UNIVERSITY OF SZEGED
Faculty of Science and Informatics
Department of Ecology
DOCTORAL SCHOOL OF ENVIRONMENTAL SCIENCES

TRUE BUGS (HETEROPTERA) AS A CONSERVATION TOOL IN HABITAT ASSESSMENT AND MONITORING: CASE STUDIES ON THE PANNONIAN SALINE GRASSLANDS

PhD dissertation

JELENA ŠEAT

Supervisor
DR ATTILA TORMA

Szeged, 2022

TABLE OF CONTENTS:

1. INTRODUCTION

1.1. Global biodiversity crisis

The broadest definition of biological diversity or biodiversity refers to the variety and variability of life. This comprehensive definition covers all levels of the biological organization, where the three key components are recognized: genetic, species (organismal) and ecosystem (ecological) diversity (Harper & Hawksworth, 1994; Sodhi & Ehrlich, 2010). Biodiversity represents a fundamental concept in global environmental management, and its social-ecological character demands the participation of a variety of scientific experts. Although ecology is underlying scientific support of the concept, 'biodiversity' actually arose from political activism and the need for a solution to manage global crisis, and therefore, biodiversity became a measure of environmental crisis. In the early 1980s, a new subdiscipline, conservation biology, emerged and its founder Michael Soulé described it as the 'science of crisis' (Robin, 2011).

The aforementioned concept of biodiversity is too broad for application in conservation practice, and there was a need for a more pragmatic approach and defining of a universal unit of biodiversity. For decades ecologists are trying to define this unit without success, although, species richness (i.e. number of species) is the most intuitive and primarily used indicator of biodiversity in conservation biology today (Magurran, 2004; Faber-Langendoen & Josse, 2010). In that manner, species richness became a currency of the diversity of life (Robin, 2011).

Why does biodiversity matter? Well-preserved biological diversity provides us food, medicines, fuel, clean water and air. Scientists and practitioners agree that diverse biological systems are more resilient to dramatic changes in the environment, since ecosystem health and biodiversity are mutually supportive (Robin, 2011). Currently, almost three-quarters of the Earth's surface has been modified, pushing nature to the small inaccessible parts of the planet (European Commission, 2020). Over the past 50 years, human activities have changed natural ecosystems largely, resulting in an irreversible loss in some aspects of biodiversity, valuable natural resources and ecosystem functions (Millennium Ecosystem Assessment, 2005). According to the last report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), 75% of the land surface has been significantly modified, 66% of the ocean area is severely impacted and over 85% of wetlands have been lost. According to the Red List criteria of the International Union for Conservation of Nature (IUCN), around 25% of animal and plant species are currently threatened by extinction, meaning, out of 8 million estimated species (75% of them are insects) around 1 million face extinction. The average abundance of native species in main terrestrial biomes decreased at least by 20%, potentially affecting ecosystem processes and indirectly, human wellbeing. The main suspects contributing to this decrease are changes in land and sea use, overexploitation, invasive species, pollution and climate change (IPBES, 2019).

Change in land use is by far the most influential of all factors in land biomes, causing the rapid decline of diversity in terrestrial and freshwater ecosystems in the past few decades (IPBES, 2019). Land-use change is a complex phenomenon, which takes many forms and results in modification of the living space of species by complete removal, fragmentation or degradation of their habitats. The main drivers of land degradation are the expansion of crop and grazing lands, unsustainable agriculture and forestry, urban expansion, infrastructure development and extractive industry. In synergy with climate change, the effects of these drivers have become even more detrimental. An increase in cropland and grazing areas and their non-sustainable management are the most prominent mechanisms of land degradation globally, and nowadays these areas cover more than one-third of the Earth's land surface (IPBES, 2018).

1.1.1. The role of European farmland in preserving biodiversity

Europe has a long history of various extensive farming traditions, as determined by soil productivity and the political history of the countries (Batáry *et al.*, 2020). This resulted in the development of mosaic-like landscapes consisting of small semi-natural habitat patches and agrarian lands in some regions, and continuous monotonous croplands or pastures in other parts of the continent. Regardless of differences (i.e. their landscape composition and configuration) of European farmlands, these areas have been attractive to many species and have been successfully supporting local biological diversity for centuries. Today the existence of some plant and animal species is completely dependent on European farmlands (European Commission, 2008). Unfortunately, effects of land abandonment (mostly in well-developed countries of Western Europe) and agricultural intensification (in former socialist countries of Central and Eastern Europe) caused the serious decline of farmland biodiversity in the past few decades (Batáry *et al.*, 2020). Only 15–25% of high-value farmland areas in Europe remain well-preserved (European Commission, 2018).

European nature conservation favours threatened species and habitats of farmlands, and it usually targets remaining natural or semi-natural fragments in the agricultural landscape (Batáry *et al*., 2020). Considering the aforementioned, there was an idea to link valuable patches of nature in order to combat habitat fragmentation, the main cause of the species extinction (Verschuuren, 2002). This idea was realized through the establishment of Natura 2000, a coherent EU-wide network of areas with high conservation importance. The network covers over 1 million km^2—almost a fifth of European territory—and is the largest of its kind in the world. Natura 2000 consists of protected nature reserves and privately owned lands as well, where human activities are daily present (European Commission, 2018). The goal of Natura 2000 is to promote positive conservation practices within agricultural, forest and fishery systems that are ecologically sustainable, socially beneficial and economically profitable. The network comprises 27,000 terrestrial and marine sites (i.e. Natura 2000 sites) which are supported by the two key documents of the European Union (EU) legislation—Habitats Directive (Council Directive 92/43/EEC) and Birds Directive (Council Directive 2009/147/EC). These two directives and Natura 2000 network aim to conserve the most valuable species and habitats in Europe in such a way, so that further loss of global biodiversity could be prevented (Verschuuren, 2002; Evans, 2012; European Commission, 2018).

Farmlands of conservation importance in the EU make up 40% of the total area included in Natura 2000, therefore, the role of farmers and extensive farming is crucial in preserving local biodiversity. Rich biodiversity here is usually related to low productive agricultural systems, such as grazed semi-natural grasslands and scrublands, croplands on poor, dry and saline soils, traditionally managed orchards, olive groves and vineyards, etc. Rural areas of the EU incorporate 58 habitat types from Annex I of the Habitats Directive considered key farmland habitats associated with extensive agriculture, whereas, 24 of these fully depend on the right agricultural practices. Annex II of the Habitats Directive lists 197 plant and animal taxa associated with agroecosystems or grasslands, and Annex I of the Birds Directive lists 62 bird species related to the same areas (European Commission, 2018).

1.2. Conservation importance of grasslands

According to the Food and Agricultural Organisation of the United Nations (FAO), grasslands in their broadest sense are the largest habitat type in the world, covering 40% of the terrestrial area of the planet excluding Greenland and Antarctica (Suttie *et al*., 2005). Grasslands have played an important role for mankind for millennia. Throughout history, grasslands were the source of arable land, hunting grounds, pastures for domesticated herbivores and beekeeping, areas where people could find medical and edible plants (European Commission, 2008; Bengtsson *et al*., 2019). Nomadic pastoralism, as an ancient form of land use, was and still is very important for humans, defining their cultural and social identity and economic systems (Kradin, 2002). This socio-economic phenomenon was particularly prominent in Eurasian steppes where semi-arid conditions make arable farming unsustainable, thus agrarian activities were livestock oriented (Wesche *et al*., 2016). In Europe, grasslands are an integral part of the cultural landscape (Török *et al*., 2011; Dengler *et al*., 2014), as extensive mixed-farming is a centuries-old tradition here (European Commission, 2008).

By their origin, grasslands can be natural, semi-natural and secondary. (i) Natural grasslands persist in isolated corners of the Earth, like mountain tops and slopes, largely controlled by natural processes (Faber-Langendoen & Josse, 2010; Török *et al*., 2018). (ii) Semi-natural grasslands are the most common type which are usually associated with traditional pastoralism. These areas are more or less modified by human activities, although their plant communities are natural (European Commission, 2008). (iii) Secondary grasslands are mostly established after clearcutting, and for instance, in Europe, these are maintained by extensive grazing and/or hay-making (Dengler *et al*., 2014; Wesche *et al*., 2016; Török *et al*., 2018). Naturalness and conservation importance, as well as, productivity and human utilization of grasslands are determined by climate, topography, soil characteristics, etc. (European Commission, 2008; Faber-Langendoen & Josse, 2010).

Grasslands have a high ecological value and provide habitats for myriad species (Peart, 2008). At the first sight, these habitats look structurally very simple, but for instance, some dry grasslands in Europe have extraordinary small-scale diversity of vascular plants. In Ukraine, almost 30% of all plant and animal taxa listed in the national Red Book are species related to Eurasian steppes (Török *et al*., 2018). Just a look at the African savanna and its megafauna gives an impressive image of a grassland richness. In Asia, steppes harbour large herds of wild ungulates like *Saiga tatarica* (Linnaeus, 1766) (Saiga antelope) and *Gazella subgutturosa* (Güldenstädt, 1780) (Goitered gazelle); Eurasian steppe has the most extensive migrations of ungulates outside Africa (Wesche *et al.*, 2016). Large wild herbivores have almost disappeared from the European steppes, however, traditionally managed grasslands by domesticated grazers are among the most species-rich habitats here and the key habitats for species like *Otis tarda* Linnaeus, 1758 (great bustard) and *Aquila heliaca* Savigny, 1809 (imperial eagle) (European Commission, 2008). The fauna and flora of European semi-natural grasslands consist of many grassland specialists, including many endemics, which thrive in low-intensity managed grasslands. A big share of threatened species in Europe are related to grassland habitats; 63% of butterfly fauna is associated with endangered dry grasslands and steppes, 59% of bird species associated with grasslands have an unfavourable conservation status (Dengler *et al*., 2014). Grasslands are home to a large number of rare and endangered species all around the world and some of these areas are global biodiversity hotspots (Török *et al*., 2018).

Besides the importance of the grasslands of the world for wildlife conservation, they also provide a wide range of ecosystem functions and services (Boch *et al*., 2021). Grasslands help in regulation and filtering water, prevent soil erosion and desertification, contribute in carbon and methane sequestration and storage, take share in oxygen production, mitigate climate change, etc. (Peart, 2008; Faber-Langendoen & Josse, 2010; Wesche *et al*., 2016; Török *et al*., 2018; Bengtsson *et al*., 2019). Grasslands store 34% of the global carbon supply in terrestrial ecosystems, thus conversion and inappropriate land-use practices can lead to massive carbon emissions (European Commission, 2008; Wesche *et al*., 2016). In farmlands, grassland patches provide a supporting system for pollination, seed dispersal and biocontrol of pests (Peart, 2008; Bengtsson *et al*., 2019).

1.2.1. Uniqueness of the Pannonian saline grasslands

The Pannonian Biogeographic Region is the westernmost part of the Eurasian steppe, covering the territory of several countries in Central and Eastern Europe (Fig. 1). The region is represented by a wide lowland, also known as Pannonian Plane or Carpathian Basin, and is surrounded by several mountains, namely, the Carpathians on the north and east and the Alps on the west. The climate here is dry continental with cold humid winters and hot dry summers with occasional droughts

(Šefferová-Stanová *et al.*, 2008; Deák *et al.*, 2014a; Eliáš *et al.*, 2020). From the middle of the 19th century landscape in this region has considerably changed; huge steppe pastures were converted to arable fields and only the saltiest and wettest patches remained (European Environment Agency, 2002; Molnar & Borhidi, 2003).

Figure 1. The Pannonian Biogeographic Region (orange area on the map).

Saline or halophytic habitats of the region encompass the whole spectrum of different habitats types, from several grasslands and wetland types to alkaline (soda) lakes. These saline habitats form the most continuous inland salt-affected landscape in Europe and cover more than 210,000 ha (Šefferová-Stanová *et al.*, 2008). All saline habitats of the Pannonian Region are listed in Annex I of the Habitats Directive by its code name 1530 *Pannonic salt steppes and salt marshes (Council Directive 92/43/EEC). Also, the habitats are marked as areas of high conservation importance, due to their restricted geographic distribution and unique taxa which cannot be found anywhere else in Europe (Šefferová-Stanová *et al.*, 2008). Besides the few well-preserved fens, saline habitats are the most natural ones among the treeless habitats in Hungary (Bölöni *et al*., 2008). Unfortunately, human activities in Europe caused a huge loss of saline habitats and in present time, only about 20% of remained are of ancient origin (European Environment Agency, 2002). It is estimated that 55% of the Pannonic salt steppes and salt marshes in the EU are already protected within Natura 2000 (Europe Commmision, 2018). Seemingly, wide areas of Pannonian saline grasslands in Hungary are well taken care of, but small grassland fragments at the edge of the ecoregion experience greater pressure and accelerated change in their original biodiversity (Rabitsch, 2012).

The uniqueness of saline grasslands is the fine-scale zonation of vegetation with around 50 distinct plant communities. At the same time, plant diversity in those communities is relatively species-poor consisting mostly of several characteristic halophytes and salt-tolerant grasses (Molnár & Borhidi, 2003; Šefferová-Stanová *et al*., 2008; Török *et al*., 2011; Deák *et al*., 2014b). However, saline grasslands are home to several plant endemics such as *Cirsium brachycephalum* Juratzka, *Limonium gmelinii* ssp. *hungarica* (Klokov), *Plantago schwarzenbergiana* Schur, *Puccinellia limosa* (Schur) Holmb. and *Aster tripolium* ssp. *pannonicum* (Jacq.) Dobrocz. (Molnár & Borhidi, 2003; Török *et al*., 2011). Compositional mosaicism of vegetation in saline grasslands is driven by microtopography, seasonal changes of astatic groundwater and salt content in the upper layer of the soil (Šefferová-Stanová *et al*., 2008; Deák *et al*., 2014b). These abiotic factors defined three main pasture types: open alkali swards, alkali steppes and alkali meadows. (i) Open alkali swards are the most affected by salts, which is concentrate in the upper soil layer and sometimes crystallize on the soil surface. During the springtime, shallow waters cover the surface of open alkali swards. These are species-poor communities mainly built by halophytes, and vegetation cover here is very sparse. (ii) Alkali steppes are dry short-grass habitats, moderately salt-affected and a bit humid in spring. According to the subordinate forbs, alkali steppes are divided into *Artemisia* alkali steppes (*Artemisia santonicum* L.) and *Achillea* alkali steppes (*Achillea setacea* Waldst. & Kit.). (iii) Alkali meadows are species-poor tall-grass stands that are exposed to low salt stress without droughts. These grasslands produce the biggest biomass among the above-mentioned and besides grazing, they can be used for hay-making too (Török *et al*., 2011; Deák *et al*., 2014b). Homogeneous stands of a single saline grassland type can be rarely found, usually patches of different grassland types form mosaic structures in the landscape (Török *et al*., 2011).

Saline grasslands have always been open habitats because salty soils and fluctuating groundwater rarely allowed the development of trees and shrubs (Molnár & Borhidi, 2003; Török *et al*., 2011). These ancient grasslands have been grazed by wild ungulates since the Pleistocene, but in the last few millennia, they have been used as low productive pastures grazed by domesticated cattle, sheep and horses. (Molnár & Borhidi, 2003; Eliáš *et al*., 2020). However, from the middle of the 19th century, drainage of marshlands and river regulations (e.g. the length of the Tisza River has been shortened by 134 km) caused the loss of many saline habitats, mostly wetlands being affected (European Environment Agency, 2002). Drainage caused salt leaching from the soils, thus, these habitats lost water and salts at the same time which assisted local extinction of halophytes (Molnár & Borhidi, 2003; Šefferová-Stanová *et al*., 2008; Deák *et al*., 2014a). On the other side, bad water management led to secondary salinization/alkalization and accidental conversion of non-alkali wetlands and grasslands to secondary saline pastures (Molnár & Borhidi, 2003; Török *et al*., 2011). Lastly, high demands for arable lands caused the disappearance of some saline grasslands and populations of unique species. Even though being unsuitable for intensive agriculture because of poor soil quality and unpredictable water fluctuations, in the post-World War II period there were and still are attempts for improvement of 'flawed' halomorphic soils, which were perceived as an economic and a political problem (Španović, 1948; Živković *et al*., 1972; Török *et al*., 2011; Manojlović, 2014). Ploughing caused loss of microrelief and characteristic zonation of saline grassland vegetation which is the hardest to recover besides the restoration of their water regime (Šefferová-Stanová *et al*., 2008; Eliáš *et al*., 2020). Also, habitat destruction leaves remaining fragments isolated from each other, so the landscape, in general, got simplified and its natural ecological network got weakened (European Environment Agency, 2002; Šefferová-Stanová *et al*., 2008).

Saline grasslands are not so sensitive to overgrazing and trampling since typical plants of saline pastures tolerate it very well (Molnár & Borhidi, 2003). However, high stocking rates during dry summers can cause total removal of vegetation and accumulation of dung, changing the chemical and physical composition of the soil and helping the proliferation of weeds and invasive plants in saline grasslands. In the cases where grazing is lacking, mowing is an alternative for grass biomass removal. Low productive saline grasslands are usually cut once a year—saline meadows in late June–July, *Puccinellia* swards in the second half of July—after the nesting season of highly protected ground-nesting birds like are *Crex crex* (Linnaeus, 1758) (corncrake), *Asio flammeus*

(Pontoppidan, 1763) (short-eared owl), *Charadrius alexandrinus* Linnaeus, 1758 (Kentish plover), *Himantopus himantopus* (Linnaeus, 1758) (black-winged stilt) and *Recurvirostra avosetta* Linnaeus, 1758 (pied avocet) (Šefferová-Stanová *et al*., 2008; Török *et al*., 2011). Regardless of a certain level of resilience of saline grasslands, these habitats still need proper conservation management. For the last 20 years, a lot of grazing experiments were executed in Hungary, and the general conclusion is the recommendation of extensive grazing by traditional breeds like Hungarian grey cattle (0.5–1 animal/ha) and racka sheep (5–7 animals/ha) for the management of the saline grasslands (Šefferová-Stanová et al., 2008; Török *et al*., 2011, 2018).

Saline grasslands of the Pannonian Region went through a lot, but their strongly stressed vegetation (e.g. exposed to salts, fluctuating water regime, droughts, grazing, burning and human activities of all kinds) still is in good shape making these semi-natural grasslands one of the best-preserved habitats in Europe (Bölöni *et al*., 2008; Török *et al*., 2011).

1.3. Insects in nature conservation

The decline of insect diversity and biomass is well documented and currently is one of the hot topics in scientific research, becoming an important political and economic issue as well (Dunn, 2005; Cardoso *et al*., 2011a; Wagner *et al*., 2021). Insects are an irreplaceable component of biodiversity and play vital roles in many ecological and environmental processes (pollination, soil formation, a food source for vertebrates, controlling mechanisms for populations of other organisms, etc.) thus, we do not know what are the potential consequences for ecosystems and human well-being if this trend of decline in insect diversity continues (Ward & Larivière, 2004; Harvey *et al*., 2020; Wagner *et al*., 2021). In the last decade, many review articles have been published on how to treat the ongoing insect crisis, some authors referred to it as 'insect apocalypse' (see Wagner *et al*., 2021), and all of them highlighted the need for joint work of scientists, governmental agencies, conservation practitioners and civil societies to set conservation priorities and take action (Cardoso *et al*., 2011b; Braby & Williams, 2016; Harvey *et al*., 2020; Hochkirch *et al*., 2020).

Insect conservation is an extremely complex issue with a lot of obstacles (many undescribed species or unsolved taxonomic status, unknown distribution, ecological functions and population trends of species, unexisting red lists and information on the conservation status of species, lack of monitoring programs and publicly available databases on insects, etc.) that will not be overcome anytime soon (Ward & Larivière, 2004; Cardoso *et al*., 2011a, 2011b; Hochkirch *et al*., 2020). Yet, our knowledge of certain species and groups still can be used in improving conservation tools and practices. For instance, well-known groups of insects are regularly used as surrogates that provide information on the health and naturalness of ecosystems, measure the success of specific management practices and restoration actions or report on the state of biodiversity (New, 1999; McGeoch, 2007; Sumways *et al*., 2020). Insect surrogates also serve as bioindicators of different taxonomic ranks and assemblage complexity; sometimes single well-known species can provide enough information, in other cases, a set of species or certain functional group(s) are used (Kremen *et al*.,1993; McGeoch *et al*., 2002; Cardoso *et al*., 2011b; Sumways *et al*., 2020). Insects have the potential to be highly specific indicators because some of them respond fast to a certain change in the environment by a rapid shift in abundance and community composition (Sumways *et al*., 2020); this sensitivity makes them potentially informative in scientifically based conservation planning (Kremen *et al*.,1993). Also, their omnipresence in ecosystems, tremendous diversity of taxa and functional groups, short life span, specialisation to microhabitats and restricted movements of some of them make insects ideal indicators of environmental change and habitat quality with higher resolution than vertebrates can ever provide (Kremen *et al*.,1993; New, 1999; Ward & Larivière, 2004; Cardoso *et al*., 2011b).

Who are good candidates for indicator insects? Sometimes species with well-known conservation status like endemics and rare species are used as bioindicators, but their restricted distribution and small detectability in samples make them not so practical for application in universal evaluation programs (Braby & Williams, 2016; Hughes *et al*., 2000). However, threatened species of a wider range usually perform well as indicators (Samways, 2005). Prominent threatened insects with good public visibility and distinct ecological requirements are often used as an 'umbrella' in conservation, aiming to protect and cover the needs of a spectrum of species (i.e. beneficiary species) in a particular area or habitat type (Roberge & Angelstam, 2003; Samways, 2005; Cardoso *et al*., 2011a). The umbrella species concept is attractive, but single species can never ensure the ecological needs of a community, therefore, a multi-species approach, based on several umbrellas which are complementary in their requirements and encompass plenty of resources and microhabitats, is a more promising alternative to the single species umbrella concept (McGeoch *et al*., 2002; Roberge & Angelstam, 2003).

