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CARABID BEETLE FAUNA (COLEOPTERA, CARABIDAE) OF PERIODICALLY FLOODED HABITATS IN THE LONJSKO POLJE NATURE PARK (CROATIA)

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Floods are one of the most important natural disturbance events in the terrestrial ecosystems of the European lowlands. River regulation has significantly altered the river banks and affected river dynamics worldwide. Lonjsko polje, a retention area along the Sava River, plays a crucial role in flood control. However, beyond its flood management function, it holds significant ecological value on regional and global scale. In this study, we aimed to assess the carabid beetle fauna of the flooded habitats of Lonjsko polje Nature Park, the forest remnant and the pasture, using pitfall traps. Altogether 3,369 carabid beetle specimens belonging to 64 species were sampled. Carabid beetle activity density was six times higher in the forest remnant than in the pasture. The assemblages of both habitat types were composed primarily of macropterous species with good dispersal abilities, which can easily move to other areas in response to flooding. In addition, open habitat and hygrophilous species prevailed in terms of abundance in both habitat types. The mosaicity of habitats, combined with traditional land management practices, pig foraging and livestock grazing, support carabid beetle fauna of high conservation value, including rare and threatened species such as *Carabus clatratus auraniensis* and *Blethisa multipunctata*.

Key words: grazing, *Carabus clatratus auraniensis*, seasonal dynamics, temporal dynamics, functional traits, wetlands

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Poplave su jedan od najvažnijih prirodnih poremećaja koji utječu na kopnene ekosustave u europskim nizinama. Regulacija rijeka značajno je promijenila obale rijeka i njihovu fluvijalnu dinamiku širom svijeta. Lonjsko polje, retencijsko područje uz rijeku Savu, ima ključnu ulogu u kontroli poplava. Međutim, osim funkcije kontroliranja poplava, ima značajnu ekološku vrijednost na regionalnoj i globalnoj razini. U ovom istraživanju željeli smo odrediti faunu trčaka poplavljenih staništa Parka prirode Lonjsko polje, šumskog fragmenta i pašnjaka, metodom lovnih posuda. Ukupno je sakupljeno 3369 jedinki trčaka svrstanih u 64 vrste. Brojnost trčaka bila je šest puta veća u šumskom fragmentu negoli na pašnjaku. Zajednice trčaka obaju staništa sastojale su se od makropternih vrsta koje imaju veliku sposobnost rasprostranjenja i lako se mogu kretati u druga područja, prilagođavajući se plavljenju. Osim toga, vrste otvorenih staništa i higrofilne vrste dominiraju brojnošću u oba tipa staništa. Mozaičnost staništa, zajedno s tradicijskim korištenjem zemljišta, poput ispaše svinja i stoke, podržala je faunu trčaka od konzervacijskog značaja, npr. *Carabus clatratus auraniensis* i *Blethisa multipunctata*.

Ključne riječi: ispaša, *Carabus clatratus auraniensis*, sezonska dinamika, vremenska dinamika, funkcionalne značajke, močvare

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INTRODUCTION

Floods are among the most important natural disturbance events in terrestrial ecosystems in floodplains (Joyce & Wade, 1998), occurring periodically and often covering large areas. Such disturbances modify landscapes and induce changes in ecosystems by altering the physical environment, which in turn impacts plant and animal communities prone to frequent changes (Bonn *et al.*, 2002; Ward *et al.*, 1999). In addition, floods are a source of spatio-temporal heterogeneity, by creating habitat mosaics of perennial and temporal waterbodies (Tockner & Stanford, 2002). Such a complex patchwork provides suitable conditions for a wide array of taxa with diverse life history traits, ranging from pioneers and species characteristic of intermediate succession stages, to species with a preference for stable habitats (Jähnig *et al.*, 2009; Poff *et al.*, 1997). In short, floodplains are among the most biodiverse and productive ecosystems globally (Tockner & Stanford, 2002; Ward *et al.*, 1999).

In Europe, natural flow dynamics is strongly degraded, with most large rivers and their floodplains altered by dikes, weirs, stone embankments or severe changes to the riverbed (Petts *et al.*, 1989). Due to intensive land-use and hydro-morphological changes, 90% of the floodplains in Europe are highly modified, putting them among the most endangered habitats (Tockner & Stanford, 2002). All these changes have profound and negative impacts on aquatic and terrestrial communities alike, with many riparian species listed as endangered in floodplains and wetlands (Tockner *et al.*, 2010; Bonn *et al.*, 2002; Walter *et al.*, 1998). As a result, ecological restoration and rehabilitation of rivers and wetlands is ongoing throughout Europe, particularly through the implementation of the Water Framework Directive, which aims to achieve and restore the "good ecological status" of water bodies (WFD, 2000/60/EC; European Commission, 2000).

In contrast to other European rivers, the floodplain of the Sava River in lowland Croatia has been largely preserved as a near-natural habitat, making it of significant ecological and nature conservation value (Schneider-Jacoby, 2005). Therefore, periodically flooded habitats, such as flooded forests, forest remnants and pastures, together with their respective waterbodies, are typical of the area of Lonjsko polje Nature Park. These habitats support numerous threatened plants, invertebrate and vertebrate species that largely depend on specific flooding regimes (e.g. Turić *et al.*, 2021; Radović & Jelaska, 2012; Topić & Vuković, 2010). In addition, these habitats are still used today for mowing and traditional extensive grazing and foraging by native breeds of pigs, cows and horses (Schneider-Jacoby, 2005; Schneider-Jacoby & Ern, 1993), such traditional land-management practices playing a crucial role in maintaining plant and invertebrate diversity (Zahn *et al.*, 2007; Watkinson & Ormerod, 2001; Falke *et al.*, 2000).

