodplain forests in neighbouring countries within the Pannonian Basin and Central Europe, including Slovenia, where phenology and monitoring of Natura 2000 saproxyllic beetles in floodplain and lowland forests have been extensively studied (Vrezec, 2008; Vrezec et al., 2012). Floodplain forests along the Mura and Danube river systems have been identified as areas of high conservation importance for saproxyllic beetles, including Habitats Directive species such as *C. cinnaberinus*, where forest continuity and the retention of old trees play a crucial role (Schlaghamerský et al., 2008; Vrezec, 2008; Vrezec et al., 2012). These regional studies consistently show that saproxyllic richness and the occurrence of habitat specialists increase with forest age, continuity, and dead-wood volume, particularly in oak-dominated floodplain systems (Buse et al., 2008; Gossner et al., 2013). Similar patterns have also been reported from Central European floodplain and lowland forests, where beetle community structure closely follows hydrological and habitat gradients (Litavský et al., 2021). Within this regional framework, Kopački rit stands out as one of the best-preserved natural floodplain systems, combining extensive old oak forests, natural hydrological dynamics, and long-term protection.

Although the field data presented in this study were collected in 2014, they should not be interpreted as outdated. Instead, they represent an essential ecological baseline that predates and directly supports subsequent developments in saproxyllic beetle research and conservation in Croatia. Since 2014, there has been a clear transition from isolated faunistic studies towards structured, policy-oriented monitoring frameworks. This transition builds directly on earlier initiatives for saproxyllic beetle monitoring in Croatia, particularly the stag beetle-based framework developed by Katušić et al. (2017), which provided the first standardised national approach to Natura 2000 saproxyllic beetles.

This process culminated in the preparation of a series of national monitoring programmes for Natura 2000 beetles within the Operational Programme Competitiveness and Cohesion (OPKK) in 2023, covering key species such as *Rhysodes sulcatus*, *Bolbelasmus unicornis*, *Limoniscus violaceus* and *Cucujus cinnaberinus* (Lauš et al., 2023a–d), *Lucanus cervus*, *Cerambyx cerdo*, *Rosalia alpina*, *Mori-mus funereus* and *Osmoderma eremita* (Šerić Jelaska &

Horvatić, 2023a–d), and *Graphoderus bilineatus* (Turić & Vignjević, 2023).

In the context of widespread insect declines reported across Central Europe, particularly in intensively managed lowland landscapes (Sánchez-Bayo & Wyckhuys, 2019; Seibold et al., 2019), the saproxylic beetle assemblages of Kopački rit represent an increasingly rare reference for near-natural floodplain forest biodiversity. The Kopački rit Nature Park thus represents not only a local hotspot of saproxylic diversity, but also a reference system of national importance for understanding, monitoring and conserving saproxylic beetles in the Continental biogeographical region with strong Pannonian biotic elements. Given the rapid loss of old-growth elements and natural floodplain dynamics across Europe, these assemblages provide a crucial benchmark for assessing the conservation status and restoration potential of lowland floodplain forests.

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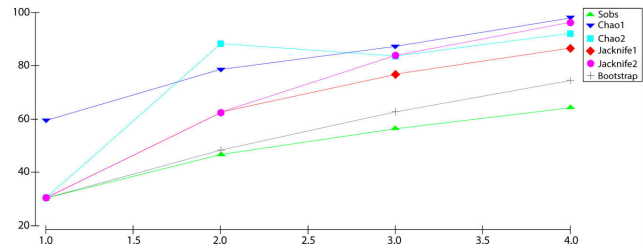


Fig. S1. Accumulation curves comparing current species richness (Sobs) with other estimators (Chao1, Chao2, Jackknife1, Jackknife2 and Bootstrap).

Table S1. A list of identified species of saproxylic beetles in the Kopački rit Nature Park with IUCN Red List Categories (Europe) followed Nieto & Alexander (2010). Number of caught individuals considering sampling method per study site are also included. Abbreviations: DD – Data Deficient, LC – Least Concern, NT – Near Threatened, CWFT – cross-vanes window flight trap, SWFT – single-plane window flight trap, PFT – pitfall trap, AT – air trap with attractant, A – oak–hornbeam forest, B – white and black poplar stands, C – white and fragile willow with blackberry.