New (1999) recognized three categories of invertebrates (refer to insects too) according to their applicability in conservation as bioindicators. (i) Well-know groups are those with well-established taxonomy, ecology and distribution of their taxa, where standard sampling and evaluation techniques can be applied and can be easily identified by amateur taxonomists (e.g. butterflies, dragonflies). (ii) Catch-up groups have moderately known ecological functions and can be involved in biodiversity assessments; these groups have great potential and their value in conservation can be increased significantly with a small effort. (iii) Black hole groups are usually poorly known with unsolved taxonomic issues, incoherent knowledge on their biology and/or distribution, and difficulties to sample them by standardized methods. Whatever are the arguments for choosing species or set of indicators, there is a consensus that the response of a bioindicator must be specific to a change in its environment, and it is the responsibility of researchers to identify and test it (Kremen *et al*.,1993; McGeoch *et al*., 2002; McGeoch, 2007). The utilization of indicator insects in environment assessment implies standardized and mutually comparable protocols of sampling and evaluation (New, 1999).

Biodiversity assessment is the first phase and foundation of any conservation planning, and its results provide arguments for the selection of the most suitable bioindicators, updates to the current conservation status of species, decisions on management and designation of new protected areas. The main forms of biodiversity assessment of insects are inventorying, mapping of species distribution, monitoring and red listing (Sumways *et al*., 2020). (i) Inventory is a state of the biodiversity at some point in time, ‘snapshot of the biodiversity’, and can refer to the biodiversity of any spatial scale, from local to regional. An inventory provides information on species richness and diversity, community composition, population structure, species of conservation interest, etc. (Samways, 2005; Braby & Williams, 2016). (ii) Mapping is a result of proper inventorying and refers to data on occurrences of individual species and their geographic distribution (Samways, 2005). These data can be used in detecting areas with the highest diversity of species, especially endangered and endemic species (i.e. biodiversity hotspots) and provide a baseline for environment-induced changes (e.g. climate change) of the species range (Cardoso *et al*., 2011b; Sumways *et al*., 2020). (iii) Monitoring is a periodical check-up of the biodiversity aiming to detect and/or measure the change from the previous assessment. Change of the biodiversity can be positive (e.g. improved by management activities) or negative (e.g. caused by harmful human impact) (Kremen *et al*.,1993; Samways, 2005; Sumways *et al*., 2020). (iv) Red listing is a process of cataloguing the species that are at some risk to be endangered or extinct. Red lists provide information on population trends and threatening factors (Samways, 2005), and are a powerful tool in lobbying for the legal protection of insect species. Red lists can provide funding for conservation projects, help in setting conservation priorities and in raising public awareness about the biodiversity crisis (Cardoso *et al*., 2011a, 2011b; Hochkirch *et al*., 2020). All aforementioned biodiversity assessment methods should have well-defined spatial and temporal scale, use standardized replicable methods and appropriate insect indicator(s), have minimal impact on evaluated species and their habitats and provide maximum information with minimal investments (Kremen *et al*.,1993; Samways, 2005; McGeoch, 2007; Hochkirch *et al*., 2020).

1.3.1. True bugs as bioindicators in terrestrial ecosystems

In the last two decades, terrestrial true bugs have been highly used as model organisms and bioindicators in ecological studies. Most of these experiments have been studying effects of grassland management, landscape heterogeneity and habitat quality on true bugs as surrogates of local biodiversity (Di Giulio *et al*., 2001; Rabitsch, 2008; Kőrösi *et al*., 2012; van Klink *et al*., 2013, 2016; Zulka *et al*., 2014; Simons *et al*., 2014a). Besides the basic descriptors of true bug communities (i.e. species richness, abundance, species composition), some studies also investigated how environmental factors determine functional and life-history traits of true bugs (Brändle *et al*., 2000; Zurbrugg & Frank, 2006; Woodcock *et al*., 2007; Simons *et al*., 2014b, 2016; Zulka *et al*., 2014; Gamez-Virues *et al*., 2015; Friess *et al*., 2017; Torma *et al*., 2017, 2019; Neff *et al*., 2019) consequently affecting the functionality of ecosystems (Neff *et al*., 2020, 2021). Moreover, herbivorous true bugs were used as model organisms in the research carried out on the relationship between body size and host range (Brändle *et al*., 2000) to test several ecological hypotheses aiming to explain distribution–abundance relationship (Friess *et al*., 2017) and in another study on the importance of plant–herbivore interactions in community assembly (Shinohara & Yoshida, 2021). In their vastly cited study, Duelli & Obrist (1998) ranked true bugs as one of the most suitable indicator groups for the evaluation of habitat quality and approximation of biodiversity in the European farmlands. The authors based their arguments on a highly significant correlation of diversity indices and total arthropod species richness.

Most of the terrestrial true bugs are phytophagous species with remarkable species richness in grassland and other open grassy habitats, therefore, they are mainly used as model organisms and indicators in these environments (Di Giulio *et al*., 2001; Achtziger *et al*., 2007; Friess *et al*., 2017). Herbivory of true bugs (with different degrees of specialization) makes them sensitive to any change in vegetation composition, structure or quality, and that is why studies on grassland management are so popular nowadays. One of the big research projects in Germany, the Biodiversity Exploratories covers 150 experimental grasslands and has been monitoring several invertebrate taxa (true bugs as well) for years to discover how management type and intensity determine biodiversity in long run and at different spatial and temporal scales (Fischer *et al*., 2010; Simons *et al*., 2014a, 2014b, 2016; Gossner *et al*., 2015b; Seibold *et al*., 2019; Neff *et al*., 2019, 2021). A similar project on grazing in coastal saline marshlands in the Netherlands was monitoring responses of true bugs and several other groups to changes caused by different grazing regimes (van Klink *et al*., 2013, 2016). Rabitsch (2008) recommended true bugs as indicators in future monitoring of conservation management in the area of the Neusiedler See-Seewinkel National Park by involving endangered true bugs, the specialists of saline and sandy habitats (Rabitsch, 2012). Duelli & Obrist (2003) stressed the convenience of using rare and endangered species in biodiversity assessments since species of high conservation importance, unlike common species, put additional worth to local biodiversity. Achtziger *et al*. (2007) considered true bugs as favourable indicators in assessments related to nature conservation because they have a high indicator value and comparatively low processing effort.

In a review article on the bioindication character of the Central European true bugs, Achtziger *et al*. (2007) gave numerous arguments for using true bugs as indicators, which greatly coincides with general criteria for the selection of terrestrial insect indicators given by McGeoch (2007). The arguments are as follows: (i) Taxonomy and systematic relationships of most of the European true bugs are stable; (ii) Knowledge of their faunistic, distribution and biology is reliable and available in various literary sources; (iii) True bugs are vastly present in all habitat types, have diverse ecological requirements, represent several trophic levels with different degrees of feeding specialization; (iv) Adults and larvae occupy the same habitat and have similar ecology; (v) True bugs have a very diverse and broad range of bionomic features (e.g. body size and shape, wing and leg length); (vi) Being the most species-rich hemimetabolous group, the number of true bug species is manageable for processing, i.e. species identification is not so complicated and time-consuming; (vii) These insects can be sampled easily by standardized methods, plus, costs of collecting and storage are low; (viii) True bugs provide a favourable ratio of number of species to number of individuals (i.e. high species richness with low abundance) and provide sufficient information for statistical analysis; (ix) The proportion of stenotopic species is high in endangered natural and semi-natural habitats. Achtziger *et al*. (2007), also, emphasized potential obstacles in the broader application of true bugs as bioindicators: (i) Number of people working on taxonomy and faunistic of true bugs are very low and some European countries do not have any heteropterist; (ii) Faunistic knowledge of different regions considerably vary, as well as, the availability of local checklists and red lists; (iii) The lack of comprehensive regional/national taxonomic keys in local languages is an issue that is not easy to solve in the near future; (iv) Our knowledge of the biology and ecology of small and hidden species is still insufficient.

Besides all limitations of using true bugs as indicators, their involvement in habitat and biodiversity assessments is increasing. As one of the ‘catch-up’ groups, true bugs have the potential to take a prominent role in the future of conservation planning and management (New, 1999). Gossner *et al*. (2015a, 2015b) provided the first open-access trait databases on 179 Central European species which can help researchers to study the roles of true bugs in terrestrial ecosystem processes. However, recognition of endangered and threatened true bug taxa is still mild and their current presence in the official red lists is very modest. For instance, the Annex II of the EU Habitats Directive lists only one alpine species from Northern and Central Europe (Council Directive 92/43/EEC; Gossner *et al*., 2018), whereas the IUCN Red List evaluated 23 true bugs and all of them are endemic to oceanic islands (IUCN, 2021). Hopefully, the growing visibility of these insects in online galleries and platforms for identification (e.g. Flickr, iNaturalist) can help with popularization and contribution to scientific research on true bugs by greater involvement of citizen scientists.

2. AIMS

True bugs have a good potential to become a staple group in all kinds of biodiversity and habitat assessments of the European mainland where the true bug fauna is well-known. The recognition of rare, endemic and endangered true bugs can raise the value of protected sites or assign the conservation significance to unprotected ones. Their numerous species have vast ecological functions and responses to environmental changes which can help to create fine-tuned and specific management according to local needs. The following aims of this thesis were addressed by using true bugs as bioindicators:

(i) Assessing the conservation status of saline grasslands at the edge of the Pannonian Region and identifying the key elements of true bug community structure in saline grasslands;
(ii) Assessing the effects of grazing as the most frequently applied management type on the biodiversity of saline grasslands;
(iii) Assessing the importance of drainage canals as secondary habitats in biodiversity conservation of saline grasslands.

The first part of the thesis is dealing with pioneer work on saline true bugs in the northern Serbian province of Vojvodina. Faunistic studies covered inventorying and mapping of saline habitat fauna with special attention to the distribution of saline specialists and potential red list candidates. Additionally, data from Serbia were used to investigate the community assembly of saline true bugs aiming to define default community structure which can be used as a reference in future monitoring programs. Establishment of minimal sampling was also explored to reduce unnecessary devastating effects to the true bugs and their habitats, but still, to provide high-quality data for statistical analyses and a good representation of the community composition (Chapter 3). The last two parts of the thesis cover two field studies conducted in Hungary. In the field experiment, grazing pressure and its effects on true bugs at different sub-community levels were investigated (i.e. functional groups, life stages). Here, the importance of season in community responses to management was also analysed (Chapter 4). The study on canals explored the supporting role of drainage canals as secondary habitats for grassland biodiversity of Hungarian farmland. Therefore, it was crucial to test how divergent is the biodiversity of canals and nearby saline grasslands and whether these habitats accommodate different true bug species and functional groups or not (Chapter 5).

The overall goal of the thesis is to contribute to the greater utilization of terrestrial true bugs as bioindicators.

3. TRUE BUGS OF SALINE GRASSLANDS AT THE EDGE OF THE PANNONIAN REGION

The northern Serbian province of Vojvodina was in focus for this phase of research, here true bug fauna was poorly explored compared to other Pannonian countries and an overall inventory of this area was necessary. The knowledge of historical data of true bugs in saline habitats of Serbia is very limited. The only notable source of earlier records is a comprehensive publication of Géza Horváth (1897) on the Hemiptera fauna of the Kingdom of Hungary when Vojvodina was a part of the Austro-Hungarian Empire. Horváth's article was a starting point for this study, thus the search for rare taxa listed by this author began by visiting historical localities more than a century later. This part of the study aimed to answer the following questions: (i) How rich is the true bug fauna nowadays in northern Serbia in comparison to historical data? (ii) How frequent and well-distributed are saline specialists and rare steppe species at the edge of the Pannonian Region?

In addition, the study investigated the nested pattern of true bug communities in the selected saline grasslands. Nested structure is a non-random pattern of species composition which refers to the situation when species present at species-poor sites constitute subsets of those present at species-richer sites (Patterson & Atmar, 1986). Studies on nestedness in terrestrial insects are relatively neglected and rare, where habitat area or habitat patch size is the best-investigated cause behind the nested pattern among insect communities (Fleishman & Murphy, 1999). The nested pattern also emerged in studies with equal-sized sampling plots, showing that not only a huge habitat area provides high species richness (species–area relationship), instead, other habitat characteristics like habitat quality are also responsible for nestedness in communities as well (Berglund & Jonsson, 2003; Hylander *et al*., 2005). Other frequently reported causes of nestedness in insects are life-history traits, habitat heterogeneity and sampling intensity (Fleishman & Murphy, 1999; Peintinger *et al*., 2003; Schouten *et al*., 2007). Considering all aforementioned causes behind nestedness, the following questions were addressed: (i) How different sampling methodologies (total inventory *vs*. standardized transects), sampling effort (total inventory *vs*. a single transect *vs*. three transects) and data type (binary *vs*. weighted) influence detection of nested pattern in true bug communities? (ii) Will true bug communities persist to show nested patterns if grass-feeders, the core of saline grassland community are excluded from the analyses? (iii) Which one of the assessed patch- and landscape-scale factors could cause nestedness in true bug communities when equal sampling effort is applied?

3.1. Materials and methods

3.1.1. Study area and sampling sites

The faunistical survey was conducted in the northern Serbian province of Vojvodina where altogether 138 sites (see section 11.1. of the Appendix for the details) were visited and sampled between 2015 and 2020 (Fig. 2). Numerous sampling sites covered a variety of habitats and vegetation types (i.e. primary and secondary saline grasslands, meadows and steppes, saline marshlands) but saline steppe vegetation was the main focus of the study. The vegetation of these grasslands was characterized by the presence of real halophytes (*Artemisia santonicum*, *Camphorosma annua* Pall., *Lepidium cartilagineum* Thell., *Plantago maritima* L., *P. schwarzenbergiana*) and dominant salt-tolerant grasses (*Puccinellia limosa*, *Festuca pseudovina* Hackel ex Wiesb.).

For studying nestedness of true bug communities, 17 saline pastures were selected as sampling sites (Fig. 2, R 2015 and R 2017 sampling sites). These grassland fragments considerably varied in size but showed well-representing vegetation and structure of a typical saline pasture in northern Serbia. The following criteria were considered during the site selection: (i) Only grasslands with typical *Artemisia* alkali steppe vegetation were selected. *Artemisia* steppes are a very characteristic and dominant vegetation type in saline pastures, recognized by *Artemisia santonicum* plants which stand out among dominant short salt-tolerant grasses, mostly represented by *Festuca pseudovina*; (ii) Exclusively grazed parts of grasslands were selected. The management can vary even within the same grassland, depending on a protected status (nature reserve or unprotected area), ownership (public or private land), etc; (iii) Parts of grasslands with homogenous plant cover were selected. Vegetation around the central point of sampling sites was relatively uniform, consisting of extensively grazed vegetation approx. 5–20 cm high (depending on the season), without shrubs and trees.

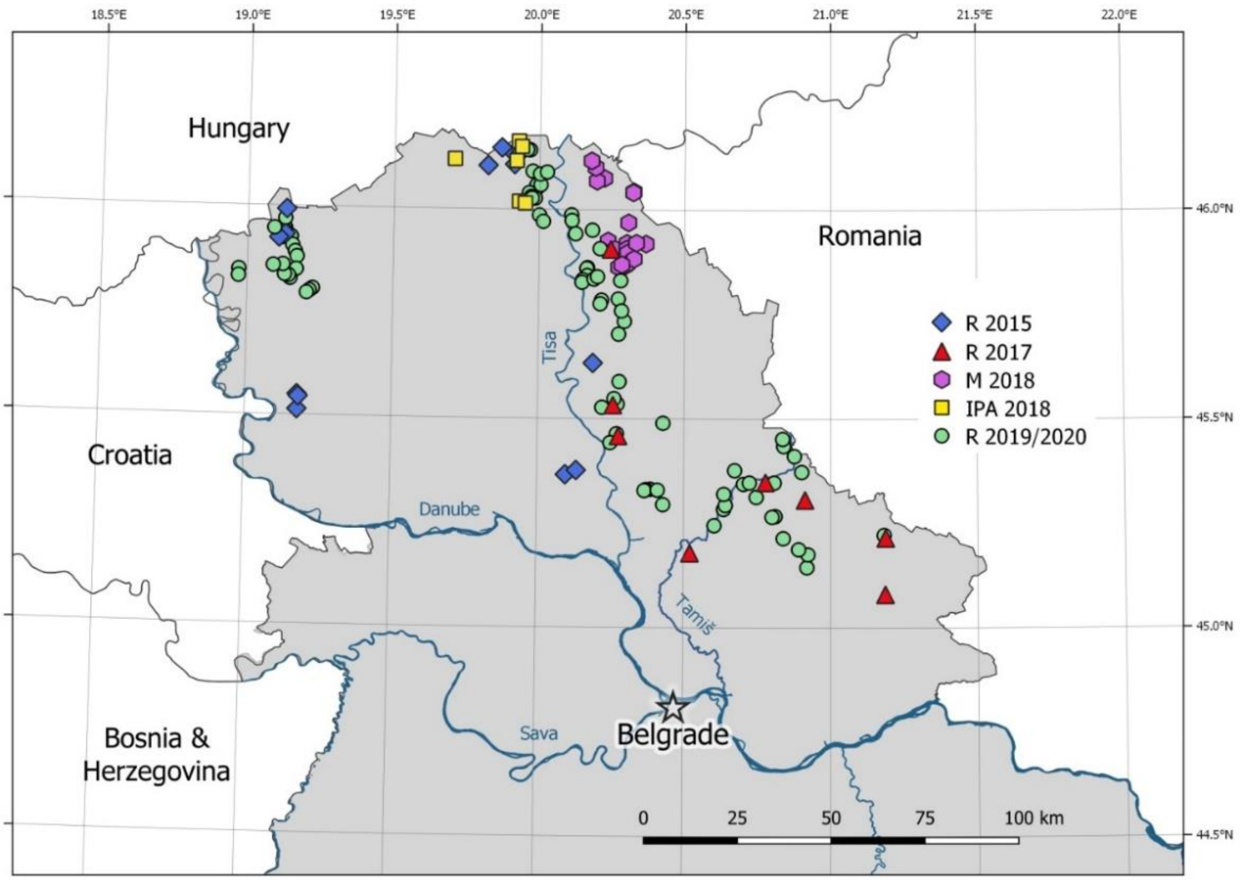

Figure 2. Distribution of sampling sites (colours and symbols refer to different projects).

3.1.2. <u>True bug sampling and identification</u>

Throughout the whole study (2015–2020) terrestrial true bugs were sampled by standard sweep-netting method, but in 2015, night sampling was also carried out; a LED/ UV 12 V lamp with 2 m × 1.8 m horizontal white cloth was installed in sampling sites. For collecting true bugs in the daytime, various sweep-net sampling procedures (total inventory, rapid assessment, targeted search for certain species, transects varying in length and number per sampling sites) were applied for the faunistic survey.

For studying nestedness, true bugs were collected every 3–4 weeks, from April to October in 2015 and 2017. In 2015, the first set of 9 sampling sites was surveyed, and in 2017, the second set of 8 sampling sites was surveyed. Three different sampling procedures were applied, varying in sampling effort and methodology: (i) In 2015, sweep-netting along a single 20 m long transect in the centre of each study site was conducted; (ii) In 2017, sampling was done along three parallel

30 m long transects per site. The starting and ending points of the transects were fixed and marked in the field to sample the same path during the whole sampling season; (iii) Lastly, in 2015, the total inventory of true bugs was applied. In this sampling procedure, consecutive samplings along random paths inside a buffer zone of approx. 100 m around central points of the sampling sites were performed. The total inventory sampling ended when a new taxon was not detected in two consecutive samples for the given sampling site and sampling occasion. All three sampling procedures were repeated seven times, i.e. seven sampling occasions for every procedure.

Samples with adult true bugs were sorted in the field immediately after sweeping. All specimens were preserved, i.e. dry stored in the freezer until identification. In the case of the total inventory, not all of the specimens were preserved and counted, because some species, e.g. *Acetropis carinata* (Herrich-Schäffer, 1841), *Amblytylus nasutus* (Kirschbaum, 1856) and *Conostethus hungaricus* are present in tens and hundreds in saline grasslands for a few weeks in May–June period. Therefore, total inventory is supposed to give information only on species richness of true bugs, in contrast, transect samples provided data on species richness and abundance.

Collected specimens of adult true bugs were identified up to species level. References used for species identification were Heiss & Péricart (1983), Kis (1984), Lehr (1988), Lis et al. (2008, 2012), Matocq & Pluot-Sigwalt (2012), Matocq (2004), Péricart (1972, 1983, 1984, 1987, 1998), Putshkov (1986), Rabitsch & Deckert (2007), Schuh *et al*. (1995), UkrBIN (2017) and Wagner & Weber (1964). Dry mounted specimens are deposited in the private collection of the author of this thesis.

Conservation status of species in the countries of the Pannonian Region mostly follows IUCN Red List categorization. In several cases there were extra categories; namely, ‘regionally extinct’ and ‘rare’, adapted to meet national conservation strategies. The following references were used to identify the conservation status of species in the Pannonian countries: Štepanovičová & Bianchi (2001) (Slovakia), Official Gazette of Slovenia (2010) (Slovenia), Rabitsch (2012) (Austria–Burgenland), Kment *et al*. (2017) (Czech Republic).