Carabid beetles, a diverse group of insects, play an important role in floodplain communities. Their assemblages in floodplains are influenced by a variety of environmental factors, including hydrology, slope, soil properties and vegetation (Jachertz *et al.*, 2019; Šustek, 1994). Carabid beetle species inhabiting riverbanks and floodplains, are adapted to natural disturbances (Bonn, 2000; Thiele, 1977). Being good fliers, they have a high dispersal ability (Bonn, 2000; Zulka, 1994) or they can escape flooding by vertical migration to higher grounds or higher vegetation (Adis & Junk, 2002; Adis *et al.*, 1997). In addition, some species may tolerate short or prolonged submersion both as adults and larvae, while others, e.g. *Bembidion minimum* (Fabricius, 1792) and *Pterostichus madidus* (Fabricius, 1792), are known to successfully use water surface tension, enabling them to avoid drowning (Thiele, 1977).

In recent years, carabid beetles have been studied in the wetland habitats of Lonjsko polje Nature Park, e.g. in forests (Durbešić *et al.*, 2000) and plant stands invaded by *Amorpha fruticosa* (Brigić *et al.*, 2014). Nevertheless, the carabid beetle fauna of this unique area is still insufficiently known, especially with regard to species composition and seasonal dynamics. Accordingly, the main aims of this study are: 1) to present carabid beetle fauna of a small forest remnant and an adjacent pasture exposed to low-density grazing in Lonjsko polje Nature Park; 2) to assess functional trait composition (flight ability, habitat and moisture preference) in the carabid beetle assemblages of the two habitat types; 3) to show the seasonal dynamics of dominant carabid beetle species and 4) to assess the relevance of the studied area for carabid beetle conservation in the Croatian context.

MATERIALS AND METHODS

Study area

This study was performed near Mužilovčica (45°23'55.67'' N, 16°41'43.05'' E) and Kratečko (45°23'52.77'' N, 16°37'57.06'' E) villages, within Lonjsko polje Nature Park (Fig. 1a). With a total area of 50,650 ha, Lonjsko polje NP is one of the largest and best-preserved wetlands in Croatia. It is included in the Ramsar List of Wetlands of International Importance and listed as an Important Bird Area (Anonymous, 2024). The region is characterised by a temperate humid climate with warm summers, with an average annual temperature of 10.5°C and an average annual precipitation of 950 mm (Zaninović *et al.*, 2008; Šegota & Filipčić, 2003).

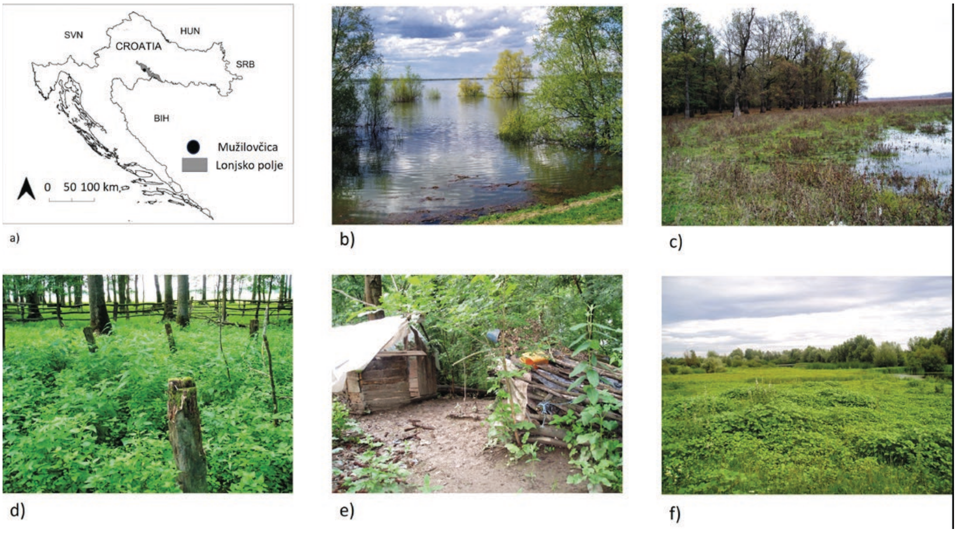

Fig. 1. Studied area in Lonjsko polje Nature Park (Croatia): a) geographical position, b) flooded pasture in May 2002 near Mužilovčica village, c) forest remnant; d) a former pig-pen in the forest remnant, e) an active pig-pen in the forest remnant, f) non-flooded pasture.

Site description

The sampling sites were in two periodically flooded habitat types, differing in the degree of habitat openness – riparian oak-ash forest remnant (16 ha) and adjacent pasture (around 800 ha). Both habitat types are used for traditional grazing, mainly by native breeds of pigs (Turopoljska šara pig), horses (Posavina horse) and cows (Schneider-Jacoby & Ern, 1993). In this area, floods last from a few days to several months and have a particularly strong impact at the beginning of the growing season, when floodwaters can reach up to 2 m in height (Fig. 1b).

The vegetation of the forest remnant belongs to ass. *Fraxino angustifoliae-Ulmetum laevis* Slavnić 1952 (Fig. 1c). It consists predominantly of indigenous species characteristic of periodically flooded habitats, with a prevalence of tree species *Fraxinus angustifolia* Vahl and *Ulmus laevis* Pallas. The species composition has changed over time due to livestock grazing and trampling. Accordingly, many herbaceous ruderal and nitrophilous species, such as *Erigeron annuus* (L.) Desf., *Oxalis fontana* Bunge, *Bidens frondosus* L., *Urtica dioica* L., *Ambrosia artemisiifolia* L., *Aristolochia clematitis* L., *Amorpha fruticosa* L., *Arctium lappa* L. and *A. minus* (Hill) Bernh. were also recorded. Of the three forest sites that were successfully sampled (see *Sampling*, below), one site was used for grazing and resting, the second site was located near a former pig-pen (Fig. 1d), while the third site was adjacent to an active pig-pen (Fig. 1e).