Scientific name	Family/Subfamily	Endangered status	Number of individuals									Σ				
			CWFT			SWFT			PFT				AT			
			A	B	C	A	B	C	A	B	C		A	B	C	
<i>Acrossus depressus</i>	Aphodiinae						1									1
<i>Melinopterus prodomus</i>	Aphodiinae					4	6					2	3			15
<i>Phalacrothous biguttatus</i>	Aphodiinae		1			2	10		1		3	6				23
<i>Volinus sticticus</i>	Aphodiinae			4		6	7				10	6				33
<i>Odonteus armiger</i>	Bolboceratidae		2													2
<i>Anaglyptus mysticus</i>	Cerambycinae	LC		1												1
<i>Aromia moschata</i>	Cerambycinae	LC		1	1			19						3		24
<i>Callidium violaceum</i>	Cerambycinae	LC					1									1
<i>Cerambyx scopoli</i>	Cerambycinae	LC	2													2
<i>Clytus arietis</i>	Cerambycinae	LC	1			1	3									5
<i>Phymatodes testaceus</i>	Cerambycinae	LC	1				1			1						3
<i>Cetonia aurata</i>	Cetoniinae		30	7	3	29	12	7	1		1	1	4			95
<i>Gnorimus variabilis</i>	Cetoniinae	NT				2	1									3
<i>Protaetia affinis</i>	Cetoniinae	DD	2								1					3
<i>Protaetia cuprea</i>	Cetoniinae		5	1	2	10	2	1	1				1			23
<i>Protaetia cuprea</i> subsp. <i>metallica</i>	Cetoniinae		4			2			1							7
<i>Protaetia lugubris</i>	Cetoniinae	LC		1	2	1	7						1			12
<i>Tropinota hirta</i>	Cetoniinae						1									1
<i>Valgus hemipterus</i>	Cetoniinae	LC	95	25	4	11	5		1		2					143
<i>Clerus mutillarius</i>	Clerinae			1												1
<i>Thanasimus formicarius</i>	Clerinae		2			1										3
<i>Cucujus cinnaberinus</i>	Cucujidae	NT	2	1												4
<i>Mycetina cruciata</i>	Endomychidae					8	2				1					11
<i>Dacne bipustulata</i>	Erotylidae	LC	2		1		1	1				1	1			7
<i>Triplax aenea</i>	Erotylidae	LC	1	1			1									3
<i>Triplax russica</i>	Erotylidae	LC	6			1										7
<i>Tritoma bipustulata</i>	Erotylidae	LC	1													1
<i>Geotrupes spiniger</i>	Geotrupidae							1								1
<i>Agapanthia</i> sp.	Lamiinae			1												1
<i>Agapanthia violacea</i>	Lamiinae			1												1
<i>Dorcadion scopoli</i>	Lamiinae				1											1
<i>Lamia textor</i>	Lamiinae										1					1
<i>Mesosa nebulosa</i>	Lamiinae					1										1
<i>Phytoecia cylindrica</i>	Lamiinae					2										2
<i>Pogonocherus hispidus</i>	Lamiinae		1				2		2							5
<i>Tetrops praeustus</i>	Lamiinae			1			1	4			1					7
<i>Alosterna tabacicolor</i>	Lepturinae		48	3			1		1							53
<i>Anoplodera sexguttata</i>	Lepturinae					1										1
<i>Dinoptera collaris</i>	Lepturinae		2										1			3
<i>Grammoptera ruficornis</i>	Lepturinae											2				2
<i>Leptura aurulenta</i>	Lepturinae		1			1										2
<i>Pseudovadonia livida</i>	Lepturinae				1											1
<i>Rhagium sycophanta</i>	Lepturinae		2	1												3
<i>Stenocorus meridianus</i>	Lepturinae			3		1										4
<i>Stenurella nigra</i>	Lepturinae			1												1
<i>Dorcus parallelipipedus</i>	Lucanidae	LC	30	53		179	68	2	34	75		8				449
<i>Lucanus cervus</i>	Lucanidae	NT	3	2		2			3	1						11
<i>Aegosoma scabricorne</i>	Prioninae	LC						1								1
<i>Pyrochroa coccinea</i>	Pyrochroidae		1							2						3
<i>Pyrochroa serraticornis</i>	Pyrochroidae		4	3		7	3									17
<i>Omoglymmius germari</i>	Rhysodinae	DD	1	1			7									9
<i>Rhysodes sulcatus</i>	Rhysodinae	DD	1													1
<i>Anomala dubia</i>	Rutelinae			1												1
<i>Omalopecta</i> sp.	Sericinae							1								1
<i>Serica brunnea</i>	Sericinae			4		1	2			1						8
<i>Bolitophagus interruptus</i>	Tenebrionidae									4			1			5
<i>Diaperis boleti</i>	Tenebrionidae		6		1	1	3			1						12
<i>Nalassus dermestoides</i>	Tenebrionidae		2		1	3		16				1				23
<i>Prionychus ater</i>	Tenebrionidae		1													1
<i>Pseudocistela ceramboides</i>	Tenebrionidae		1													1
<i>Stenomax aeneus</i>	Tenebrionidae		5			7										12
<i>Tenebrio</i> sp.	Tenebrionidae									4						4
<i>Uloma culinaris</i>	Tenebrionidae									4						4
<i>Tillus elongatus</i>	Tillinae			1												1