3.1.3. Vegetation sampling

Vegetation data were collected from May to September in 2017 and from May to June in 2018, where each sampling site was visited twice within the survey period. In May–June period (the first sampling) diversity of saline grassland is at its peak, but this is also a very unstable period and after rain, grasslands can be covered by shallow waters. In these circumstances, the vegetation survey could not be performed at some sampling sites in 2017 and therefore, was performed the following year. July–September period (the second sampling) is more stable, the soil is completely dry and vegetation is quite sparse and degraded by grazing.

In each sampling site, one 5 m × 5 m plot was fixed in the field. Every vegetation plot was established in the centre of a sampling site, covering the area of fixed transects and surveyed by using the standard methodology of the Braun-Blanquet cover–abundance scale (Braun-Blanquet, 1928, 1964; Horvat *et al*., 1950). The species richness of plants and their diversity (Shannon diversity index) were used as robust measures of possible habitat heterogeneity of sampling sites (Tab. 1).

Table 1. Landscape and vegetation features of surveyed saline grasslands.

	500 m buffer	1000 m buffer	
	Mean (min–max)	Mean (min–max)	Mean (min–max)
Grassland (%)	65.26 (21.59–90.91)	48.69 (14.02–77.54)	–
Arable land (%)	29.63 (4.17–74.32)	44.38 (18.88–80.80)	–
Shrubs and trees (%)	3.02 (0–18.08)	3.62 (0–13.84)	–
Orchard (%)	0.21 (0–1.75)	0.82 (0–5.22)	–
Uninhabited area (%)	1.85 (0–7.31)	2.45 (0.43–7.83)	–
Diversity index of land cover classes	0.73 (0.39–1.20)	0.88 (0.63–1.23)	–
Grassland patch size (ha)	–	–	147.60 (6.49–757.56)
Species richness of plants	–	–	12.17 (7–17)
Shannon's diversity index of plants	–	–	1.75 (0.62–2.60)

3.1.4. Data on landscape composition

Landscape features of the surrounding of sampling sites were derived from satellite images (XYZ Tile Layer, approx. 1:2,500 scale) in QGIS 3.4.7 Madeira software (QGIS Development Team, 2020). Satellite images helped in the mapping of present land covers in buffer zones of 500 m (lower scale) and 1,000 m (higher scale) from the centre of a sampling site. The selection of buffers was based on the literature review of similar studies which highlighted 500 m and 1,000 m buffers as the most appropriate (influencing) scale for arthropods in the agricultural landscape of Central Europe (Torma & Császár, 2013; Torma *et al*., 2014, 2018).

Five different land cover classes were distinguished: grassland, arable land, an area covered by shrubs and trees, orchard and 'uninhabited area' for terrestrial true bugs, i.e. water bodies and different man-made objects like roads, railways, houses, etc. In satellite images, it was not possible to distinguish precise area under *Artemisia* alkali steppe, thus the whole grassy area was put under 'grassland' category. The areas of all present land cover classes were measured and calculated as a percentile share in both buffer zones. The diversity of local landscapes was calculated by the Shannon-Wiener formula (Tab. 1).

3.1.5. Data analysis

Datasets were analysed for nestedness in the form of both binary and weighted matrices (except total inventory data) using package 'FALCON' (Beckett *et al*., 2014) in R Statistical Environment (R Core Team, 2022). To analyse binary matrices, NODF (Nestedness metric based on Overlap and Decreasing Fill) (Almeida-Neto *et al*., 2008) and spectral radius (Staniczenko *et al*., 2013) metrics were used to measure the degree of nestedness, and to weighted ones, WNODF (Weighted NODF) (Almeida-Neto & Ulrich, 2011) and spectral radius were applied. NODF is one of the most popular metrics and is known as independent of matrix shape and size, thus it is a perfect metric for the comparison of matrices varying in these features (Almeida-Neto *et al*., 2008; Ulrich *et al*., 2009). WNODF has the same logic as NODF but it is adjusted for quantitative data. Spectral radius is one of the newest metrics which could be applied to both, binary and quantitative data.

To test the statistical significance of nestedness in the binary matrices Swappable–Swappable (SS) and Cored–Cored (CC) models were used, and for weighted matrices Binary

Shuffle (BS) and Row Column Totals Average (RCTA) models were used. Requirements for choosing null models were that they have to conserve the size (number of rows and columns) and fill (percentage of filled cells in a matrix) of an original matrix. Additionally, one null model from the pair should be more strict by conserving some of the core structures found in the input matrix (CC and RCTA) (Beckett *et al.*, 2014). The most conservative Fixed–Fixed (FF) model was avoided because its column and row sums are strictly maintained and placement of species in such matrix is not random (Ulrich & Gotelli, 2012). Also, very liberal null models which vary in size and fill were not used because they are prone to Type I error, a tendency to falsely detect nestedness (Ulrich *et al*., 2009). The size of a null ensemble was 1,000 matrices.

The *sortVar* function in 'FALCON' was run to sort rows and columns in a way to maximize the nestedness of the input matrix and give a single robust nestedness value (Beckett *et al*., 2014). Based on this, factors that could cause the given ordering of sampling sites in matrices and nested patterns in communities were analysed. Spearman's rank correlation method was applied to test possible correlations between the site ordering and assessing true bug and vegetation data and landscape features of sampling sites as well.

3.2. Results

True bug fauna of saline grasslands

During the study 16,103 specimens were collected and 210 species were identified (see section 11.2. of the Appendix for the full list of species). The most important findings were records of new species from Serbian fauna—*Agramma* (*Agramma*) *ruficorne* (Germar, 1835), *Chlamydatus* (*Chlamydatus*) *saltitans* (Fallén, 1807), *Solenoxyphus fuscovenosus* (Fieber, 1864), *Lygaeosoma anatolicum* Seidenstücker, 1960, *Emblethis brachynotus* Horváth, 1897, *Geotomus punctulatus* (Costa, 1847) and *Phimodera flori* Fieber, 1863.

One of the main goals of the study was also the search for saline specialists and rare steppe species previously reported from northern Serbia. Therefore, rediscoveries are categorized in two groups: (i) on the basis of the last published records more than a century ago by Horváth (*Compsidolon* (*Apsinthophylus*) *pumilum* (Jakovlev, 1876), *Conostethus hungaricus* Wagner, 1941, *Criocoris sulcicornis* (Kirschbaum, 1856), *Crypsinus angustatus* (Baerensprung, 1859));

and (ii) on the basis of the last published records more than 50 years ago by other authors (*Acalypta gracilis* (Fieber, 1844), *Aoploscelis bivirgata* (Costa, 1853)). However, a few more interesting species mentioned by Horváth (1897) are still waiting to be rediscovered in Vojvodina—*Anapus longicornis* Jakovlev, 1882, *Megalocoleus dissimilis* (Reuter, 1876), *Diomphalus hispidulus* Fieber, 1864, *Geocoris arenarius* (Jakovlev, 1867) (syn. *Geocoris sirulus* var. *arenarius*) (Protić, 1998, 2001, 2011a, 2011b).

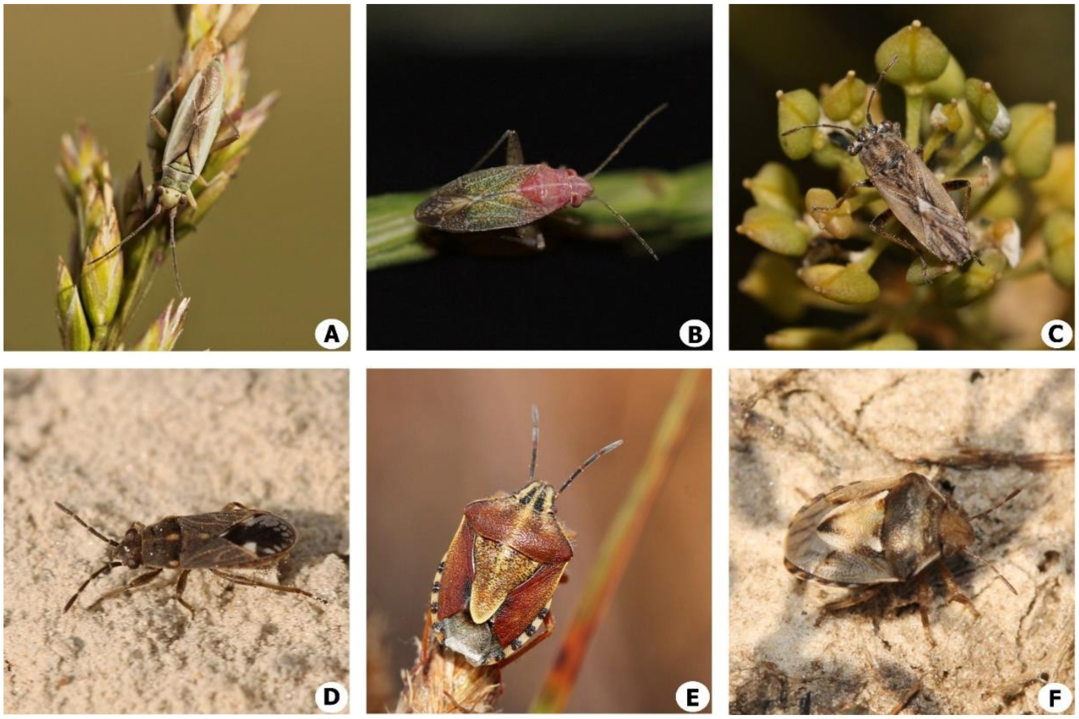

Figure 3. True bugs species related to the Pannonian saline grasslands—A. *Conostethus hungaricus*, B. *Solenoxyphus fuscovenosus*, C. *Henestaris halophilus*, D. *Lygaeosoma anatolicum*, E. *Antheminia varicornis*, F. *Crypsinus angustatus*.

<u>Nested true bug communities of saline grasslands</u>

Regardless of the different sampling procedures, a minority of species, i.e. grass-feeders (transects 20 m—27.5% and 3 × 30 m—23.8% of the recorded species) constituted a large share of the total abundance of true bugs sampled along transects (transects 20 m—65.7% and 3 × 30 m—78.8% of the collected individuals) (Tab. 2). It seems the number of collected grass-feeding species was similar when different sampling methodologies were applied, but the number of non-grass-feeding species considerably increased with the intensification of the sampling effort.

Table 2. Summarized data of species richness and abundance of true bugs according to the applied sampling procedure

		Full data				Grass-feeders data				Non grass-feeders data			
Sampling procedure	Data type	Species richness	Mean of species richness (min–max)	Abundance	Mean of abundance (min–max)	Species richness	Mean of species richness (min–max)	Abundance	Mean of abundance (min–max)	Species richness	Mean of species richness (min–max)	Abundance	Mean of abundance (min–max)
Transect 20 m	Binary & weighted	58	15 (10–22)	979	108.77 (15–206)	16	7.22 (3–10)	624	69.33 (6–204)	42	7.77 (2–13)	355	39.44 (2–68)
Transect 3 × 30 m	Binary & weighted	84	27.12 (16–42)	5264	658 (47–2221)	20	11 (8–17)	4153	519.12 (26–2134)	64	16.12 (8–25)	1111	138.87 (21–252)
Total inventory	Binary	153	58.55 (47–70)	–	–	24	16.44 (14–21)	–	–	129	42.11 (31–54)	–	–

A number of collected specimens for total inventory is not given because of the data irrelevancy to the study.

Analyses of nestedness in the true bug communities showed notable consistency in reporting the nested pattern, irrespective of the applied metrics, type and completeness of the data (Tab. 3). In analyses of binary data, total inventory seems to be the most reliable method. Both types of applied transects had similar power in detecting significant nestedness in the case of binary and weighted data. Spectral radius, compared to NODF and WNODF, recognized nested patterns more often, even when the conservative null models were applied.

Table 3. Effects of metrics, null model and data completeness in detecting a nested pattern in saline grassland true bug communities. Abbreviations: SR–spectral radius, SS–Swappable–Swappable, CC–Cored–Cored, BS–Binary Shuffle, RCTA–Row Column Totals Average.

	Matrix fill[1]	Null model	Metrics	Z	p-value	Metrics	Z	p-value
FULL DATASETS								
Binary			NODF			SR		
Total inventory	38.3%	SS	50.897	**12.576**	**≤0.001**	17.973	**25.514**	**≤0.001**
		CC	50.897	**3.595**	**≤0.001**	17.973	**4.997**	**≤0.001**
Transects 3 × 30 m	32.3%	SS	43.016	**7.935**	**≤0.001**	10.761	**13.024**	**≤0.001**
		CC	43.016	**2.106**	**0.023**	10.761	**3.128**	**≤0.001**
Transects 20 m	25.9%	SS	34.048	**5.125**	**≤0.001**	8.285	**11.607**	**≤0.001**
		CC	34.048	**1.732**	**0.047**	8.285	**3.744**	**≤0.001**
Weighted			WNODF			SR		
Transects 3 × 30 m	32.3%	BS	24.505	**5.623**	**≤0.001**	1846.934	**3.781**	**≤0.001**
		RCTA	24.505	-1.557	0.931	1846.934	**32.167**	**≤0.001**
Transects 20 m	25.9%	BS	20.080	**4.638**	**≤0.001**	158.808	0.440	0.299
		RCTA	20.080	-2.920	0.997	158.808	**26.192**	**≤0.001**
DATASETS WITHOUT GRASS-FEEDERS								
Binary			NODF			SR		
Total inventory	32.6%	SS	43.249	**9.779**	**≤0.001**	14.313	**18.916**	**≤0.001**
		CC	43.249	**2.809**	**0.007**	14.313	**4.078**	**≤0.001**
Transects 3 × 30 m	25.2%	SS	29.654	**3.729**	**≤0.001**	7.361	**7.275**	**≤0.001**
		CC	29.654	0.806	0.208	7.361	**1.917**	**0.033**
Transects 20 m	18.5%	SS	20.916	**2.571**	**0.007**	4.936	**4.274**	**0.002**
		CC	20.917	1.044	0.139	4.936	1.612	0.057
Weighted			WNODF			SR		
Transects 3 × 30 m	25.2%	BS	13.257	**2.319**	**0.008**	230.785	0.150	0.423
		RCTA	13.257	-4.357	1.000	230.785	**12.273**	**≤0.001**
Transects 20 m	18.5%	BS	9.497	**2.757**	**≤0.001**	81.306	**2.595**	**0.013**
		RCTA	9.497	-3.888	1.000	81.306	**11.831**	**≤0.001**

[1] Matrix fill represents % of occupied cells in a matrix. Binary and weighted matrices of the same dataset have the same fill value.

With the decrease of sampling effort, it seems that all metrics gradually lose power to detect significant nestedness and this corresponds to matrix fill, i.e. species occurrences in different sites (Tab. 3). The trend is especially evident when grass-feeders were excluded from the analyses, those impoverished matrices were still significantly nested in some case.

True bug species richness of a sampling site was the only factor significantly correlated to site rank in matrices and greatly induced nestedness (Tab. 4). However, when abundance data were included and the diversity of true bug communities calculated the correlation became insignificant. Plant cover features showed almost no influence on the nested pattern in true bug communities. A significant correlation was found only between plant species richness and site ranking in transect 3 × 30 m. None of the landscape features (grassland patch size, grassland share, land cover diversity) correlated to sampling site ranking.

Table 4. Results of Spearman's rank correlation analysis given in a ρ (rho) coefficient values.

	Ranked sampling sites in a matrix			
/ Sampling site	Total inventory (binary)	Transect 3 × 30 m (binary/weighted)[a]	Transect 20 m (binary)	Transect 20 m (weighted)
Species richness of true bugs	**-0.996*****	**-0.994*****	**-0.996*****	**-0.996*****
Shannon's diversity index of true bugs	–	-0.190	-0.600	-0.550
Species richness of plants	0.374	**0.826***	0.196	0.272
Shannon's diversity index of plants	-0.084	0.610	-0.050	-0.033
Diversity index of land cover classes in buffer of 500 m	-0.483	-0.524	-0.167	-0.267
Diversity index of land cover classes in buffer of 1000 m	-0.467	-0.381	-0.167	-0.217
Grassland share in a buffer 500 m (%)	0.467	0.452	0.117	0.233
Grassland share in a buffer 1000 m (%)	0.617	0.548	0.067	0.183
Grassland patch size (ha)	0.567	0.500	0.083	0.117

[a] Site ranking was the same for binary and weighted matrices in transects 3 × 30 m.
*** $p \leq 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$

3.3. Discussion

Among many dwellers of saline habitats in Serbia, species strongly connected to salt-affected areas are of special interest in conservation and can be divided into three groups: trophic specialists, habitat specialists and species associated with saline grasslands in the Pannonian Region (Fig. 3). (i) Trophic specialists (*Solenoxyphus fuscovenosus*, *Antheminia varicornis* (Jakovlev, 1874)) always appear in combination with a host plant specialized to salty soil, i.e. halophytes. (ii) Habitat specialists (*Conostethus hungaricus*, *Henestaris halophilus* (Burmeister, 1835)) do not have a preference for a single host plant or the host is not known, and typically are present in *Artemisia* steppe of the Pannonian Region. (iii) The last group consists of species which are highly associated with saline grasslands in the region but have broader distribution and can be found along the coasts of the Mediterranean Sea and the Black Sea (*Lygaeosoma anatolicum, Peritrechus meridionalis* Puton, 1877, *Crypsinus angustatus*) (Fig. 4).

Regardless of their exclusivity and prioritization in conservation, saline specialists can be highly frequent and even dominant in a certain season (e.g. *Conostethus hungaricus*) or in a certain vegetation type (e.g. *Solenoxyphus fuscovenosus*, *Antheminia varicornis*). However, we have no sufficient information on the distribution and biology of rare species in the Pannonian part of Serbia, thus they deserve a special place in red lists and conservation planning. There are 10 species with a maximum of three records or a maximum of three known locations in Serbia on the list of true bugs from saline grasslands. The cause of data scarcity on these species has to be explored, but species in the data deficient category should be treated as threatened, following the precautionary principle (Rabitsch, 2012).

What has to be done to achieve a better future for true bug species in saline habitats? A good solution could be to produce a regional red list of true bugs of the Pannonian Region. National red lists also have a purpose but in a different context and scale. An extensive evaluation of saline areas in Hungary is very important as it is the central country of the region, where the core populations of saline specialists are likely to be present. Well-preserved habitats and populations in Hungary could eventually also maintain the species elsewhere in the Pannonian Region. Until then, pressures on the saline habitat fragments should be reduced, mainly those coming from agriculture (Rabitsch, 2012).

Passive sampling was shown to be one of the determinants of nested pattern in spatially isolated communities but have received very little attention in studies on nestedness (Cutler, 1994). A study on orthopteran communities in the Netherlands showed that variations in sampling intensity among sampling sites had a strong impact on the observed degree of nestedness (Schouten *et al*., 2007). In this study, three sampling procedures were varying in intensity of true bug sampling and showed that even the minimal sampling effort—collecting of true bugs along single 20 m long transect—resulted in detecting significant nestedness. Therefore, there is no need for extreme time-consuming total inventory to be used in similar future studies on true bugs but there should be an awareness of a gradual decrease in pattern detection according to sampling effort reduction.

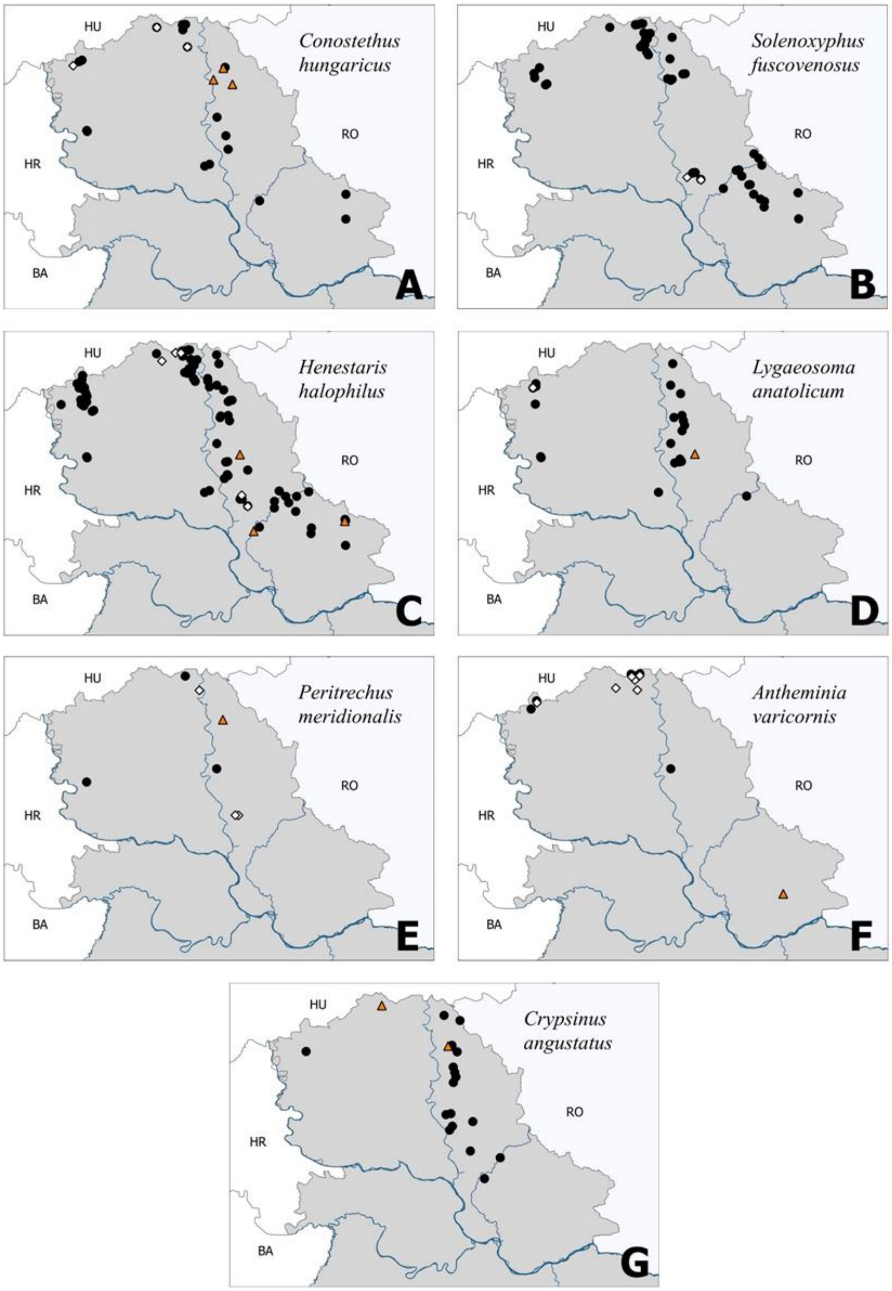

Figure 4. Distribution of saline specialists and species highly associated with saline habitats in northern Serbia (black dots—records of this study, white diamonds—records in Alciphron database on Serbian insects, orange triangles—literature data and/or specimens in the collection of Natural History Museum in Belgrade).