Pasture sites, connected to a nearby old oxbow, differed with respect to flooding – one site remained unflooded but was surrounded by high water during floods and resembled an island, while the other site was in the middle of the pasture and was completely flooded in spring (see *Sampling*, below; Fig. 1f). The vegetation of the pasture has some characteristics of ass. *Xanthietum italici* Timar ex Mititelu et Barabaş 1972, but grazing has caused changes in floristic composition and structure. Thus, next to indigenous species, e.g. *Lolium perenne* L., *Trifolium fragiferum* L. and *T. repens* L., the extensively used pasture is dominated by non-native invasive, e.g. *Asclepias syriaca* L. and *Ambrosia artemisiifolia* L. and ruderal species, e.g. *Rorippa sylvestris* (L.) Bess.

Sampling and identification

Carabid beetles were sampled using pitfall traps, within the two habitat types, isolated forest remnants and adjacent pastures, at six sites per habitat type and with five pitfall traps per site, i.e. 60 pitfall traps in total. Traps were placed five meters apart and consisted of a polyethylene cup (8.5 cm wide and 12.0 cm deep, V = 2,5 dm^3) with an outer 35 cm PVC pipe, flush with the ground surface. The PVC pipes were used because of livestock grazing. Cups were filled with a solution of wine vinegar, ethanol and water (1:1:1), to which a drop of neutrally-smelling detergent was added to reduce surface tension. A Styrofoam roof protected the contents of the cups from rain and litter, and a thin needle was used to perforate the cups at a height of 6 cm, to avoid possible flooding. Sampling sites were at least 50 m apart. However, due to heavy trampling by livestock and pigs, three sites in the forest remnant and four in the pasture were lost. Thus, in all 25 pitfall traps were functional. Field research took place between April and November 2002. Samples were collected twice a month.

Carabid beetles were identified using Müller-Motzfeld (2006), Turin *et al.* (2003) and Trautner & Geigenmüller (1987). Nomenclature follows Löbl & Löbl (2017). Samples are deposited in the Department of Biology, Faculty of Science, University of Zagreb.

Data analysis

For the analysis, the samples from the whole season per habitat type were pooled. Abundance data were expressed both (1) as totals per habitat type and (2) standardised to the number of individuals per trap to account for trap losses and unequal sampling between habitat types. The dominance was presented as the percentage of a particular carabid beetle species in the assemblages. The categories were used according to Tietze (1973): dominant species (>5%), subdominant species (1–4.99%), recendent species (0.5–0.99%), and subrecendent species (0.01–0.49%). Rank abundance curves are constructed per habitat type and based on the portion of each species in the assemblage. Functional trait values were assigned to carabid beetle species based on relevant literature (Homburg *et al.*, 2014; Brigić *et al.*, 2009; Turin *et al.*, 2003; Hůrka, 1996; Wachmann *et al.*, 1995; Lindroth, 1992) and expert knowledge. Each species was assigned to one of the categories for the following functional traits: habitat preference - open habitat species, generalist or forest specialist; flight ability – brachypterous, dimorphic or macropterous; and moisture preference – hygrophilous, mesophilous or xerophilous. Seasonal dynamics of the most abundant species were shown as total activity density (N) per month. Conservation status of the collected carabid beetles was assessed in accordance with the Croatian Red List of Carabid Beetles (Vujčić-Karlo *et al.*, 2007).

RESULTS

Carabid beetle occurrence and assemblage structure

Altogether 3,369 carabid beetle specimens belonging to 64 species were sampled (Tab. 1). The most species-rich habitat was forest remnant, with 3,344 specimens and 58 species (1,115 individuals per site). In the pasture, only 354 carabid beetle specimens and 45 species were recorded (177 individuals per site). About two-thirds of the species occurred in both habitat types (39 species, 60.9% of the total catch).

Tab. 1. Carabid beetles recorded in the forest remnant and adjacent pasture in the Lonjsko polje Nature Park (Croatia). Species are represented by the total number of individuals (N) and standardized to the number of individuals per trap (n), with dominant species presented in bold. Forest remnant totals are based on three sampling sites, while pasture totals are based on two sites. Species richness (S), activity density (N) and Berger-Parker dominance (d) of carabid beetles are shown separately for each habitat type, together with the number of unique species, and in total.

Species name	Forest remnant		Pasture		Total (N)
	Total (N)	Standardized (n)	Total (N)	Standardized (n)	
Agonum gracile Sturm, 1824	3	0.2			3
Agonum lugens (Duftschmid, 1812)	16	1.1			16
Agonum viduum (Panzer, 1796)	12	0.8	3	0.3	15
Amara communis (Panzer, 1797)			5	0.5	5
Anchomenus dorsalis (Pontoppidan, 1763)	117	7.8			117
Anisodactylus binotatus (Fabricius, 1787)	79	5.3	5	0.5	84
Anisodactylus signatus (Panzer, 1796)	4	0.3	3	0.3	7
Asaphidion flavipes (Linné, 1758)	33	2.2			33
Badister bullatus (Schrank, 1798)	2	0.1			2
Badister lacertosus Sturm, 1815	1	0.1			1
Badister sodalis (Duftschmid, 1812)	2	0.1			2