Grass-feeders are the most abundant and the most represented in saline grasslands, they are the core of a true bug community and to some extent, their exclusion from the analyses could be considered as reduced sampling effort. However, true bug communities without grass-feeders continued to be nested which means grass-feeders were not responsible for this structural pattern, but less numerous polyphagous generalists were. Patterson & Brown (1991) claimed one of the conditions for a nested pattern to exist is that relationships among species and their niches need to be organized hierarchically, i.e. fewer resources overlapping and tendency to have less specialized community members. In other words, generalist species use resources hierarchically and a larger share of generalists will ensure highly nested communities. A similar explanation was given by Nielsen & Bascompte (2007) who analysed plant–pollinator networks and showed that nestedness is less sensitive to sampling effort if a network contains a core group of generalists interacting with each other. They also demonstrated how nestedness is more sensitive to network (matrix) size and fill. This study confirmed this as well by showing how a higher number of species (matrix size) and more frequent species occurrences in different sites (matrix fill) provided higher values of nestedness and a more steady pattern.

Habitat area (habitat patch size) is known to be one of the most important factors that determine species composition patterns in fragmented landscapes (Watling & Donnelly, 2006; Schouten *et al*., 2007; Menezes & Fernandez, 2013; Matthews *et al*., 2015). Nevertheless, several studies found that species richness varies and nested pattern occurs among habitat patches of uniform size as well (Berglund & Jonsson, 2003; Hylander *et al*., 2005). The results of this study showed no correlation between grassland patch size and site ranking in nested matrices, which corresponds to the results obtained by other authors that nestedness is not necessarily affected by the habitat area. Matthews *et al*. (2015) suggested that rigorous analysis is needed to investigate the actual role of the habitat area in driving nestedness in habitat islands.

Besides the habitat area, the other landscape features also do not contribute significantly to the nested pattern in true bug communities and there are two possible explanations for this. The first could be that majority of saline grassland true bugs are generalist species, commonly present in surrounding terrestrial habitats and landscape matrix thus, a higher diversity of land cover classes does not necessarily mean higher species richness. In the modified landscape of the Pannonian plain, neighbouring semi-natural grasslands and similar man-made grassy habitats such as grass margins along ditches, roadside verges and dikes, may share a lot of species and have very similar insect communities (see e.g. Torma & Császár (2013) for dikes, Torma *et al*. (2018) for ditches, Kaur *et al*. (2019) for road verges).

The second possible explanation could be that true bugs like many other invertebrates use space at a fine scale (Gallé *et al*., 1988; Wright *et al*., 1998; Kőrösi *et al*., 2012). In this case, habitat nestedness is the factor that drives communities and causes the nested pattern. Habitats are nested if many discrete habitats (microhabitats) can be recognized at one site and if there is a gradient in habitat complexity among sites (Hylander *et al*., 2005). As mentioned before, one of the most characteristic features of saline grasslands is the fine-scale mosaics of halophytic vegetation patches within a very limited area (Molnár & Borhidi, 2003; Deák *et al*., 2014b). Even though *Artemisia* alkali steppe vegetation in the study looked relatively uniform throughout surveyed grasslands, there had to be certain variations in habitat complexity considering the differences in recorded species of true bugs among sampling sites. Schouten *et al*. (2007) showed a strong relationship between habitat diversity and orthopteran species ordering in the matrix. Several other studies also reported that orthopteran populations can persist for a long time in very small high-quality habitat patches in fragmented European landscapes (Schouten *et al*., 2007; Poniatowski & Fartmann, 2010; Löffler *et al*., 2020). Therefore, if the high-quality habitat elements are well-preserved, the reduction in patch size does not necessarily imply loss of fine-grained habitat heterogeneity (Berglund & Jonsson, 2003). This could explain why grassland patch size was not an important factor in determining the nestedness of true bugs in saline grasslands, and why some of the smallest patches in the study sustained richer true bug fauna than huge ones.

In this study, plant species richness and plant diversity were used as indicators of habitat heterogeneity but it seems that these vegetation descriptors are too robust to define the complexity of an *Artemisia* alkali steppe. It could also be that many abiotic and biotic factors affect habitat heterogeneity so more details on microclimate parameters or fine vegetation structure might explain these grasslands better. Ulrich *et al*. (2009) highlighted disturbance as a habitat quality feature and one of the causes of nestedness. In that case, management (moving, grazing) or lack of it (abandonment), as well as its intensity, could determine a nested pattern in true bugs.

What is the conservation application of nestedness for grassland true bugs? (i) Tool in biodiversity assessment. Nestedness analysis can give us information about habitat fragments with the highest species diversity and habitat complexity, but also, which one is the richest in exclusive species (idiosyncratic species) and rare resources (idiosyncratic sites) (Atmar & Patterson, 1993;

Hylander *et al*., 2005; Ulrich *et al*., 2009). (ii) Tool in detecting ecological mechanisms which shape communities. Investigating the origin of a community nestedness can help in identifying site characteristic–species trait causations (Ulrich *et al*., 2009).

4. TRUE BUGS IN THE ASSESSMENT OF SALINE GRASSLAND MANAGEMENT

Alkali meadows (hereafter wet saline grasslands) and *Artemisia* salt steppes (hereafter dry saline grasslands) are among the most common saline grassland types of the Pannonian Region and habitats which cover the widest area in Hungary and Serbia (Molnár & Borhidi, 2003; Lakušić *et al*., 2005). (i) Wet grassland patches developed in depressions where groundwater is close to the surface. The vegetation of these grasslands is generally tall and dense, dominated by the grass species like *Alopecurus pratensis* L. and *Agrostis stolonifera* L. Plant biomass production in wet grasslands is comparatively greater than in dry ones. (ii) Dry grasslands developed at relatively higher elevations of microrelief and are characterized by short and sparse vegetation. The dominant plant species in these habitats is short-growing grass *Festuca pseudovina* and the characteristic subordinate species *Artemisia sanctonicum* (Török *et al*., 2011, 2018; Deák *et al*., 2014b).

Following the contrasting vegetation structure and microclimate, different true bug communities inhabit dry and wet saline grasslands (Torma *et al*., 2019), therefore, those communities may respond uniquely to the environmental changes induced by the same management regime. Accordingly, the following questions were addressed: (i) Do species richness, abundance and functional trait values of opposite groups within the true bug community (plant- *vs*. ground-dwellers, adults *vs*. nymphs) differ between grazed and ungrazed parts? (ii) Do season (spring *vs*. summer) and vegetation type (wet *vs*. dry saline grassland) influence the effects of grazing on true bugs? (iii) How divergent are the true bug communities of wet and dry saline grasslands?

4.1. Materials and methods

4.1.1. Study area and sampling sites

The study was conducted in the Körös-Maros National Park in southern Hungary and one of its Natura 2000 and nationally protected areas, Csanádi puszták (Fig. 5). The dominant open semi-natural habitat type in the region is a loess steppe, but saline vegetation developed in depressions of solonetz soils. In the past, an extensive area of loess steppes was ploughed and transformed into arable land, however, some localities like Csanádi puszták still preserve the original vegetation of saline grasslands. Csanádi puszták has total area of 4,057 ha and consists of three separate grasslands—Kopáncs, Montág and Királyhegyesi pusztas (Fig. 5). Wet and dry saline grassland patches cover 22.1% and 26.5% of the protected area, respectively (Molnár *et al.*, 2016).

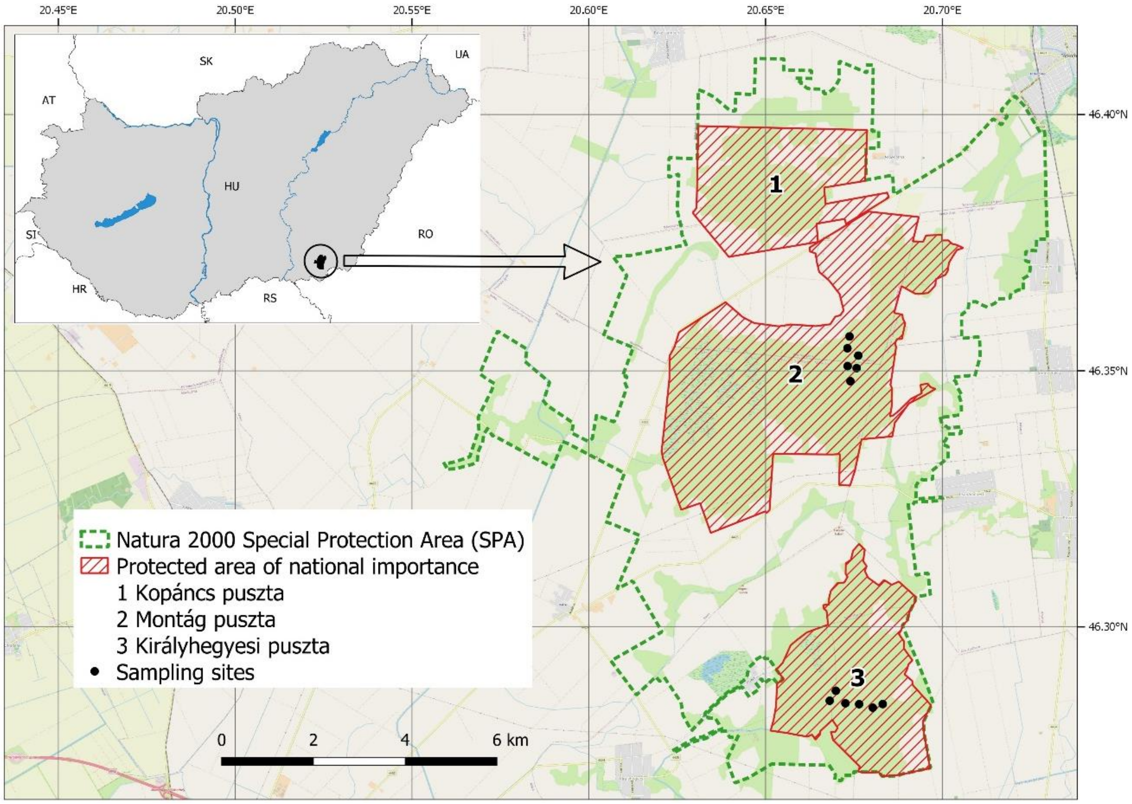

Figure 5. Study area and sampling sites in Csanádi puszták.

The sampling sites for this study were located in Királyhegyesi and Montág pusztas, where Hungarian Grey Cattle have been herded since 2006. The livestock density in this area is 0.5 animals/ha but has slightly varied between the two grasslands over the years. In 2018, the year of the study, 400 ha of the study area in Királyhegyesi puszta was grazed by 160 cows, whereas in the Montág puszta *c*. 800 ha was grazed by 170 cows and a similar number of calves.

A sampling site was defined as a 50 m × 100 m fenced area (hereafter experimental plot) with an inner ungrazed area and extensively grazed grassland outside the fence (Fig. 6). In total 12 sampling sites were surveyed, 6 in each saline grassland type, with a minimum distance of 100 m among them. All experimental plots were established in locations where the vegetation visually looked quite homogenous and before the start of the grazing season in early spring.

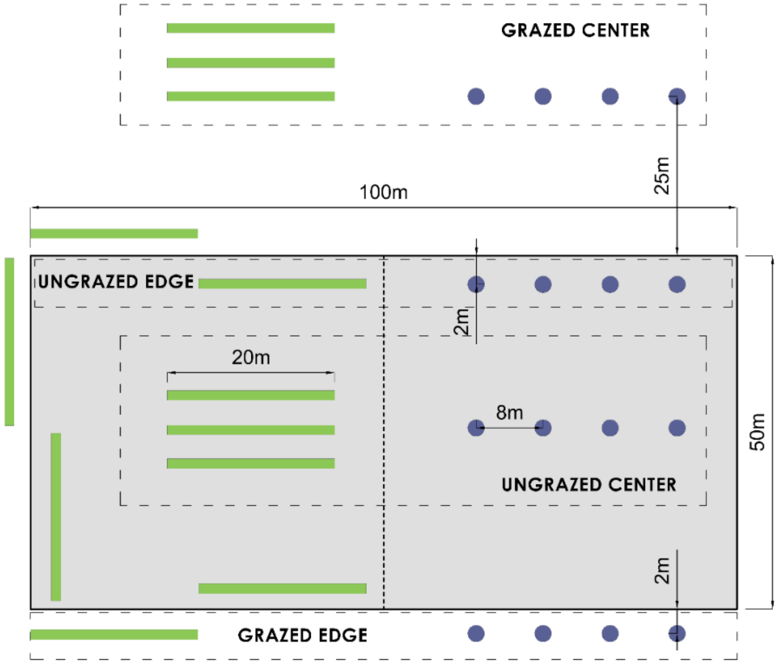

Figure 6. Experimental design and organisation of a sampling site (green stripes—sweeping transects, blue-grey dots—pitfall traps).

4.1.2. True bugs sampling and identification

Each experimental plot was divided into two equal subplots (50 m × 50 m) to implement two different collecting methods for true bugs (sweep-netting and pitfall-trapping) without interfering with each other (Fig. 6). Sweep-netting is the standard method for collecting plant-dwelling insects, like are most of the true bugs. On the other hand, pitfall-trapping is not typical for true bug sampling, but it is widely used for catching ground-dwelling arthropods. For pitfall traps, 500 ml white plastic cups with a diameter of 8.5 cm filled with 50% ethylene-glycol and a water solution containing a few drops of odourless detergent to preserve the sample and to reduce the chance of escaping were used. The traps were fitted with transparent plastic funnels to reduce vertebrate bycatches and to increase trapping efficiency and placed a plastic roof above each trap was placed to prevent the dilution of the preservative.

The sampling of true bugs was conducted in four different regimes: (i) in the centre of an experimental plot (ungrazed centre), (ii) at the inner sides of a plot (ungrazed edge), (iii) at the outer sides of a plot (grazed edge) and (iv) at the distance of 25 m from a plot (grazed centre). In total 2×4×12 statistical samples were obtained (2 sampling types × 4 sampling regimes × 12 sampling sites), but a single statistical sample consists of pooled samples collected by sweeping along three constant 20 m long transects (i.e. 3 × 25 sweeps) or samples collected by four pitfall traps in a row with an inter distance of 8 m in one of the aforementioned regimes (192 traps were instaled in total) (Fig. 6). All of the collected samples were placed in plastic bags filled with 70% ethanol and stored in a freezer until identification.

The procedure of species identification in adult true bugs is explained in section 3.1.2., where, nymphs were classified as morphospecies because of the lack of reliable literature for nymph identification up to the species level. True bugs collected in Hungarian saline grasslands are stored at the Department of Ecology, University of Szeged.

Aiming to investigate the effects of early and late grazing season on true bugs, two sampling periods were designated. True bugs were firstly sampled in Montág puszta by the method of sweep-netting on 10 May 2018, whereas, pitfall traps were installed in the field from 10 to 23 May 2018. The second sampling was done in Királyhegyesi puszta where sweep-netting was applied on 11 June 2018 and pitfall-trapping from 12 to 21 June 2018.

4.1.3. Attributes of the true bug communities

Species richness, abundance and values of the community-weighted mean (CWM) are proven to provide comparable information in community-level studies (Simons *et al*., 2016; Neff *et al*., 2019; Torma *et al*., 2019) and were used in this study to measure the responses of true bugs to cattle grazing and habitat type. Species richness and abundance are fundamentals in the quantification of community diversity and composition, they have been mainly used as descriptors in ecology and conservation studies. CWM calculates community trait values (based on species functional traits) weighted by species abundances to give information on attributes of the community which can be related to certain environmental factors.

CWM values of body size, feeding specialization and preference for habitat humidity of true bugs were used for further analysis (Tab. 5). Body size was defined as the mean length of an adult body, thus this trait was not analyzed for nymphs because of the presence of more developmental stages of nymphs in samples and differences in their sizes. In the case of feeding specialization, true bugs were categorized as monophagous (feed on one plant species or species from one genus), oligophagous (feed on species from the same family of plants) or polyphagous (feed on species from multiple plant families). Based on the preference for habitat humidity, species were divided into five groups, those which prefer dry, mostly dry, semi-humid, humid habitats and species which are indifferent to habitat humidity. All information on functional traits of the true bugs were taken from the available literature and databases (Wagner & Weber, 1964; Péricart, 1972, 1983, 1984, 1987, 1998; Wachmann *et al*., 2004, 2006, 2007, 2008; Gossner *et al*., 2015a, 2015b; UkrBIN, 2017).

Table 5. Community attributes analyzed in the study.

Attribute	Values
Species richness	Number of species
Abundance	Number of specimens
CWM body size	Body length in mm
CWM feeding specialization	0–monophagous, 0.5–oligophagous, 1–polyphagous
CWM humidity preference	0–dry, 0.25–mostly dry, 0.5– indifferent to humidity, 0.75–semi-humid, 1–humid

4.1.4. Data analysis

To detect possible edge effects and analyze the response of true bugs to grazing in different grassland types, generalized linear mixed models (GLMM) were applied by using the R package ‘lme4’ (R Core Team, 2020; Bates *et al*., 2015). Species richness, abundance and CWM trait values of true bugs were used as response variables. Vegetation type (wet *vs.* dry grassland), management treatment (grazed *vs.* ungrazed) and location of a sample (edge *vs*. centre) were used as explanatory variables, whereas the experimental plot was considered as a random effect. Interactions of the main effects were also incorporated into the models.

In the case of response variable species richness, *glmer* function with Poisson distribution setup was applied, on the other hand, for abundance data, negative binomial models were run with the help of *glmer.nb* function. In models with functional traits as a response, *lmer* function was used and CWM values were previously calculated by *functcomp* function in the 'FD' package (Laliberté & Legendre, 2010). *Anova* function of the 'car' package (Fox & Weisberg, 2019) was used to test the statistics of the GLMMs.

For the visualization of true bug communities in dry and wet saline grasslands, non-metric multidimensional scaling (NMDS) was applied as the ordination method and for this purpose *metaMDS* function of 'vegan' was used (Oksanen *et al.*, 2017).

To detect species associated with a certain vegetation type or with grazed/ungrazed parts of grasslands, the indicator species approach was applied (Dufrêne & Legendre, 1997) using *multipatt* function with the *IndVal.g* setting in the R package 'indicspecies' (De Cáceres & Legendre, 2009). The statistical significance of the species indicator values was assessed by a permutation test using 10,000 permutations.

4.2. Results

The number of adult true bugs collected during this study was 32,748 (pitfall-trapping—261 specimens, sweep-netting—32,487 specimens) which belong to 88 species (pitfall-trapping—37 species, sweep-netting—65 species). The number of collected nymphs by sweep-netting was 3,315 which belong to 34 morphospecies. The data on nymphs collected by pitfall traps was not analyzed because only a few specimens were collected.

The most frequent species in pitfall traps caught were *Acalypta marginata* (Wolff, 1804), *Peritrechus gracilicornis* Puton, 1877 and *Lygaeosoma anatolicum* with a frequency of 13.41%, 13.41% and 11.88%, respectively. The most frequent species collected by sweep-netting were specialized grass-feeders *Acetropis carinata, A. longirostris* Puton, 1875 and *Amblytylus nasutus* with a frequency of 69.26%, 10.85% and 9.56%, respectively. In the case of nymphs, the most frequent morphospecies collected by sweep-netting were 'Acetropis carinata', 'Stenodema calcarata' and 'Rhopalus parumpunctatus' with a frequency of 37.92%, 16.08% and 9.38%, respectively.

The results of GLMMs showed that true bug communities of saline grasslands were mostly shaped by vegetation type and management (Tab. 6). The location of a sample (i.e. samples taken from an edge or a centre of an ungrazed experimental plot or a grazed surrounding grassland) was the least important factor in shaping true bug communities. Only some minor edge effect was reported in ground-dwelling true bug communities (see section 11.3. of the Appendix).

Table 6. Effects of vegetation type (wet/dry), management (grazed/ungrazed) and location of the sample (edge/centre) on saline grassland true bug communities explained by GLMMs.