Species name	Forest remnant		Pasture		Total (N)
	Total (N)	Standardized (n)	Total (N)	Standardized (n)	
Badister unipustulatus Bonelli, 1813	4	0.3	2	0.2	6
Bembidion biguttatum (Fabricius, 1779)	26	1.7	14	1.4	40
Bembidion gilvipes Sturm, 1825	15	1	1	0.1	16
Bembidion lampros (Herbst, 1784)	20	1.3	5	0.5	25
Bembidion octomaculatum (Goeze, 1777)	1	0.1			1
Bembidion semipunctatum (Donovan, 1806)	4	0.3	4	0.4	8
Blethisa multipunctata (Linné, 1758)			1	0.1	1
Calathus melanocephalus (Linné, 1758)			1	0.1	1
Callistus lunatus (Fabricius, 1775)	1	0.1			1
Carabus cancellatus Dejean, 1826	678	45.2	59	5.9	737
Carabus clatratus auraniensis J.Müller, 1903	26	1.7	9	0.9	35
Carabus granulatus Linné, 1758	179	11.9	5	0.5	184
Chlaenius nigricornis (Fabricius, 1787)	47	3.1	7	0.7	54
Chlaenius spoliatus (P. Rossi, 1792)			1	0.1	1
Chlaenius tristis (Schaller, 1783)	2	0.1			2
Clivina fossor (Linné, 1758)	42	2.8	20	2	62
Diachromus germanus (Linné, 1758)			2	0.2	2
Dyschirius globosus (Herbst, 1784)	215	14.3	8	0.8	223
Elaphrus cupreus Duftschmid, 1812	6	0.4	9	0.9	15
Harpalus affinis (Schrank, 1781)	1	0.1	12	1.2	13
Harpalus atratus Latreille, 1804	2	0.1			2
Harpalus cupreus Faldermann, 1836	1	0.1	4	0.4	5
Harpalus flavescens (Piller & Mitterpacher, 1783)	1	0.1	2	0.2	3
Harpalus marginellus Gyllenhal, 1827	40	2.7	5	0.5	45
Harpalus progrediens Schauberger, 1922	1	0.1			1
Harpalus rufipes (DeGere, 1774)	820	54.7	63	6.3	883
Harpalus smaragdinus (Duftschmid, 1812)	1	0.1	1	0.1	2
Leistus ferrugineus (Linné, 1758)	2	0.1			2
Limodromus assimilis (Paykull, 1790)	209	13.9	3	0.3	212
Limodromus krynickii (Sperk, 1835)	1	0.1	1	0.1	2
Loricera pilicornis (Fabricius, 1775)	9	0.6	2	0.2	11
Nebria brevicollis (Fabricius, 1792)	2	0.1	3	0.3	5
Ophonus diffinis (Dejean, 1829)	2	0.1			2
Ophonus rupicola (Sturm, 1818)			3	0.3	3
Panagaeus cruxmajor (Linné, 1758)	1	0.1	1	0.1	2
Platynus livens (Gyllenhal, 1810)	69	4.6			69
Platynus scrobiculatus (Fabricius, 1801)	4	0.3	2	0.2	6
Poecilus cupreus (Linné, 1758)	481	32.1	68	6.8	549
Pterostichus anthracinus (Illiger, 1798)	63	4.2	4	0.4	67
Pterostichus gracilis (Dejean, 1828)	8	0.5	1	0.1	9
Pterostichus melanarius (Illiger, 1798)	1	0.1	1	0.1	2
Pterostichus melas (Creutzer, 1799)	21	1.4	1	0.1	22
Pterostichus minor (Gyllenhal, 1827)	1	0.1	1	0.1	2
Pterostichus niger (Schaller, 1783)	5	0.3	3	0.3	8
Pterostichus ovoideus (Sturm, 1824)	3	0.2			3
Pterostichus strenuus (Panzer, 1796)	5	0.3	1	0.1	6
Pterostichus vernalis (Panzer, 1796)	11	0.7	1	0.1	12
Stenolophus marginatus Dejean, 1829	1	0.1			1

Species name	Forest remnant		Pasture		Total (N)
	Total (N)	Standardized (n)	Total (N)	Standardized (n)	
Stenolophus teutonus (Schrank, 1781)	27	1.8	1	0.1	28
Stomis pumicatus (Panzer, 1796)	3	0.2			3
Syntomus obscuroguttatus (Duftschmid, 1812)	2	0.1			2
Tachys bistriatus (Duftschmid, 1812)	3	0.2	1	0.1	4
Zabrus tenebrioides (Goeze, 1777)	8	0.5	5	0.5	13
Species richness (S)	**58**	**3.9**	**45**	**4.5**	**64**
Activity density (N, total)	**3344**	**222.9**	**354**	**35.4**	**3698**
Berger-Parker dominance indeks	**0.25**		**0.19**		**0.24**
Number of unique species	**19**		**6**		

The number of species unique to a particular habitat type was high in the forest remnant (19 species, 32.8% of the total catch in this habitat type) and included the following species: *Agonum gracile*, *A. lugens*, *Anchomenus dorsalis*, *Asaphidion flavipes*, *Badister bullatus*, *B. lacertosus*, *B. sodalis*, *Bembidion octomaculatum*, *Callistus lunatus*, *Chlaenius tristis*, *Harpalus atratus*, *H. progrediens*, *Leistus ferrugineus*, *Ophonus diffinis*, *Platynus livens*, *Pterostichus ovoideus*, *Stenolophus marginatus*, *Stomis pumicatus* and *Syntomus obscuroguttatus* (Tab. 2). In contrast, only six unique species occurred on the pasture (13.3% of the total catch in that habitat type): *Amara communis*, *Blethisa multipunctata*, *Calathus melanocephalus*, *Chlaenius spoliatus*, *Diachromus germanus* and *Ophonus rupicola* (Tab. 2).

Rank-abundance curves (Fig. 2, Tab. 2) show that six species dominated the total catch: *Harpalus rufipes*, *Carabus cancellatus, Poecilus cupreus, Dyschirius globosus*, *Limodromus assimilis* and *Carabus granulatus*, accounting for 75.39% of the catch. Together with *C. granulatus*, the above-mentioned species were also dominant in the forest remnant (Tab. 2). In the pasture, four species prevailed in abundance: *P. cupreus, H. rufipes*, *C. cancellatus,* and *Clivina fossor* (Tab. 2). The subdominant species were particularly abundant in the pasture (15 species), followed by the forest remnant (7 species). The recendent species were almost twice as abundant in the pasture (11 species) as in the forest remnant (6 species, Tab. 2). The forest remnant was characterized by an exceptionally high number of subrecendent (sporadic) species (39 species), followed by the pasture (15 species).