		Vegetation		Management		Location		Veg.×Man.		Veg.×Loc.	
MAY		χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p
Pitfall trap (adults)	Species richness	0.065	0.798	0.066	0.798	0.000	1.000	0.276	0.599	0.067	0.796
	Abundance	0.316	0.574	1.081	0.298	2.114	0.146	0.112	0.738	0.002	0.962
	CWM size	**4.019**	**0.045**	0.638	0.424	0.059	0.807	0.907	0.341	2.150	0.142
	CWM humidity	0.185	0.667	**4.629**	**0.031**	0.103	0.748	0.049	0.825	0.135	0.713
	CWM feeding	0.000	0.990	3.577	0.058	0.016	0.900	**4.150**	**0.042**	2.748	0.097
Sweep-net (adults)	Species richness	3.498	0.061	0.247	0.619	0.248	0.618	0.323	0.569	0.004	0.947
	Abundance	0.162	0.688	0.075	0.784	0.779	0.377	0.038	0.845	1.513	0.219
	CWM size	2.569	0.109	**9.109**	**0.002**	0.034	0.853	**9.937**	**0.002**	0.278	0.598
	CWM humidity	**7.641**	**0.006**	**8.443**	**0.004**	0.139	0.708	**21.008**	**≤0.001**	0.008	0.927
	CWM feeding	3.671	0.055	1.062	0.303	0.004	0.949	1.684	0.194	0.125	0.724
Sweep-net (nymphs)	Species richness	1.579	0.209	0.053	0.818	0.472	0.492	0.000	0.988	0.351	0.553
	Abundance	3.055	0.080	**8.084**	**0.004**	3.300	0.069	0.000	0.992	0.339	0.559
	CWM humidity	2.420	0.119	1.242	0.265	0.010	0.917	**4.581**	**0.032**	1.492	0.221
	CWM feeding	0.042	0.836	0.743	0.388	0.019	0.891	0.644	0.422	2.132	0.144
JUNE											
Pitfall trap (adults)	Species richness	0.252	0.615	0.010	0.919	0.820	0.365	0.269	0.604	1.175	0.278
	Abundance	0.161	0.688	0.075	0.784	0.779	0.377	0.038	0.845	1.513	0.219
	CWM size	3.529	0.060	1.368	0.242	0.001	0.969	0.429	0.512	0.418	0.518
	CWM humidity	0.634	0.428	0.317	0.573	1.813	0.178	0.002	0.959	0.831	0.362
	CWM feeding	3.495	0.061	0.187	0.665	**6.710**	**0.009**	2.584	0.108	1.591	0.207
Sweep-net (adults)	Species richness	**4.843**	**0.028**	**4.284**	**0.038**	0.048	0.827	2.199	0.138	0.606	0.436
	Abundance	**45.190**	**≤0.001**	**28.829**	**≤0.001**	0.674	0.412	0.808	0.368	0.151	0.698
	CWM size	**12.194**	**≤0.001**	0.319	0.572	0.250	0.617	0.491	0.483	0.195	0.659
	CWM humidity	**121.953**	**≤0.001**	3.006	0.083	3.664	0.056	0.927	0.335	0.559	0.455
	CWM feeding	**25.904**	**≤0.001**	0.619	0.431	1.276	0.258	0.626	0.429	0.019	0.889
Sweep-net (nymphs)	Species richness	3.810	0.051	2.079	0.149	1.581	0.208	0.699	0.403	0.973	0.324
	Abundance	0.264	0.607	**30.219**	**≤0.001**	3.793	0.051	**8.573**	**0.003**	2.148	0.143
	CWM humidity	**69.496**	**≤0.001**	0.125	0.724	0.004	0.949	1.262	0.261	0.923	0.337
	CWM feeding	**23.174**	**≤0.001**	1.373	0.241	0.004	0.947	0.301	0.583	0.095	0.757

Ground-dwelling true bugs (pitfall-trapping)

In May, only functional traits of ground-dwelling true bugs were affected by management and vegetation. The interaction of management and vegetation determined the feeding preference of ground-dwellers. Wet saline grasslands had a bigger share of polyphagous true bugs than dry ones, also, polyphagy was favoured in their ungrazed parts, whereas oligophagous herbivores were more frequent in grazed parts of wet grasslands (Fig. 8a). The results on humidity preference showed that grazed parts of sampling sites were dominated by individuals which prefer drier habitats regardless of the vegetation type (Fig. 8c). The size of ground-dwelling true bugs was on average higher in wet compared to dry grasslands (Fig. 9a).

In June, feeding preference of ground-dwelling true bugs was influenced by the edge effect in wet saline grasslands and the community structure was shifted towards polyphagous individuals in the centre of sites (grazed and ungrazed) compared to their edges (Tab. 6, section 11.3. of the Appendix).

The NMDS ordination showed high overlapping of ground-dwelling communities from wet and dry saline grasslands in May, but the major separation was detected among communities in June (Fig. 10).

Plant-dwelling adult true bugs (sweep-netting)

In May, some functional traits of plant-dwelling true bug communities were strongly influenced by joined effects of management and vegetation. According to humidity preference, wet saline grasslands were occupied by bigger size true bugs who favoured habitats with greater humidity compared to dry grasslands and this was especially prominent in ungrazed experimental plots of wet grasslands (Fig. 8c, 9a).

In June, species richness and abundance were determined by vegetation and management, where dry saline grasslands had a higher number of species and specimens compared to wet ones, but also, ungrazed parts of dry and wet grasslands were richer in true bugs than grazed ones (Fig. 7b, 7d). Functional traits of plant-dwelling true bugs were strongly and entirely affected by vegetation type. Dry saline grasslands promoted communities that consisted of bigger size and drought-tolerant polyphagous herbivores (Fig. 8b, 8d, 9b)

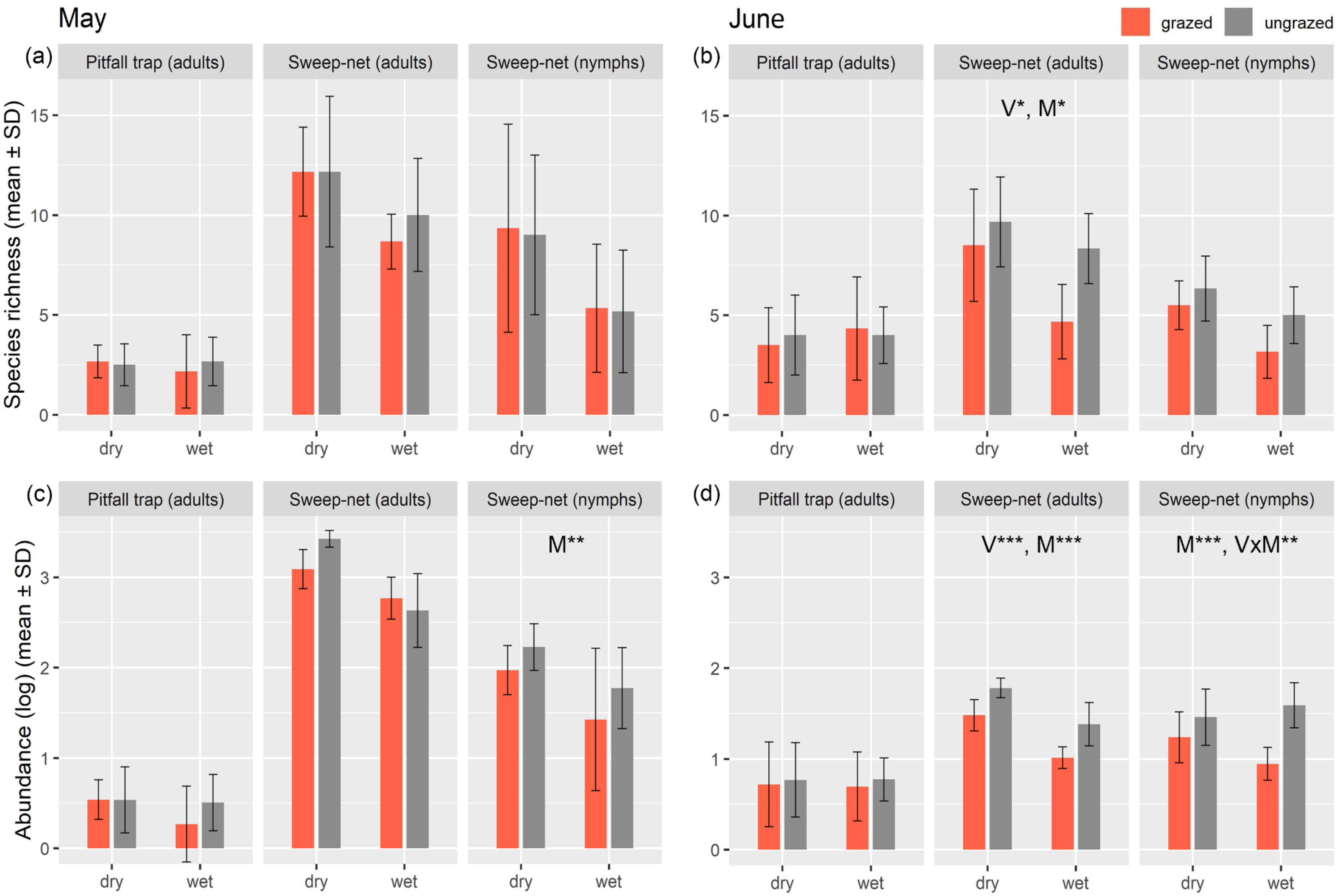

Figure 7. Effects of management (grazed *vs*. ungrazed) and vegetation type (dry *vs*. wet) on species richness and abundance of true bugs in saline grasslands according to GLMMs. Significant results are marked with asterisks (*** p ≤ 0.001, ** p ≤ 0.01, * p ≤ 0.05). Abbreviations: V–vegetation type, M–management.

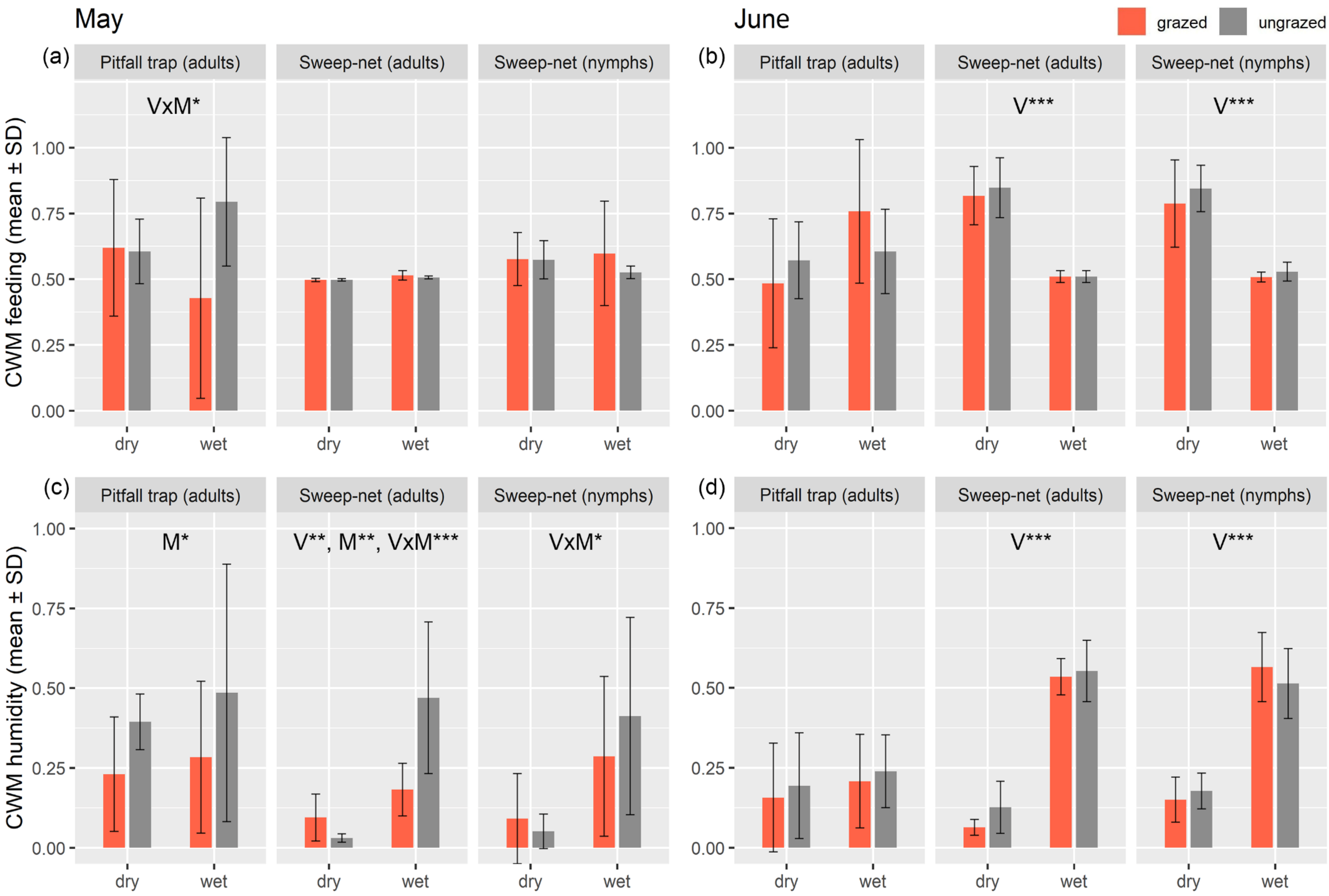

Figure 8. Effects of management (grazed *vs*. ungrazed) and vegetation type (dry *vs*. wet) on feeding specialization and humidity preference of true bugs in saline grasslands according to GLMMs. Significant results are marked with asterisks (*** $p \leq 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$). Abbreviations: V–vegetation type, M–management.

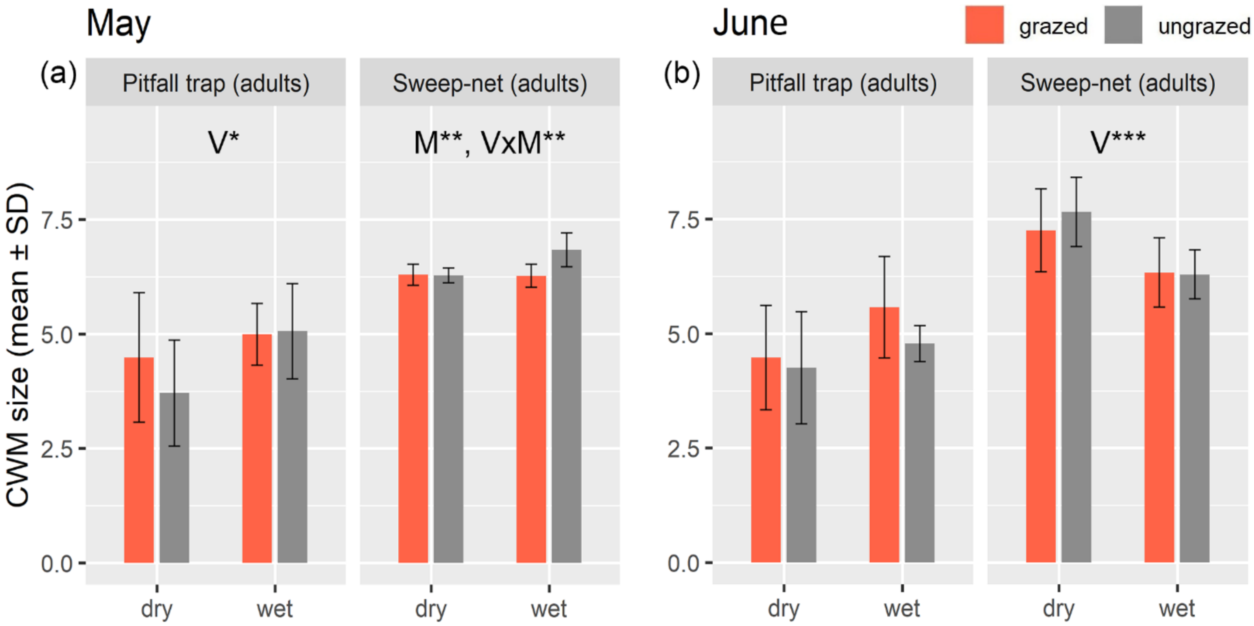

Figure 9. Effects of management (grazed *vs*. ungrazed) and vegetation type (dry *vs*. wet) on body size of true bugs in saline grasslands according to GLMMs. Significant results are marked with asterisks (*** $p \leq 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$). Abbreviations: V–vegetation type, M–management.

The NMDS results showed small overlapping of plant-dwelling true bug communities from different grasslands in May, but they diverged completely in June (Fig. 10).

Plant-dwelling juvenile true bugs (sweep-netting)

In May, the abundance of plant-dwelling nymphs was affected by management, where ungrazed parts of grasslands held more nymphs (Fig. 7c). Also, the combined effects of management and vegetation defined community structure by promoting nymphs with higher preference for more humid habitats in wet saline grassland, especially in their ungrazed parts compared to grazed ones (Fig. 8c).

In June, management and vegetation strongly influenced nymph communities, resulting in a higher number of individuals in wet compared to dry grasslands and in ungrazed compared to grazed parts regardless of the vegetation type (Fig. 7d). Similar to the results of plant-dwelling adults, functional traits of plant-dwelling nymphs were affected by vegetation type only, where dry grasslands held a higher amount of polyphagous true bugs preferring dry habitats (Fig. 8b, 8d).

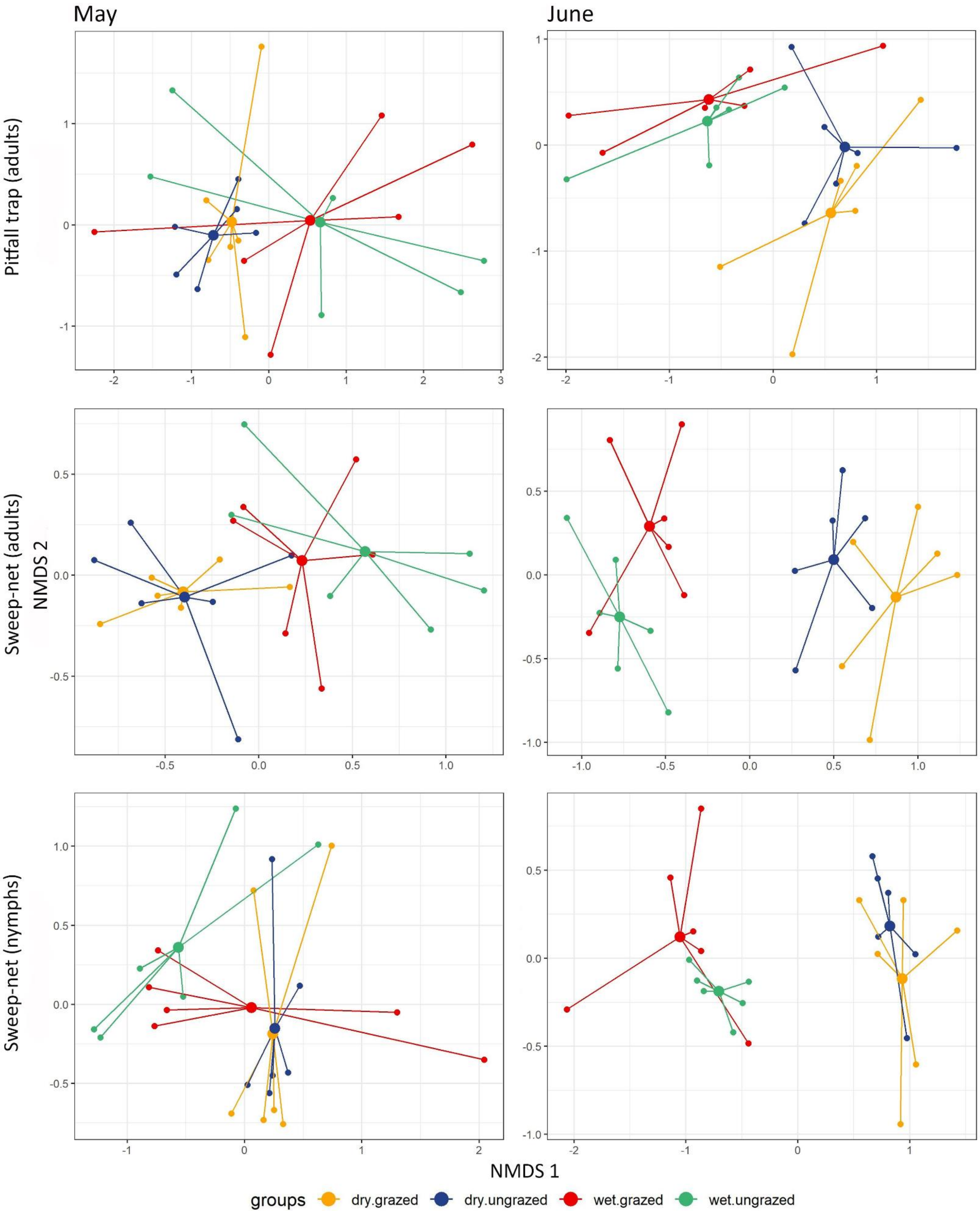

Figure 10. NMDS scatter plots of community composition on saline grassland true bugs depending on season and vegetation type.

The NMDS ordination analysis showed a great similarity between communities from grazed wet grasslands and those from dry ones in May. However, the strict separation of wet and dry grasslands (irrespective of the grazing treatment) was observed in June (Fig. 10).

Table 7. Indicator species of dry and wet saline grasslands. Two components of the indicator value measure habitat specificity (A) and habitat fidelity (B).

MAY	A	B	Stat.	p-value	JUNE	A	B	Stat.	p-value
Sweep-net (adults)									
Dry saline grasslands									
*Acetropis carinata**	0.825	1.000	0.908	≤0.001	*Rhopalus parumpunctatus**	0.997	1.000	0.999	≤0.001
Leptopterna ferrugata	0.987	0.833	0.907	≤0.001	*Stictopleurus abutilon**	1.000	0.833	0.913	≤0.001
Europiella artemisiae	0.983	0.833	0.905	≤0.001	*Dolycoris baccarum**	1.000	0.667	0.816	≤0.001
*Amblytylus nasutus**	0.760	1.000	0.872	0.002	*Geocoris grylloides*	0.944	0.667	0.793	0.004
Sciocoris sulcatus	0.970	0.750	0.853	0.002	*Camptopus lateralis*	1.000	0.500	0.707	0.013
Geocoris grylloides	0.942	0.750	0.841	0.003	*Chorosoma schillingii*	0.968	0.500	0.696	0.023
Amblytylus concolor	1.000	0.667	0.816	≤0.001	*Aelia acuminata*	1.000	0.417	0.645	0.036
Chorosoma schillingii	0.980	0.667	0.808	≤0.001					
Metopoplax origani	0.720	0.833	0.775	0.040					
*+ Peritrechus gracilicornis**									
Wet saline grasslands									
Polymerus vulneratus	0.852	0.667	0.754	0.037	*Stenodema calcarata*	0.978	0.917	0.947	≤0.001
Stenodema calcarata	0.996	0.500	0.706	0.032	*Myrmus miriformis**	1.000	0.667	0.816	≤0.001
*Peritrechus nubilus**	1.000	0.417	0.645	0.041	*Amblytylus nasutus*	1.000	0.417	0.645	0.037
*Sciocoris distinctus**	1.000	0.417	0.645	0.038	*+ Acetropis longirostris**				
Pitfall trap (adults)									
Dry saline grasslands									
*Acalypta marginata**	0.900	0.833	0.866	≤0.001	*Acalypta gracilis*	0.954	0.667	0.798	0.006
					Lygaeosoma anatolicum	0.965	0.583	0.750	0.011
Wet saline grasslands									
					Hallodapus montandoni	1.000	0.583	0.764	0.005
					Peritrechus nubilus	0.937	0.500	0.685	0.041

* Indicator species of a dry or wet saline grassland, but also an indicator of its ungrazed parts.
+ Indicators species of ungrazed areas of grassland, but not an indicator of the vegetation type.

Indicator species analysis listed 17 indicator species from dry saline grasslands and 7 indicators from wet saline grassland habitats (Tab. 7). A large number of indicator species among plant-dwellers were expected considering that number of species collected by sweep-netting was twice more than those recorded in pitfall traps. A greater number of indicator species of the dry saline grasslands compared to the wet ones followed species richness patterns between the two vegetation types. Also, the distribution of indicator species confirmed the May–June disparity, where plant-dwelling indicators had a bigger share in May communities, but the ground-dwelling one had more representatives in June.

In the results, the dominance of specialized grass-feeders was observed—*Acetropis carinata*, *A. longirostris*, *Aelia acuminata* (Linnaeus, 1758), *Amblytylus concolor* Jakovlev, 1877, *A. nasutus*, *Chorosoma schillingii* (Schilling, 1829), *Leptopterna ferrugata* (Fallén, 1807), *Myrmus miriformis* (Fallén, 1807), *Sciocoris distinctus* Fieber, 1851, *S. sulcatus* Fieber, 1851, *Stenodema calcarata* (Fallén, 1807). Several species showed persistence in communities throughout the season and were detected as indicators in May and June, as well. Therefore, *Geocoris grylloides* (Linnaeus, 1761) and *Ch. schillingii* were indicator species of dry saline grasslands and *S. calcarata* and *Peritrechus nubilus* (Fallén, 1807) of the wet ones. Species *A. nasutus* is an exceptional case by being recognized as an indicator of dry grasslands in May but shifted to wet grasslands in June. All species in the list of indicators are common members of saline grassland true bug communities, but *Lygaeosoma anatolicum* is the only one primarily associated with saline grasslands in the Pannonian Region.

4.3. Discussion

The study on grazing exclusion revealed that true bug communities were significantly affected by vegetation type, management and their interactions. However, these effects varied among different sub-community levels (i.e. plant-dwellers and ground-dwellers) and different seasons. Also, results of NMDS ordination and indicator species analysis confirmed that the species composition of true bugs in saline grasslands was different in May and June.

Seasonal dynamics regulate abiotic and biotic environments for all grassland inhabitants. Abiotic factors (i.e. water availability and salinity of the soil) determine the type of vegetation which will be established with all its structural, compositional and microclimate features (Šefferová-Stanová *et al*., 2008; Török *et al*., 2011; Deák *et al*., 2014b). Seasonal shifts in plant communities of saline grasslands are well documented (Tóth, 2010), however, changes in true bug communities observed in the field have not been systematically investigated before, except for one small pilot study (Šeat & Torma, 2018).

The season greatly influenced the effects of grazing on true bug communities. Grazing was the main factor that determined the functional attributes of true bug communities in May, but in June, it affected their species richness and especially abundance. In spring, dry (*Artemisia* salt steppe) and wet saline grasslands (alkali meadows) provide similar resources and environments for true bugs (Torma *et al*., 2019), this was confirmed by the dominance of oligophagous grass-feeders in both grassland types. Grass-feeding true bugs in different saline grasslands thrive for 2 to 3 weeks in May and early June (depending on the year) when the grassy vegetation is at its peak. During this period, dry saline grasslands are still relatively humid (Šefferová-Stanová *et al*., 2008; Török *et al*., 2011), keeping stands of *Festuca pseudovina* fresh for numerous sap-feeding insects like true bugs. According to changes of vegetation, populations of species like *Acetropis carinata*, *Amblytylus nasustus* and *Conostethus hungaricus* grow rapidly and can be collected in tens and hundreds of specimens in a single sampling occasion (Torma *et al*., 2010, 2017, 2019; Šeat & Torma, 2018). Removal of grass biomass by spring grazing was the most influential factor for true bugs in more productive wet saline grasslands. Presumably, in denser and higher vegetation, grazing caused more pronounced changes in habitat structure and microclimate, causing the shift in community composition of true bugs to more drought-tolerant and smaller size species. The dominance of smaller species (i.e. smaller body volume) was also reported in intensively managed and disturbed grasslands in the early season (Simons *et al*., 2016; Neff *et al*., 2020).

Later in the season, effects of vegetation type dominated in shaping true bug communities, and this was already reported in previous studies on different characteristic grasslands of the Pannonian Region (Torma *et al*., 2010, 2014, 2017, 2019). In summer, water in the upper soil layer evaporates rapidly from the sparse dry saline grasslands and this is the signal for the shift in plant community composition (Šefferová-Stanová *et al*., 2008; Török *et al*., 2011). At the same time, dense vegetation cover and lower position in microtopography make wet saline grassland less prone to drying (Molnár & Borhidi, 2003; Török *et al*., 2011). All aforementioned create greater differences in vegetation and habitat features in the two grassland types; dry grasslands compared to wet ones become dryer, warmer with specific food sources (e.g. *Artemisia santonicum*, *Camphorosma annua*) for specialist herbivores (Torma *et al*., 2017). With the seasonal changes, plant-dwelling true bug communities of dry saline grasslands were on average represented by bigger and more polyphagous species, whereas, specialized grass-feeders in foraging fresh food moved to wet grasslands. This is supported in the case of grass-feeding *Amblytylus nasutus*, identified as an indicator of dry saline grasslands in May and of wet saline grasslands in June. Previous data from Serbia (Chapter 3, i.e. Šeat & Nadaždin, 2021) confirmed that *A. nasutus* is present in *Artemisia* salt steppes mostly in May with a few records from early June. Regardless of the harsh and dynamic environment of dry saline grasslands, they were more heterogeneous habitats in comparison to wet ones (Torma *et al*., 2017) and harbour more species and more individuals of plant-dwelling true bugs throughout the season. In grasslands, plant diversity and diversity of herbivorous true bugs are usually positively correlated (Torma & Császár, 2013; Simons *et al*., 2014b).

All aforementioned habitat changes in saline grasslands greatly influenced communities of plant-dwellers, supporting the bottom-up hypothesis according to which insect herbivore communities (consumers) are regulated by vegetation (producers) (Zhu *et al*., 2012; Neff *et al*., 2020). Bottom-up control is the theoretical foundation of using true bugs as indicators in grassland management (Kőrösi *et al*., 2012; Simons *et al*., 2014b; Torma *et al*., 2019). However, there is no evidence that ground-dwelling true bugs are regulated in the same way (Kőrösi *et al*., 2012), and studies analyzing particularly ground-dwelling true bugs are missing. In this study, ground-dwellers showed minor sensitivity to changes in vegetation cover, caused by management or seasonal dynamics. The explanation for the lack of response of ground-dwellers could be that (i) pitfall traps are not an efficient collecting method and/or (ii) vegetation structure above ground does not influence habitat quality for true bugs on ground level. A total number of specimens collected in this study by pitfall-trapping is more than a hundred times lower than the number of collected specimens by sweep-netting, and this fact could lead to the conclusion that insufficient sample size caused the absence of statistically significant results. The second explanation would be that ground-dwelling true bugs do not use above-ground plant biomass as a food source or microclimate buffer. Most of the species recorded in this study were trophic opportunists and habitat generalists without specific ecological requirements, so grazing had no impact on habitat quality or resource availability for these species. Similarly, a decrease in vegetation height by management was not affecting communities of ground-dwelling beetles as well (Tscharntke & Greiler, 1995; Torma *et al*., 2019) and vegetation height (here as a measure of management intensity) was not a predictor of species richness of ground-dwelling true bugs either (Kőrösi *et al*., 2012).

Besides ground-dwellers, nymphs of true bugs are also rarely involved in similar grassland assessments, mostly because of difficulties related to their identification (Zurbrügg & Frank, 2006; Rabitsch, 2008). Young true bugs do not have sex organs and the identification of many species relies on characteristics of genital apparatus of their adult counterpart (see Wagner & Weber, 1964). Use of morphospecies in defining species or 'morphospecies' richness and community composition was the closest to precise species identification (Duelli & Obrist, 2003; McGeoch, 2007). In this study, communities of plant-dwelling nymphs more or less mirrored patterns of plant-dwelling adults in all aspects i.e., species richness, abundance and CWM values. This was expected considering that true bug nymphs' ecological requirements are very similar to those of adults of the same species, except for reduced dispersal abilities, but they usually have the same trophic behaviour and live in the same habitats with adults (Di Giulio *et al*., 2001; Zurbrügg & Frank, 2006; Achtziger *et al*., 2007). Using morphospecies, as a tool for the distinction of different taxa of true bugs, principally provides information on basic community composition patterns relevant for rapid assessment of management success. True bug nymphs can be very abundant in grasslands, contributing to the pressure of herbivorous insects on producers (Tscharntke & Greiler, 1995; Zurbrügg & Frank, 2006), but also provide a great food source for invertebrates and small vertebrate predators (Zahn *et al*., 2010; Neff *et al*., 2020). In this way, true bug nymphs could significantly influence ecosystem functioning and structure of food webs (see Weisser & Siemann, 2008), especially in spring when a new generation of specialized grass-feeding Mirids (e.g. *Acetropis carinata*, *Amblytylus nasutus*, *Conostethus hungaricus*) start to hatch and become one of the most abundant insect groups in saline grasslands.

Indicator species analysis showed the dominance of grass-feeders, in both, dry and wet saline grasslands. Recorded grass-feeding species appeared to have preference for a certain grassland type and many of them were indicators of ungrazed parts as well. Indicators of ungrazed grasslands in some sense showed persistence on higher taxa levels; genera *Acetropis*, *Peritrechus* and those from the Rhopalidae family (*Rhopalus*, *Stictopleurus* and *Myrmus*) indicated towards more complex vegetation structure regardless of vegetation type. Selective grazing by large herbivores is one of those factors that can change vegetation structure and composition significantly (Zhu *et al*., 2012; van Klink *et al*., 2014; Li *et al*., 2021). For instance, in dry saline grasslands *Artemisia santonicum* is the subordinate plant and known as unpalatable for cattle, so even in intensively grazed pastures, stands of this plant are intact. *Europiella artemisie* is specialised to feed on species of the *Artemisia* genus (Wachmann *et al*., 2004) and a reliable indicator of dry saline grasslands since there is no host plant in the wet grassland type. Similar host–true bug interaction exists in German coastal salt marshes between *A. maritima* and its specialist *E. decolor*. *E. decolor* had a higher abundance in grazed habitats where its host plant could thrive in conditions of reduced shade from the surrounding grasses (van Klink *et al*., 2013). In this sense, alternative management practices, like the annual mowing of dry saline grasslands, could diminish habitat heterogeneity (Dítě *et al*., 2013; Dítětová *et al*., 2016; Torma *et al*., 2019) and jeopardize the persistence of species related to *A. santonicum* and other unpalatable plants which provide a primary food source for a few trophic specialists and alternative food for many polyphagous species in saline grasslands (see Wachmann *et al*., 2004, 2006, 2007, 2008).

After all, dry (*Artemisia* salt steppe) and wet (alkali meadows) saline grasslands in the Pannonian Region support different communities of true bugs in the herb layer, however, the separation of communities on the ground level is not so clear. This divergence in plant-dwelling communities is more evident in summer when the distinction between two grasslands types is greater which influences the response of true bugs to management. On the one hand, spring grazing can significantly modify the community composition of true bugs, particularly in wet saline grasslands. Moreover, in summer, the strong differences between wet and dry vegetation types determine the community composition of true bugs and summer grazing can have a generally negative effect on true bugs, regardless of the grassland type they inhabit. Disentangling these effects is important and should be considered in future conservation management planning.

5. THE ROLE OF DRAINAGE CANALS IN PRESERVING SALINE GRASSLAND TRUE BUGS

The lowland of central Hungary (Danube-Tisza interfluve) used to be a mosaic of wetlands, grasslands and forested patches. From the middle of the 20th century, the whole landscape changed markedly when a dense network of drainage canals covered the region to free the land from water and make it suitable for intensive agriculture. In a few decades, most of the wetlands disappeared or spontaneously turned into dryer habitats (Biró *et al*., 2007). Later, aridification was pushed further by climate change (Pongrácz *et al*., 2011), extraction of groundwater for irrigation and excessive afforestation (Tölgyesi *et al*., 2020).

Although canals had a great contribution to biodiversity loss worldwide, nowadays, conservationists start to recognize their potential as refugia for native species in intensively managed areas. Despite the contradictory roles of canals in the past and present, their conservation value is recognized and especially importance in agricultural landscapes where canals should take a share in conservation planning and agri-environmental schemes (Blomqvist *et al*., 2009; van Dijk *et al*., 2013). This study aims to contribute to a better understanding of the conservation role of the drainage canal network in central Hungary. More specifically, the following research questions were addressed: (i) How well do drainage canals represent true bug communities from semi-natural grasslands of high conservation value and can they properly support them? (ii) What landscape- and canal-scale factors define a canal as an adequate secondary habitat for grassland true bugs? (iii) What trait syndromes of true bugs are favoured by saline canals and nearby saline grasslands? (iv) What are the rarest, most common and characteristic true bug species of saline habitats in Kiskunság?

5.1. Materials and methods

5.1.1. Study area and sampling sites

The study area covers part of the Danube-Tisza interfluve of central Hungary and overlaps with the protected area of Kiskunság National Park (Fig. 11). This region is known for its well-preserved sandy habitats and landscapes like forest-steppe and sand dunes, however, the substrate here is diverse thus certain zonality of the soils can be recognized. The coarse sand prevails in the central zone of the region, saline loam along the bordering rivers (Danube and Tisza) and peaty loam (fen substrate) between the sandy and saline zones. Isolated patches of salt-affected and peat soils can also be present azonally in the depressions of the central part (Pásztor *et al.*, 2018). Considering uniform elevation and climate of the Danube-Tisza interfluve, the substrate stays as the main determinant of the vegetation and habitat formation. According to dominant soil types, the main open habitats present here are fen, sandy and saline grasslands, and marshlands (Biró *et al.*, 2007, 2008; Molnár *et al.*, 2008).

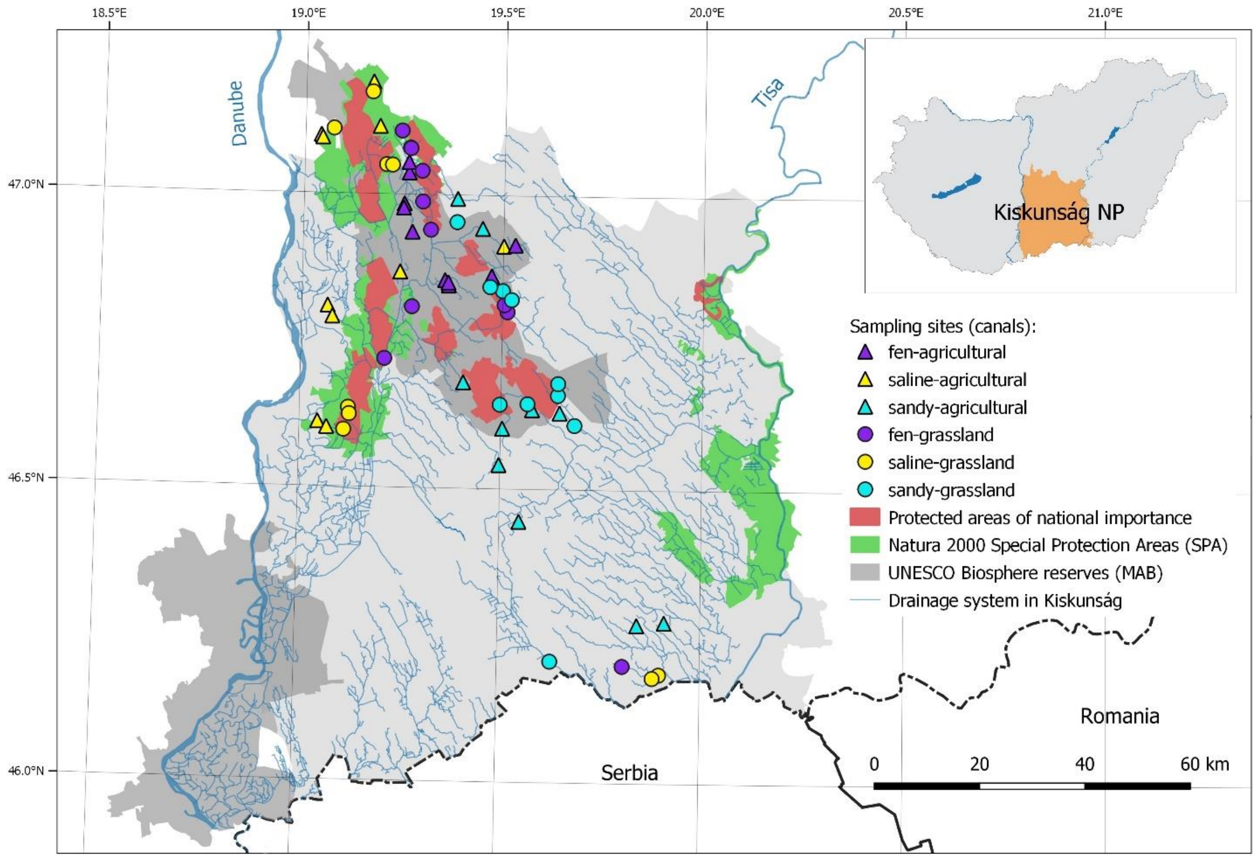

Figure 11. The study area of the Kiskunság National Park with the sampling sites.

The first type of sampling site was a 200 m long section of agricultural (bordering annual cropland by both sides) or grassland (bordering extensively used semi-natural grassland by both sides) drainage canal. In total 60 canals were surveyed, 30 of each surrounding landscape matrix type. Additional characterization of the canals was based on the substrate and size. In consistence with soil distinctions, three habitat types were recognized in canals: fen, saline habitat and sandy habitat (20 of each type) (Fig. 11). Two categories of canals' sizes were considered for the survey, small and large ones (30 of each). Small canals had a depth of 0.7 ± 0.2 m (mean ± SD) and a width of 3.6 ± 1.4 m, the large ones had a depth of 1.7 ± 0.5 m and a width of 6.8 ± 2.0 m, banks included. All aforementioned attributes of canals led to five replicates for each of the 12 combinations (2 landscape matrices × 3 habitats × 2 sizes). Most of the sampled canals are dry nowadays, only temporary filled with water in spring and after heavy rains. Very large arterial canals with constant water cover were avoided, as well as, canals dredged within the past 10 years.

The second type of sampling site was a 5 m × 200 m transect in a grassland area (hereafter reference transect) parallel to every grassland canal, approx. 50 m from them. Those semi-natural grasslands are the closest to what is considered authentic and native vegetation of the region. In total 30 reference transects were sampled corresponding to the number of grassland canals. The sampling of reference transects was performed following the protocol of the canal sampling.

5.1.2. Vegetation sampling

Vegetation was sampled on several occasions during the second half of June 2018. Plants' species were recorded in evenly spaced 1 m^2 plots and 8 plots were selected per sampling site. In canals, four plots were placed on the dry slopes of the bank and four plots at the canal bottom or adjacent to the bottom in case if water level was too high. In total 480 plots were selected in canals plus 240 in reference transects. Additionally, the abundance of reeds and woody vegetation was assessed and the measure was the cumulative length of the covered canal bank with a resolution of 1 m. Each bank was measured separately, leading to a maximum abundance of 400 m for reeds and woody vegetation, respectively.