Species traits

In terms of functional traits, the abundance of carabid beetles with an affinity for open habitats was very high both in the forest remnant and in the pasture, reaching over 50% of the catch in each respective habitat type, followed by the abundance of generalist or shade-tolerant species (Fig. 3ad). In contrast, the abundance of forest species was rather low in both habitat types (11.9% in the forest remnant and 7.9%; Fig. 3ad); with the exception of *L. assimilis*, forest species were mostly subrecendent and rarely subdominant in the assemblage (Tab. 2). As expected, abundances of hygrophilous (forest remnant - 36.5%; pasture - 48.3%) and mesophilous (38.7%; 28.5%) carabid beetles were high in both habitat types (Fig. 3cf). In terms of flight ability, the abundance of macropterous species was very high in both habitat types, reaching over 60% of the catch in each (Fig. 3be). The abundance of brachypterous carabid beetles was higher in the forest remnant than in the pasture, while dimorphic species were similarly represented in both habitat types (Fig. 3be).

Tab. 2. Dominance of carabid beetle species in two habitat types (forest remnant and adjacent pasture) in the Lonjsko polje Nature Park. Frequencies of individuals captured per species are shown in brackets.

	Dominant species (> 5%)	Subdominant species (4.99 % - 1.00 %)	Recendent species (0.99 % - 0.5 %)
Total	*Harpalus rufipes* (23.88%)	*Carabus granulatus* (4.98%)	*Carabus clatratus auraniensis* (0.95%)
	Carabus cancellatus (19.93%)	*Anchomenus dorsalis* (3.16%)	*Asaphidion flavipes* (0.89%)
	Poecilus cupreus (14.85%)	*Anisodactylus binotatus* (2.27%)	*Stenolophus teutonus* (0.76%)
	Dyschirius globosus (6.03%)	*Platynus livens* (1.87%)	*Bembidion lampros* (0.68%)
	Limodromus assimilis (5.73%)	*Pterostichus anthracinus* (1.81%)	*Pterostichus melas* (0.59%)
		Clivina fossor (1.68%)	
		Chlaenius nigricornis (1.41%)	
		Harpalus marginellus (1.22%)	
		Bembidion biguttatum (1.08%)	
Forest remnant	*Harpalus rufipes* (24.52%)	*Anchomenus dorsalis* (3.50%)	*Asaphidion flavipes* (0.99%)
	Carabus cancellatus (20.28%)	*Anisodactylus binotatus* (2.36%)	*Stenolophus teutonus* (0.81%)
	Poecilus cupreus (14.38%)	*Platynus livens* (2.06%)	*Bembidion biguttatum* (0.78%)
	Dyschirius globosus (6.43%)	*Pterostichus anthracinus* (1.88%)	*Carabus clatratus auraniensis* (0.78%)
	Limodromus assimilis (6.25%)	*Chlaenius nigricornis* (1.41%)	*Pterostichus melas* (0.63%)
	Carabus granulatus (5.35%)	*Clivina fossor* (1.26%)	*Bembidion lampros* (0.60%)
		Harpalus marginellus (1.2%)	
Pasture	*Poecilus cupreus* (19.21%)	*Bembidion biguttatum* (3.95%)	*Agonum viduum* (0.85%)
	Harpalus rufipes (17.80%)	*Harpalus affinis* (3.39%)	*Anisodactylus signatus* (0.85%)
	Carabus cancellatus (16.67%)	*Carabus clatratus auraniensis* (2.54%)	*Nebria brevicollis* (0.85%)
	Clivina fossor (5.65%)	*Elaphrus cupreus* (2.54%)	*Ophonus rupicola* (0.85%)
		Dyschirius globosus (2.26%)	*Limodromus assimilis* (0.85%)
		Chlaenius nigricornis (1.98%)	*Pterostichus niger* (0.85%)
		Amara communis (1.41%)	*Badister unipustulatus* (0.56%)
		Anisodactylus binotatus (1.41%)	*Diachromus germanus* (0.56%)
		Bembidion lampros (1.41%)	*Harpalus flavescens* (0.56%)
		Carabus granulatus (1.41%)	*Loricera pilicornis* (0.56%)
		Harpalus marginellus (1.41%)	*Platynus scrobiculatus* (0.56%)
		Zabrus tenebrioides (1.41%)	
		Bembidion semipunctatum (1.13%)	
		Harpalus cupreus (1.13%)	
		Pterostichus anthracinus (1.13%)	

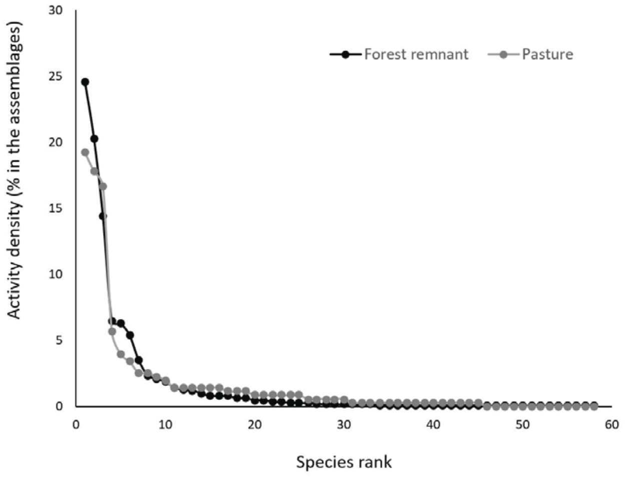

Fig. 2. Rank abundance curves of carabid beetle assemblages in two habitat types: forest remnant (black) and adjacent pasture (grey) in the Lonjsko polje Nature Park (Croatia).