5.1.3. True bugs sampling and identification

The sampling of true bugs was done by standard sweep-netting method alongside 200 m canal section or reference transect. One sample contained specimens swept from four evenly spaced 25 m long sub-transects inside of canal or reference transect (i.e. 4 × 25 sweeps). All collected samples were placed in plastic bags filled with 70% ethanol and stored in a freezer until identification. Only data on adult true bugs were used for this study and the procedure of species identification is explained in section 3.1.2. True bugs collected in the Kiskunság are stored at the Department of Ecology, University of Szeged. To record most of the seasonal changes in true bug communities, three sampling periods were designated in 2018. The first sampling period was done from 15 to 24 May, the second from 9 to 17 July and the third from 5 to 18 September.

5.1.4. True bug traits

To investigate what true bug functional and life-history traits or their combinations correspond with certain saline habitats, six traits which had the potential to describe the diversity of different salt-affected environments (Tab. 8) were selected as follows: (i) Body size which was defined as the mean length of an adult body; (ii) Dispersal ability which was based on wing length category where apterous specimens lack wings or they are extremely reduced, brachypterous specimens have shortened wings and macropterous are those with full (maximum) wing length; (iii) Herbivorous true bugs were categorized as monophagous, oligophagous or polyphagous; (iv) Overwintering stage—three possible stages in hemimetabolous development of true bugs: egg, nymph and adult; (v) Humidity preference and (vi) Shade tolerance were further divided into five categories, starting with the preference for humid and shaded forest-like habitats to completely open and dry grassland-like habitat types. All information on traits of the true bugs were taken from the literature (Wagner & Weber, 1964; Péricart, 1972, 1983, 1984, 1987, 1998; Wachmann *et al*., 2004, 2006, 2007, 2008; Gossner *et al*., 2015a, 2015b; UkrBIN, 2017).

Table 8. True bug traits analyzed in the study.

Trait	Values
Body size	Body length in mm
Dispersal ability	0–apterous, 0.25–mostly brachypterous, 0.5–brachypterous, 0.75–mostly macropterous, 1–macropterous
Specialization of herbivores	0–polyphagous, 0.5–oligophagous, 1–monophagous
Overwintering stage	0–egg, 0.5–nymp, 1–adult
Humidity preference	0–humid, 0.25–semi-humid, 0.5–indifference to humidity, 0.75–mostly dry, 1–dry
Shade tolerance	0–shaded, 0.25–semi-shaded, 0.5–indifference to shade, 0.75–open to partly shaded, 1–open

5.1.5. Data analysis

Linear mixed-effects models (LMMs) were applied to evaluate how environmental factors determine the true bug species richness. According to the species pool hypothesis of Zobel *et al.* (1998), different species pool sizes can be expected in different habitats, making comparisons across habitats difficult. Therefore, standardization of the species richness scores of canals to habitat-specific average reference species richness scores was performed. The result of standardization was ‘species excess’, a value that represented proportional excess or deficit of species richness compared to habitat-specific reference averages. The species excesses were expressed as percentages. The use of species excesses, equalling the proportional added value of canals to landscape-wide diversity, allowed between-habitat comparisons by ruling out the effect of the differently sized species pools of different habitats. The following equation was used for the calculations:

$$E_i = \frac{\left(C_i - \left(\sum_{j=1}^{n} R_j\right)/n\right) \times 100}{\left(\sum_{j=1}^{n} R_j\right)/n},$$

where E_i is the habitat-specific species excess of the i^{th} sampling unit of a canal (true bugs collected by 25 sweeps), C_i is the species richness of this sampling unit, R_j is the species richness of the j^{th} sampling unit of any of the reference transects belonging to the same habitat type as the canal and n is the number of such reference sampling units.

The species excess was considered biotic response variable and explanatory variables were landscape matrix, habitat, size, and season as categorical ones, and abundance of woody vegetation and reeds as continuous. Canal identity was a random effect in the models. Explanatory variables were also checked for multicollinearity; generalized variance inflation factors ranged between 1.00 and 1.62, thus, all variables were included in the final models.

The mean score of species excesses in each level of the categorical explanatory variables (landscape matrix, habitat, size and season) was also checked, to see whether it differed from the reference level, i.e. from the score 0. For the analysis, reduced models were used including only one explanatory variable at a time and the random term of canal identity if multiple data were available for each canal.

Models were prepared in the R environment (R Core Team, 2020) using the *lmer* function from the ‘lme4’ package (Bates *et al*., 2015). Generalized variance inflation factors were calculated with the *vif* function of the ‘car’ package (Fox & Weisberg, 2019). The significance of the explanatory variables was tested using the *ANOVA* function (‘car’ package). Pairwise comparisons of the three-level variable (habitat and season) in models were performed with the *emmeans* function of the ‘emmeans’ package (Lenth, 2020).

For further analyses, pooled data were used; data collected at one sampling site (8 vegetation plots or 4 × 25 sweeps in the case of true bugs) were pooled making one statistical sample. Additionally, data from different seasons were also pooled to create joined species composition matrix of true bugs. Reference transects were treated as the third level of the surrounding landscape matrix and incorporated into the analyses.

True bugs data from different habitats (defined by substrate and/or landscape matrix) were used to analyze dissimilarity in their community composition by applying permutational multivariate analysis of variance (PERMANOVA) in the R environment. Overall dissimilarity was tested with the help of *adonis* function of the ‘vegan’ package (Oksanen *et al*., 2017), whereas pairwise comparisons were done by *pairwise.adonis* function of the ‘pairwiseAdonis’ package (Martinez Arbizu, 2020).

RLQ and the fourth-corner analyses were applied to investigate how environmental factors shape true bug community composition and what habitat attributes are associated with certain traits of true bugs. Both methods are based on the analysis of the fourth-corner matrix, which crosses species traits and environmental variables weighted by species abundances. The input matrices for the resulting fourth-corner matrix are R table (samples × environmental attributes), L table (samples × species) and Q table (species × species traits). These two methods were applied together to complement each other; RLQ is a multivariate ordination technique that summarizes the joint structure among the three tables, whereas the fourth-corner tests individual trait–environment relationships (Dray *et al*., 2014). To perform these analyses correctly, the instructions of Kleyer *et al.* (2012) and Dray *et al*. (2014) were followed.

The R table for this study had sampling sites (20 saline canals + 10 reference transects, i.e. saline grasslands) for ‘samples’ and landscape matrix, the abundance of reeds and woody vegetation, species richness of plants and invasive plans for ‘environmental attributes’. The L table was a typical species composition matrix (i.e. sampling sites × true bug species). The Q table was based on true bug traits described in section 6.1.4 (Tab. 8).

To carry out analyses of RLQ and the fourth-corner, the ‘ade4’ package (Dray & Dufour, 2007) was applied in R. Functions *estim_ncpPCA* and *imputePCA* of the package ‘missMDA’ (Josse & Husson, 2016) were applied to estimate and fill missing values in Q table in order to perform correct principal component analysis (PCA) which preceded RLQ. The significance of RLQ and the fourth-corner models was tested using 9,999 permutations. To separate functional groups of true bugs, hierarchical cluster analysis was applied. Thereafter, analysis of variance (ANOVA) and Tukey’s HSD tests were performed to validate the distinction of traits values among species clusters.

Commonness index was calculated for saline habitat true bugs aiming to detect the rarest and the most common species in the dataset. Commonness index estimates a probability for each species to be common (1) or rare (0) based on abundance–occupancy information from species composition matrix. Commonness indices were calculated in R with the help of the ‘FuzzyQ’ package and its *fuzzyq* function. To assess the accuracy of the indices within a 95% confidence interval, bootstrapping with 1,000 replicates was applied (Balbuena *et al*., 2021a, 2021b).

5.2. Results

Table 9. Recorded species richness of true bugs depending on surrounding landscape matrix, habitat type and the sampling season.

	Level	Species richness	No. of specimens	Singletons
Landscape matrix	Agricultural canals	188	7854	20
	Grassland canals	171	8034	14
	Reference grasslands	164	13982	11
Habitat (substrate)	Fens	166	6744	14
	Saline habitats	167	12146	10
	Sandy habitats	185	10980	21
Season	May	175	16500	19
	July	167	7767	19
	September	122	5603	7

During the study, 242 species of true bugs were identified from 29,870 adult specimens. The total number of species that occurred in the canals was 218 and 80 of them were collected only there (saline canals' species richness: agricultural—199, grassland—99), whereas 26 species were exclusive for reference grasslands (number of species recorded in saline grasslands—99). Species richness of different habitats (according to soil types and landscape matrix) and in different seasons are given in the summary table (Tab. 9).

True bug species richness in canals determined by environmental factors: a linear mixed-effects model (LMM) approach

According to LMMs results, species excesses were affected only by landscape matrix and season, with higher scores in agricultural canals than in grassland ones, and higher scores in summer than in spring. Compared to the reference transects, the statistics confirmed significant species excess in agricultural canals but not in grassland ones, in large canals but not in small ones and on sandy habitat but not in fen or saline habitats. Species excess was highly positive in summer, but a significant difference was also confirmed for autumnal data (Fig. 12, Tab. 10).

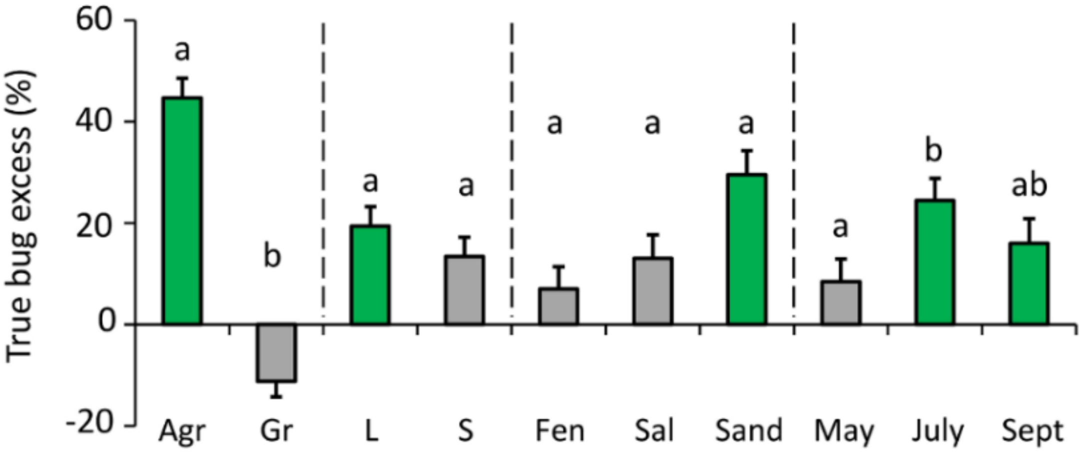

Figure 12. The effects of landscape matrix, canal size, habitat (substrate) type and season on the species excesses of true bugs. Different lowercase letters within each canal parameter identify significantly different groups. Green shading indicates a significantly positive difference from the reference level (i.e. the 0 score), whereas grey shading is used when no significant difference was detected from the reference level. Agr: agricultural canal, Gra: grassland canal, L: large canal, S: small canal, Fen: fen habitat, Sal: saline habitat, Sand: sandy habitat.

Table 10. **A**. Test results of the reduced models which tested whether the levels of the categorical variables differ from the reference levels. **B**. Test results of the fixed factors of the full models. **C**. Pairwise comparisons of the full models are shown for factors with more than two levels (habitat and season) and with significant effects.

A		t	p-value
Landscape matrix	Agri. canal	**6.38**	**<0.001**
	Grass. canal	-1.58	0.120
Size	Large	**2.14**	**0.037**
	Small	1.50	0.139
Habitat (substrate)	Fen	0.49	0.625
	Saline	0.91	0.369
	Sandy	**2.86**	**0.006**
Season	May	1.22	0.220
	July	**3.58**	**<0.001**
	September	**2.35**	**0.019**

B	χ^2	p-value
Reed	1.65	0.199
Woody	2.82	0.093
Matrix	**37.85**	**<0.001**
Size	1.86	0.172
Habitat	2.07	0.356
Season	**9.87**	**0.007**

C	t-ratio	p-value
Fen–Saline	–	–
Fen–Sandy	–	–
Saline–Sandy	–	–
July–May	**3.14**	**0.005**
July–Sept	1.65	0.224
May–Sept	-1.50	0.294

<u>True bug traits–saline habitat relationships explained by RLQ and fourth-corner analyses</u>

PERMANOVA showed that all habitat types, whether the definition was based on substrate type or landscape matrix, have distinctive true bug communities. However, pairwise comparisons of agricultural canals have not distinguished fen from saline or sandy habitats by their community composition of true bugs, only saline *vs*. sandy communities were identified as separated entities (Tab. 11).

Total inertia of RLQ analysis had a value of 1.93 and was explained by 4 axes in total (projected inertia: 68.85%, 31.00%, 0.13%, 0.02%) where the first two axes described 99.85% of the variation. Overall RLQ model was significant at p-value = 0.021, whereas Model 2 (permuted site vectors, i.e. rows of L table) and Model 4 (permuted species vectors, i.e. columns of L table) were significant for p-value = 0.022 and p-value = 0.014, respectively.

The ordination biplot of RLQ analysis showed a certain grouping of true bug functional and life-history traits with environmental attributes along the two main axes (Fig. 13a): (i) Along the horizontal axis, grassland canals are opposed (i.e. negatively correlated by the fourth-corner analysis) to true bugs which prefer dry habitats and have higher dispersive abilities. Reference saline grasslands are opposed to species that overwinter in the adult stage, (ii) Along the vertical axis, an association of agrarian canals, invasive plants and woody vegetation are opposed to true bugs which prefer open habitats. According to results of fourth-corner analysis, bigger sized true bugs were positively correlated with agrarian canals and a higher number of invasive plant species in a habitat, whereas overwintering in the adult stage was significantly associated with grassland canals. The feeding behaviour of herbivores was not correlated with any of the landscape- or canal-scale features (see section 12.4. of the Appendix for the details), whereas canal size and reed abundance were excluded from the analysis because they showed no effect on true bugs.

Table 11. Dissimilarity in the true bug community composition of different habitats (for pairwise comparisons adjusted p-values with Bonferroni correction are indicated).

Habitat (substrate or matrix)	Pairs of habitats	F-model	R^2	p-value
Fen		3.669	**0.202**	**0.001**
Saline habitat		5.342	**0.283**	**0.001**
Sandy habitat		3.708	**0.216**	**0.001**
Agricultural canal (AC)		1.910	**0.124**	**0.007**
Grassland canal (GC)		6.375	**0.313**	**0.001**
Reference grassland (RG)		4.023	**0.223**	**0.001**
Fen	AC vs. GC	3.594	**0.159**	**0.003**
	AC vs. RG	3.871	**0.169**	**0.003**
	GC vs. RG	3.552	**0.151**	**0.003**
Saline habitat	AC vs. GC	6.840	**0.275**	**0.003**
	AC vs. RG	3.424	**0.160**	**0.003**
	GC vs. RG	6.108	**0.253**	**0.003**
Sandy habitat	AC vs. GC	1.725	**0.087**	**0.042**
	AC vs. RG	5.770	**0.243**	**0.006**
	GC vs. RG	3.846	**0.176**	**0.003**
Agricultural canal	Fen vs. Saline	1.423	0.073	0.297
	Fen vs. Sandy	1.484	0.076	0.222
	Saline vs. Sandy	2.766	**0.133**	**0.003**
Grassland canal	Fen vs. Saline	7.775	**0.290**	**0.003**
	Fen vs. Sandy	3.726	**0.164**	**0.003**
	Saline vs. Sandy	7.937	**0.306**	**0.003**
Reference grassland	Fen vs. Saline	3.095	**0.140**	**0.003**
	Fen vs. Sandy	6.065	**0.242**	**0.003**
	Saline vs. Sandy	3.153	**0.149**	**0.006**

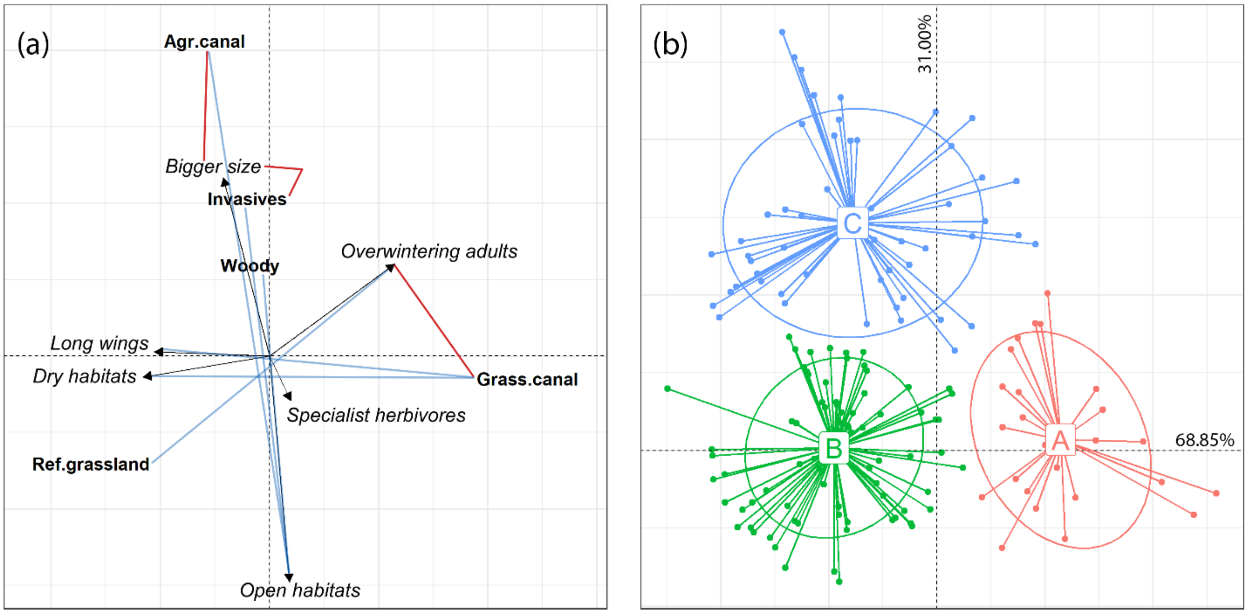

Figure 13. Results of the RLQ analysis: (a) True bug trait–environment features ordination biplot is complemented with correlation lines of fourth-corner analysis. True bug traits are given in italic, environmental attributes are boldface. Red lines refer to significantly positive correlations and light blue to significantly negative correlations of attributes. The highest values of true bug traits are pointed by arrows. (b) The ordination plot of species scores is based on values of true bugs' functional and life-history traits. Species clusters (A, B and C) are defined by hierarchical cluster analysis.

Hierarchical clustering defined three species clusters (i.e. trait syndromes) of true bugs according to analyzed functional and life-history traits (Fig. 13b). Trait partitioning among clusters was tested with ANOVA to check the validity of clusters as distinguishable groups (Fig. 14). At first glance separation along axes divided clusters on (A and B) and above (C) horizontal axis, and on the left (B and C) and right (A) of the vertical axis. The horizontal axis divided small-bodied species which prefer open grassland-like habitats (A and B) from larger species of semi-shaded habitats (C). The vertical axes separated species into those with longer wings and better dispersal abilities (B and C) and those which on average are more brachypterous and less dispersive (A). Species from the A-cluster also showed high preference for more humid habitats and almost exclusive oligophagy. B-cluster species are the only group that have a bigger share of species that overwinter as eggs and favours the driest habitat types. Additionally, B-cluster species altogether with those from C-cluster have more polyphagous herbivores. C-cluster species are mostly associated with saline habitats of medium humidity.