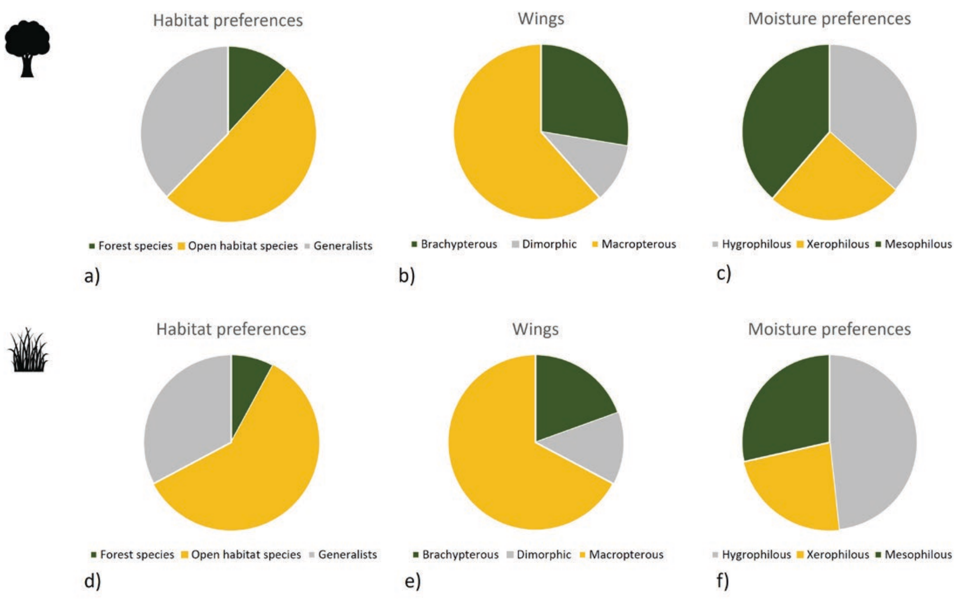

Fig. 3. Proportion of abundances per functional trait group in the forest remnant and adjacent pasture in the Lonjsko polje Nature Park (Croatia): habitat preferences: a) and d); wing development: b) and e); moisture preference: c) and f).

Seasonal activity patterns

In the forest remnant, activity density of *H. rufipes* peaked in June, remaining relatively high in July, and another peak was recorded in August (Fig. 4a). *Carabus cancellatus* was found from May to November, with the maximum seasonal activity in August (Fig. 4b), whereas in the pasture, the species was first recorded in July and reached its activity peak in September (Fig. 4b). From October, the total number of specimens decreased in both habitat types. The seasonal activity patterns of *D. globosus*, *L. assimilis* and *P. cupreus* were quite similar in the forest remnant, with the surface activity maximums of all three species recorded in June, and their activity decreasing significantly in the following months. However, a slight increase in the number of *D. globosus* and *L. assimilis* specimens was observed in autumn (Fig. 4de). The activity of *D. globosus*, *L. assimilis*, *P. cupreus* and *H. rufipes* (Fig. 4acde) in the pasture was uniformly low, with the exception of a distinct peak in the activity of *P. cupreus* in May (Fig. 4c). In the forest remnant, activity density of *C. granulatus* peaked in July and decreased in the following months, while its activity density was uniformly low in the pasture (Fig. 4f).

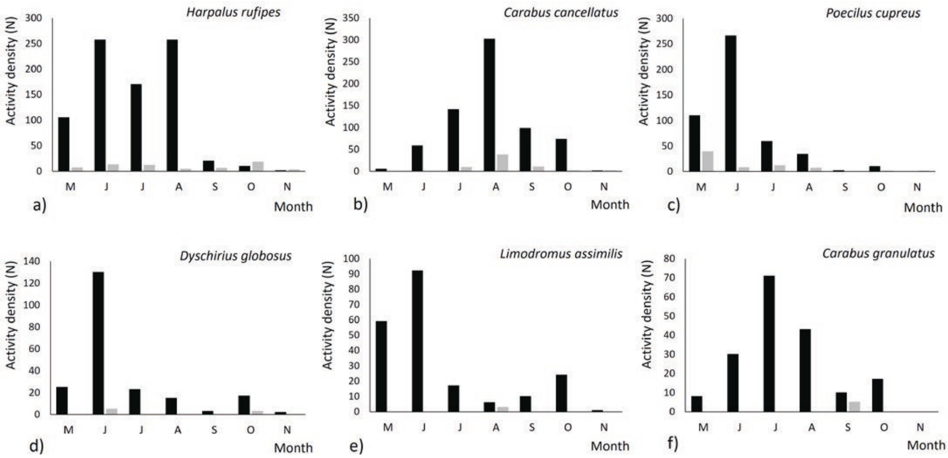

Fig. 4. Seasonal activity density of carabid beetle species in the forest remnant (black) and adjacent pasture (grey) in the Lonjsko polje Nature Park (Croatia). Seasonal dynamics is shown for species recorded in abundance higher than 4.5% of the total catch. Data were obtained from five pitfall traps per site (forest remnant n = 3 sites, pasture n = 2 sites).

Carabid species of conservation interest

Altogether 16 carabid beetle species included in the Croatian Red List (Vujčić-Karlo *et al.*, 2007) were found in the study area. *Carabus clatratus auraniensis*, a critically endangered species (CR), was found in both habitat types, but it was most abundant in the forest remnant site adjacent to an active pig-pen. Other threatened species occurred in low frequencies: *C. tristis* (EN) and *Bembidion octomaculatum* (VU) were found exclusively in the forest remnant, while *B. multipunctata* (VU) occurred only in the flooded pasture. In addition, three near-threatened (NT) species (*C. cancellatus*, *Panagaeus cruxmajor* and *Pterostichus gracilis*) and nine least-concern (LC) species (*Badister unipustulatus, Elaphrus cupreus, Harpalus cupreus, H. flavescens, H. smaragdinus, Loricera pilicornis, Pterostichus minor, S. marginatus* and *S. pumicatus*) were recorded.

DISCUSSION

Carabid beetle diversity of the study area

The results of this study unambiguously show that the periodically flooded habitats of the Lonjsko polje Nature Park are characterized by a high carabid beetle species richness, which corroborates previous findings for the area (Brigić *et al.*, 2014). This could be explained by the disturbance caused by periodical floods and extensive grazing, resulting in a high spatio-temporal diversity of habitats. All the known records, show that Lonjsko polje Nature Park is inhabited by 99 carabid beetle species (Brigić *et al.*, 2014; Durbešić *et al.*, 2000). Similarly, high carabid beetle species richness has been observed in other floodplains, e.g. of the Oka and Morava rivers (Trushitsyna *et al.*, 2016; Zulka, 1994) or in various salt wetlands (Amri *et al.*, 2019, Andujar *et al.*, 2001). However, the carabid beetle diversity of the Lonjsko polje Nature Parke is far from being fully explored, as currently known data are based on a few habitat types surveyed (e.g., meadows, stands invaded by *Amorpha*, shrubs, forest remnants) with a relatively small number of pitfall traps used and the sampling performed during a single vegetation season. Therefore, the carabid beetle species richness is expected to be still greater if other habitat types (e.g., river banks, various flooded and non-flooded forests, and agricultural habitats) are sampled over multiple vegetation seasons, with additional sampling techniques (e.g., window traps, light traps and hand sampling).

Carabid beetle assemblage composition and structure

In this study, higher species richness and abundance of carabid beetles were found in the forest remnant than in the pasture. Carabid beetle fauna of the forest remnant was highly heterogenous, as it was composed of species typical of: meadows (e.g., *H. rufipes* and *P, cupreus*), floodplains (e.g. *A. flavipes*, *A. dorsalis, Agonum lugens, P. livens*, etc.), riparian habitats (e.g. *Bembidion* sp., *Agonum* sp., *Pterostichus anthracinus*) and, to a smaller extent, of forest species (e.g. *L. assimilis, L. krynickii, Pterostichus niger*). Additionally, two widespread species with habitat preferences ranging from moist to wet habitats, *C. cancellatus* and *C. granulatus*, dominated the forest remnant assemblages. It is important to highlight that the forest remnant lacks the typical composition of carabid beetle fauna of flooded *Quercus* forests in Croatia (e.g. Vujčić-Karlo & Durbešić, 2004), possibly due to the size and shape of the forest remnant and edge structure. In particular, *Carabus ullrichi,* a large-sized, brachypterous species with poor dispersal ability, inhabiting *Quercus* forests (Turin *et al.*, 2003), was not recorded in this study. Similarly, neither *Carabus coriaceus* nor *Abax* sp. were recorded. Most importantly, all previously mentioned species inhabit flooded *Quercus* forests in Croatia (Vujčić-Karlo & Durbešić, 2004). Additionally, typical forest species such as *L. krynickii and P. scrobiculatus,* were recorded in low abundance in the investigated forest remnant (Šustek, 1994).

High species richness of the forest remnant could be due to immigration of carabid beetles from adjacent habitats, periodical floods and/or animal disturbances. High abundance of meadow species, *H. rufipes* and *P. cupreus,* with great dispersal abilities, indicates that abrupt forest edges could be prone to invasion from adjacent areas, corroborating findings from floodplain forests in Moravia and Slovakia (Šustek, 1994). This is further confirmed by high occurrence of sporadic or migrant species in the forest remnant, such as *Badister* sp., *Chlaenius tristis*, several *Harpalus* species, etc. In particular, *H. rufipes* has a high migration potential and under unfavorable conditions the species is most probably capable of large-scale migrations (Sienkiewicz & Żmihorski, 2012). Periodical flooding shapes carabid beetle assemblages, leading to qualitative and quantitative changes in carabid beetle assemblages (Sienkiewicz & Żmihorski, 2012; Günther & Assmann, 2005). In the study area, carabid assemblages are also likely influenced by the the foraging of pigs and livestock grazing. This small-scale animal disturbance affects habitat structure and resource availability: 1) small patches of stagnant water are created, interchanging with bare soil and resulting in greater spatio-temporal structural diversity; 2) soil invertebrates are supplied with new resources such as excrement and carrion, likely supporting their greater abundance (Poschlod *et al.*, 2002; Kerovec *et al.*, 2001). Previous studies showed that low to medium intensity grazing enhances carabid beetle species richness and abundance (Melis *et al.*, 2007; Wallis De Vries *et al.*, 2007; Falke *et al.*, 2000).

Although the periodic floods did not inundate the pasture site, they have indirectly affected carabid beetle species composition, as the site was completely surrounded by water, at least 1 m high, for a minimum of 30 days. Therefore, carabid beetle assemblages consisted of both species from the nearby patch and open habitat species that may rapidly respond to changes in habitat (e.g. *H. rufipes*, *P. cupreus, Bembidion* sp., *Diachromus germanus,* several other *Harpalus* species). These are mainly eurytopic macropterous species, some of which dominated the site in terms of abundance. Furthermore, some highly hygrophilous taxa, such as *Agonum* and *Bembidion*, may quickly recolonize the available space after floods (Bonn, 2000). However, open habitat species such as *Brachinus crepitans* and *Ophonus diffinis*, previously recorded in high abundance in the Lonjsko polje Nature Park (Brigić *et al.*, 2014), most probably cannot tolerate prolonged floods. Immigration of carabids from adjacent habitats occurs several days after flood pulse and the retreat of high waters, in line with Sienkiewicz & Żmihorski (2012).

Most of the recorded species, both in the forest remnant and the pasture, are macropterous and have very good dispersal abilities (e.g. *A. flavipes*, *A. dorsalis, Agonum* sp.*, Bembidion* sp., *Platynus livens*). These species are adapted to periodical floods, and can quickly abandon the area and repopulate it once the conditions become suitable again (Bonn, 2000; Šustek, 1994; Zulka, 1994). Some carabid beetles are even capable of swimming, in particular *C. clatratus auraniensis,* which dives and hunts in the water (Turin *et al.*, 2003; Thiele, 1977). Furthermore, during the field work we observed *L. assimilis* successfully using water surface tension to cross small patches of stagnant water. Similar observations were documented for other hygrophilous and larger carabid beetle species, e.g. *B. multipunctata*, *P. cupreus* and *Pterostichus niger* (Sienkiewicz & Żmihorski, 2012). Also, trees may provide additional opportunities for surviving floods, especially for brachypterous species that may hide under the bark of drifting wood (Zulka, 1994) or by vertical migration onto tree trunks (Adis *et al.*, 1997).

Seasonal dynamics

Our results show that seasonal dynamics differ between large-bodied (*C. cancellatus* and C. *granulatus*) and medium to small sized carabid beetle species (*H. rufipes*, *P. cupreus*, *L. assimilis* and *D. globosus*). Maximum activity peaks of the latter were observed in spring (June), in line with other studies (Lindroth, 1992). *Poecilus cupreus*, *L. assimilis* and *D. globosus* are spring breeders, hibernating as adults (Lindroth, 1992), while *H. rufipes* is an autumn breeder, hibernating in a larval stage and to lesser extent as an adult (Lindroth, 1992). Maximum activity peaks of large sized *Carabus* species were recorded in summer (July-August), corroborating previous studies (c.f. in Turin *et al.*, 2003). Both *C. cancellatus* and C. *granulatus* are spring breeders, and are active from May to September (Turin *et al.*, 2003). Interestingly, the maximum activity peak of *C. cancellatus* in the non-flooded *Amorpha* stands in the Lonjsko polje Nature Park was recorded in May as in most other studies (Brigić, unpublished data; c.f. Turin *et al.*, 2003). This indicates that periodical floods may cause shifts in seasonal dynamics and/or enhanced foraging activity of the species, but this remains to be investigated in the future.

Conservation value of the study area

Many species from the present study are rare or sporadic, not only in Croatia but also in Europe (Turin *et al.*, 2003), therefore the investigated area is of a substantial conservation interest. A vivid example is *C. clatratus auraniensis*, a strongly hygrophilous species, inhabiting mainly marshes, peat bogs, swampy reedlands and wet grasslands, but also muddy shores of rivers and lakes (Turin *et al.*, 2003). In the Lonjsko polje area, habitats have retained original soil properties, vegetation and hydrology required to support the occurrence of this potential flagship species. Small patches of stagnant, shallow water (10-30 cm), as well as the surrounding drier (but still moist) habitat sections are preferred by the species (Turin *et al.*, 2003); such suitable microhabitats are created by the rooting of pigs and the grazing of livestock. *Carabus clatratus auraniensis* is one of the most localized and highly endangered species in Europe, reported as threatened or extinct in several European countries (Assmann, 2003). In the past, it was a widely distributed Asian-European species, but nowadays it is critically endangered due to habitat loss caused by drainage, lowering ground water levels and cultivation or even predation by invasive species (Casale & Busato, 2008; Assmann, 2003). In the Mediterranean, the species is seriously threatened by cultivation and urbanization (Forel & Laplat, 1995; Casale *et al.*, 1982). During the last 60 years, such activities have resulted in the extinction of this species in Vrana Lake, a Mediterranean wetland in Croatia. Based on the current knowledge, in Croatia this species occurs in the Lonjsko polje and Kopački rit area (Brigić *et al.*, 2024 in review). Other very rare species recorded in this study, e.g. *C. tristis, B. multipunctata, B. octomaculatum, L. krynickii,* are endangered in Croatia due to habitat degradation and loss (Vujčić-Karlo *et al.*, 2007).

In conclusion, this study suggests that the mosaicity of small habitats, combined with traditional land management practices, can support carabid beetle fauna with considerable conservation interest not only for Croatia, but also at the European level. However, carabid beetle species may be lost by intensification or abandonment of traditional land management practices and vegetation succession (Grandchamp *et al.*, 2005; Falke *et al.*, 2000). In particular, depopulation of villages and changes in the traditional lifestyle in Lonjsko polje Nature Park, have caused severe decrease of stocking rates (Schneider-Jacoby, 2002) and resulted in the expansion of invasive species, particularly *A. fruticosa*. Such changes were already detrimental to the existing grassland plant communities (Poschlod *et al.*, 2002) and have also affected some globally threatened birds, such as corncrakes (*Crex crex,* Linné, 1758) (Dumbović, 2003), and different waterfowl species that have lost suitable feeding sites (Gugić, 2008). With respect to carabid beetles, such changes might be advantageous for relatively eurytopic and widespread species, but stenotopic and highly hygrophilous carabid beetles will certainly show negative responses both at the species and the assemblage level (Brigić *et al.*, 2014). Moreover, a serious threat not only to the carabid beetle fauna, but also to the overall biodiversity of Lonjsko polje Nature Park are plans for the construction of a multipurpose Danube-Sava channel which might affect the flood dynamics (Schneider-Jacoby, 2002; Jakovac, 1999). Therefore, it is imperative to develop strategies for sustainable river basin management in order to preserve the high biodiversity of Lonjsko polje Nature Park.

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