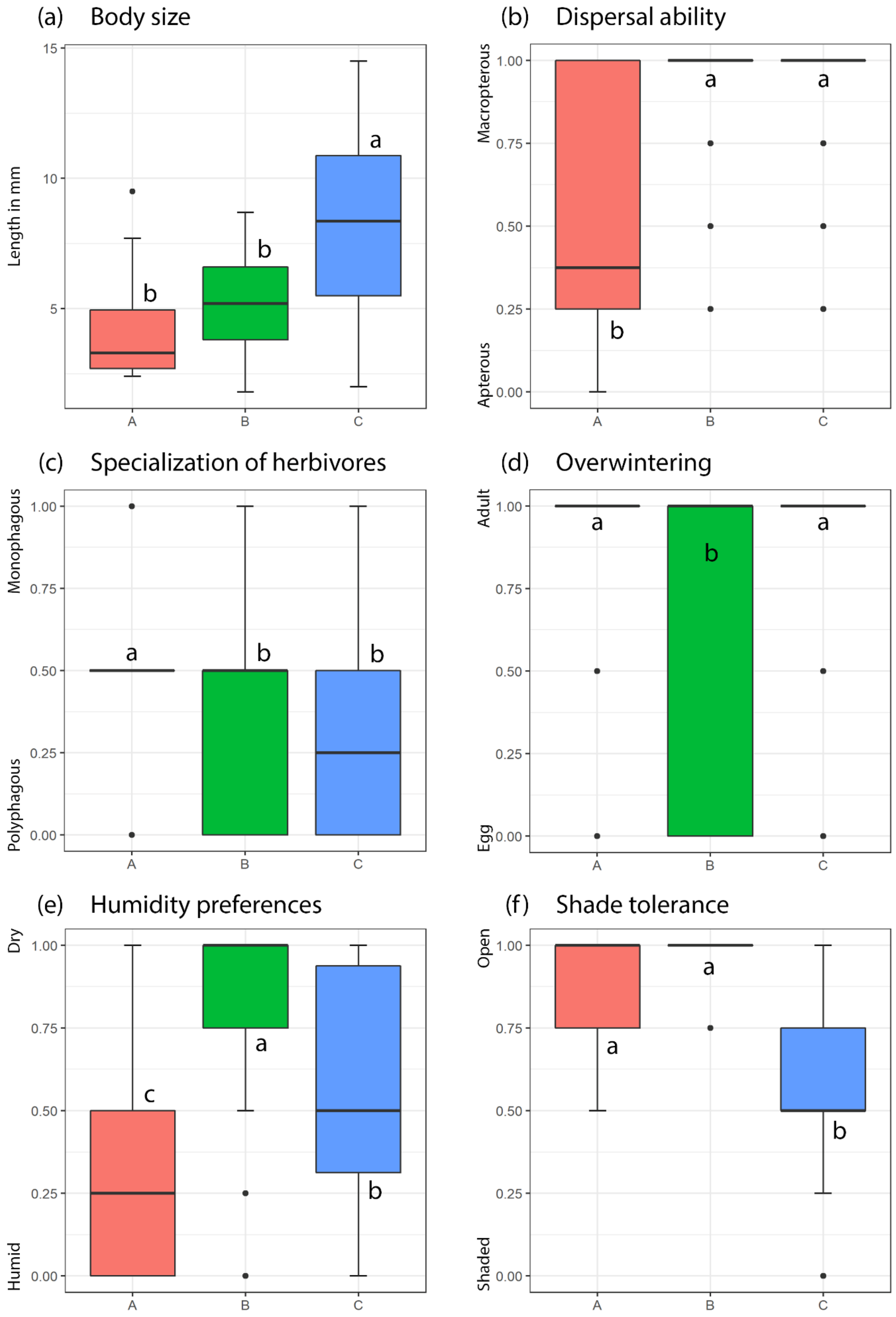

Figure 14. True bug traits partitioned among three species clusters (A, B and C). Correlation ratio values of true bugs' traits are given: body size = 0.558, dispersal ability = 0.547, specialization of herbivores = 0.277, overwintering stage = 0.304, humidity preference = 0.527, shade tolerance = 0.677. Different lowercase letters identify significantly different groups.

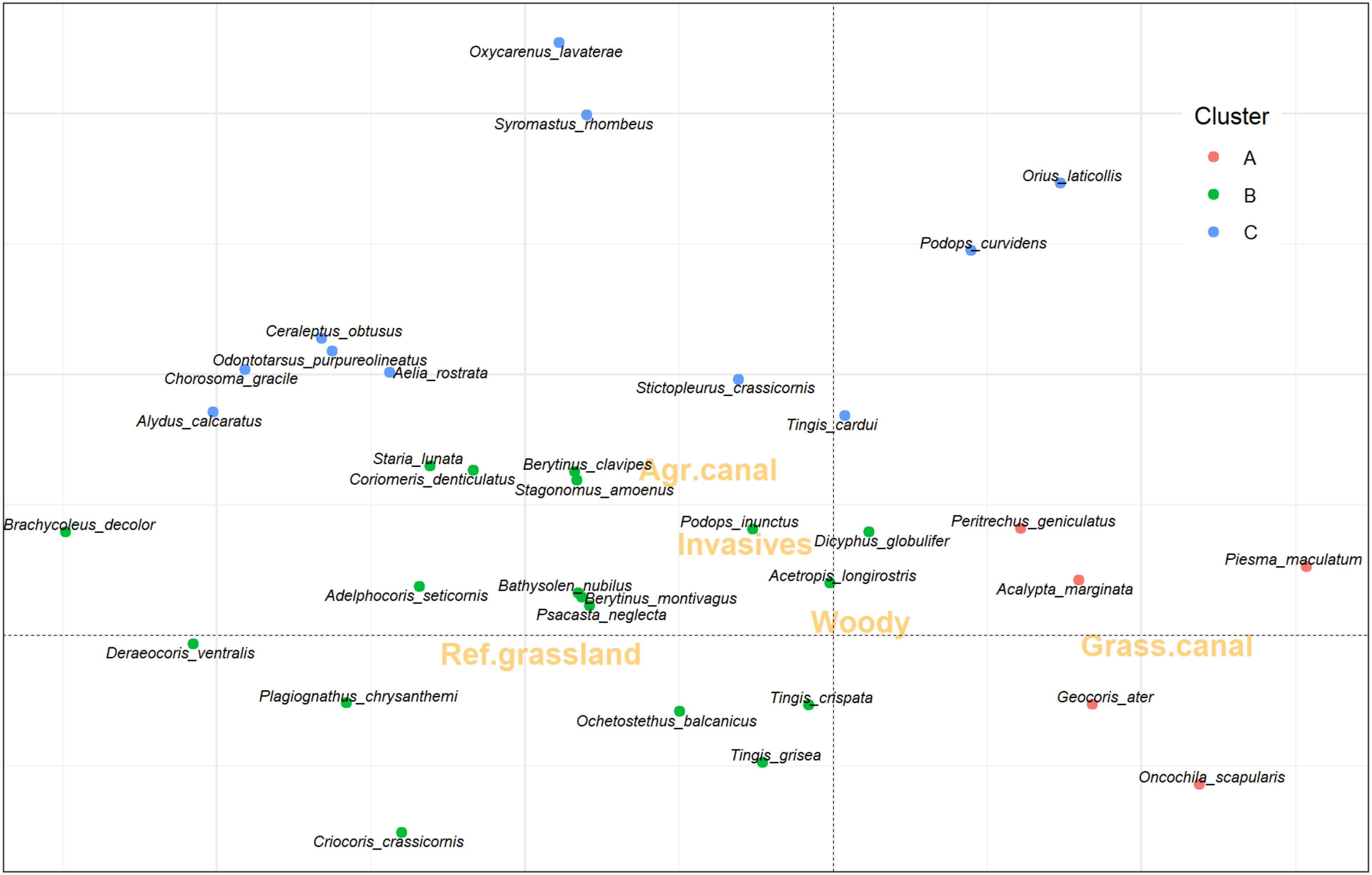

Figure 15. Ordination biplot of the environment features and true bug singletons recorded in saline canals and saline grasslands of Kiskunság. Allochthonous species *Nezara viridula* and *Corythucha arcuata* were also represented by singletons but not shown here. The colour of the dots refers to the species cluster to which a species belongs.

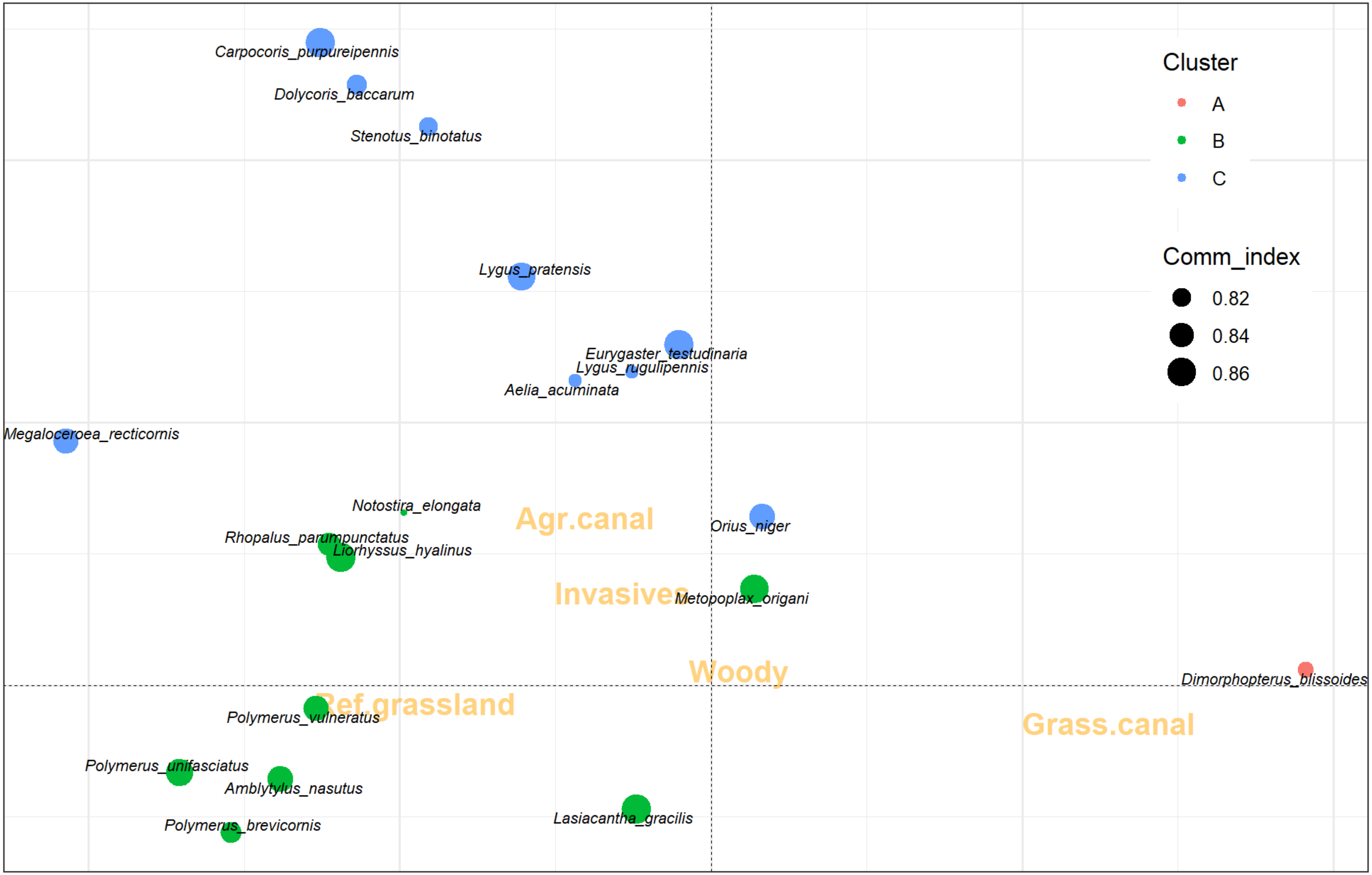

Figure 16. Ordination biplot of the environment features and the most frequently recorded true bug species in saline canals and saline grasslands of Kiskunság. The size of dots refers to the value of the commonness index and the colour of the dots refers to the species cluster to which a species belongs.

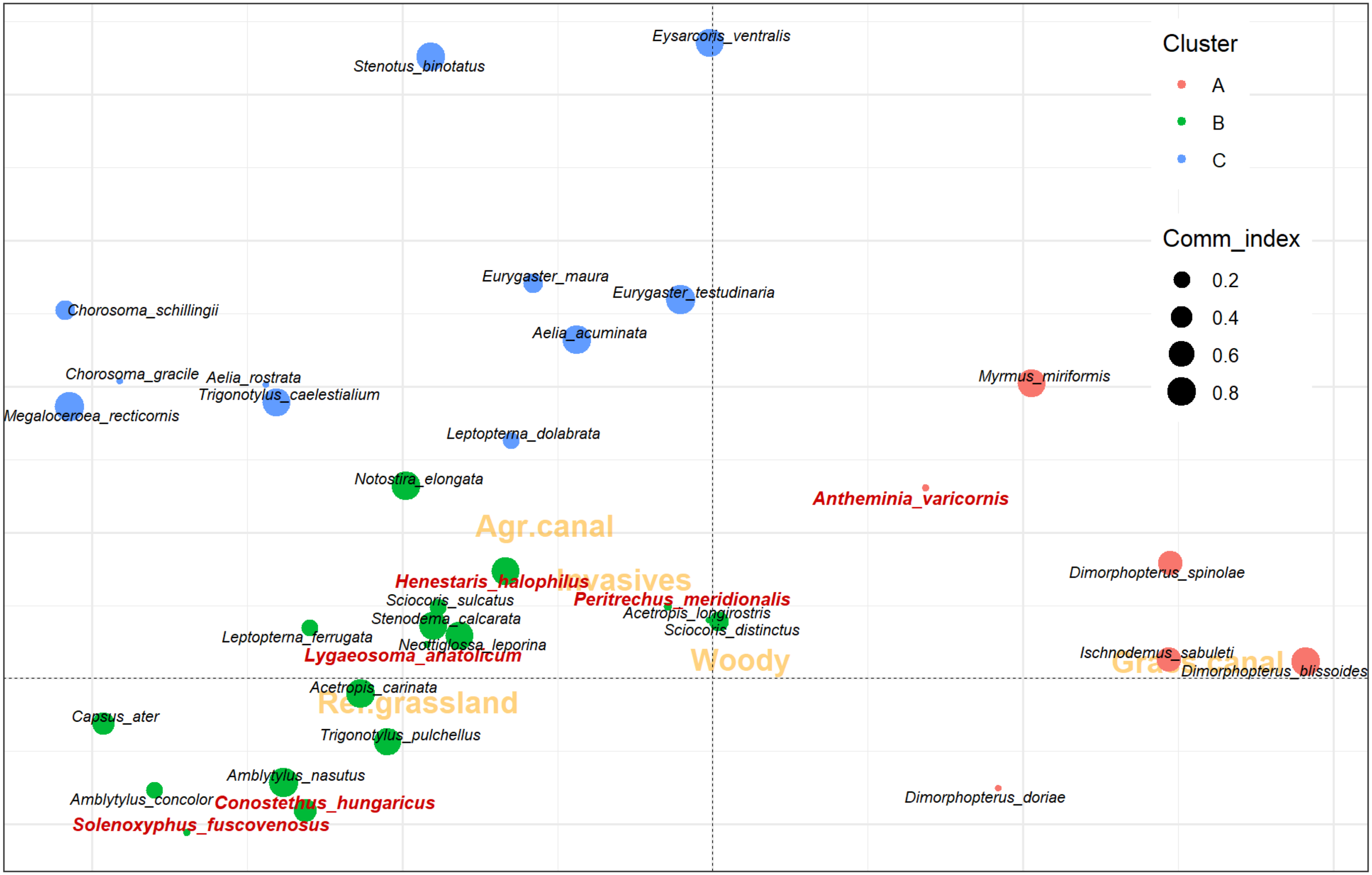

Figure 17. Ordination biplot of the environment features and the exclusive grass-feeders together with habitat specialists (red boldface letters) in saline canals and saline grasslands of Kiskunság. The size of dots refers to the value of the commonness index and the colour of the dots refers to the species cluster to which a species belongs.

Analysis of rare and common species of saline habitats resulted in 115 rare and 52 common species (see section 12.5. of the Appendix for the details). According to species cluster affiliations, A-cluster had 16 rare and 10 common species, B-cluster had 63 rare and 24 common, C-cluster had 36 rare and 18 common species. A big share of species had very low values of commonness index (less than 0.1), but not all rare species can be treated the same way as extremely rarely recorded ones were represented with singletons. Distribution of singletons (commonness index < 0.042) among clusters was 19.23% in the A-cluster, 20.69% species in the B-cluster and 24.07% in the C-cluster which means that the rarest species are evenly distributed among three species clusters, i.e. trait syndromes (Fig. 15). Among singletons, allochthonous invasive species *Nezara viridula* (Linnaeus, 1758) and *Corythucha arcuata* (Say, 1832) were also recorded, both of them were collected from agrarian saline canals and belong to C-cluster. The percentage of most common species (commonness index > 0.8) in the dataset was present with 3.85% in A-cluster, 10.35% in B-cluster and 16.67% in C-cluster. Out of 19, the most frequently recorded 7 species were exclusive grass-feeders (Fig. 16, 17).

The samples collected from saline canals and grasslands of Kiskunság also held specimens of saline habitats specialists (Fig. 17). Specialists species were mostly members of the B-cluster and *Antheminia varicornis* was the only one in A-cluster. C-cluster had no saline specialist true bugs. All specialists were considered as rare according to the value of their commonness index, except *Henstaris halophilus* which was recognized as the only common species in the dataset. However, *Conostethus hungaricus* was on the border to be considered as common species (commonness index = 0.48). None of the saline habitat specialists was represented with singletons. Out of 30 sampling sites characterized as saline habitats, specialist species were sampled from 13 locations, 9 reference grasslands, 3 grassland canals and 1 agrarian canal. *A. varicorinis* was collected from the agrarian and one natural canal howere, *H. halophilus* as the most frequent specialist was recorded in 3 grassland canals out of 9 locations in total.

5.3. Discussion

Landscape matrix and season end up being the most influential factors in shaping species richness and community composition of true bugs in drainage canals of Kiskunság. Areas bordering canals (cropland or semi-natural grassland) determined the conservation value of a canal and its suitability for saline specialists. The season is known to affect true bug communities in saline grasslands (Chapter 4), but it seems that can be applied to all open grassland-like habitats in this dry region where water availability defines the seasonal dynamics of vegetation (Biró *et al*., 2007) and related arthropod communities (Tölgyesi *et al*., 2021). Additional analysis of habitats on different substrates also affected true bugs and recognized those communities as distinctive entities. Other canals' attributes (i.e. canal size, species richness of plants and invasive plants, the abundance of reed and woody vegetation) had a negligible effect on local true bug fauna.

Agrarian saline canals followed the trend of all agrarian canals in the region, with the highest number of species among the same-substrate habitats and many singletons. In comparison to habitat groups of the same matrix category (e.g. grassland canals, reference grasslands), the separation of true bug communities from agricultural canals was not so clear, which means that even different substrates of these canals provided a similar environment and resources for true bugs. The alikeness of all considered agricultural canals might come from the similarity of vegetation; many invasive and ruderal plant species were shared among agricultural canals on different soils. True bug fauna from saline agricultural canals mostly consisted of generalists and the occasional presence of allochthonous invasive species. Agrarian canals provide environmental heterogeneity (Stein *et al*., 2014), not offered by semi-natural grasslands or surrounding croplands. Robust invasive plants and woody vegetation in these habitats increased habitat complexity and upgraded vegetation structure (López-Pintor *et al*., 2006; Herzon & Helenius, 2008), this was followed by the creation of new microhabitats and new food sources, which had not been available before and eventually caused the enrichment in true bug diversity. This boost in species number is not necessarily good, because of the presence of a large share of generalists in the community and the replacement of specialists may cause functional homogenization and reduction in the conservation value of a habitat (Blomqvist *et al*., 2003; Clavel *et al*., 2011). Regardless of it, agricultural canals yield many opportunities from which true bug species in the region can benefit (Herzon & Helenius, 2008).

Grassland canals were more similar in species richness of true bugs to corresponding reference grasslands, but their community composition was distinctive. In the case of saline grassland canals, it looks like they create an environment similar to salt-affected wetlands of the region (Biró *et al*., 2007; Molnár *et al*., 2008). Remnants of salt marsh vegetation were more frequent in these canals than in agrarian ones and provided better support for marshland true bug fauna and saline specialists. *Antheminia varicornis* is a trophic specialist that feeds on *Bolboschoenus maritimus* (L.) Palla (Wagner, 1965; Wachmann *et al*., 2008; Rabitsch, 2012), a sage species common in saline marshlands of the Panonnain Region (Molnár *et al*., 2008; Deak *et al*., 2014a). *Henestaris halophilus* was the most common saline habitat specialist in Kiskunság and was also occasionally present in saline grassland canals. *H. halophilus* prefers very dry and poor saline grasslands (Wagner, 1965; Wachmann *et al*., 2007; Rabitsch, 2012), and those canals can support this species as well. It seems that the slopes of these canals mimic the effect of naturally occurring microtopography unique to a saline grassland-marshland mosaic of the region (Molnár & Borhidi, 2003; Šefferová-Stanová *et al*., 2008). A gradient in water availability and salt content is present on the slopes of canals, consequently, this creates characteristic zonation of saline vegetation, from salt marsh vegetation on the bottom to *Artemisia* salt steppe on the top (Molnár & Borhidi, 2003; Šefferová-Stanová *et al*., 2008; Deák *et al*., 2014b). Vegetation diversity generates opportunities for many true bug species and habitat specialists, however, a small area of slopes limits the carrying capacity of canals and they should not be considered as long term surrogates for saline grassland and marshland areas.

Based on functional and life-history traits of true bugs, three trait syndromes were recognized which separated species from saline habitats in three species clusters. Species of A- and B-clusters were associated with open grassland-like habitats and adapted to specific regional ecological conditions. The difference between those two is that A-cluster contained species of low dispersive abilities with preference for humid grasslands and saline marshlands, whereas B-cluster comprised highly mobile and xerophilous species like the majority of species in dry saline grasslands. It is known that high dispersal and disturbance avoiding abilities are promoted by intense grassland management (Neff *et al*., 2020) and considering that saline grasslands are regularly grazed or mown, it can be assumed that these grasslands may favour better dispersers. Although management applied in saline grasslands of the Pannonian Region is of low intensity, according to regulations of Natura 2000 and nationally protected areas, Torma *et al*. (2019) suggested that even low-intensity management regimes could influence the dispersal abilities of saline true bug communities. Lastly, C-cluster species were associated with agricultural canals, less hostile environments than nearby semi-natural grasslands. These communities mostly consisted of bigger size habitat generalists with good dispersal abilities; the high colonization potential of these species is a result of conquering wide cropland areas to reach isolated agricultural canals (Seibold *et al*., 2019; Batáry *et al*., 2020).

Rare species in the study were mostly associated with reference grasslands which means that dry saline grasslands are irreplaceable habitats for original true bug fauna; most saline habitat specialists were associated with the same habitats as well (*Henestaris halophilus*, *Conostethus hungaricus*, *Solenoxyphus fuscovenosus*, *Lygaeosoma anatolicum*, *Peritrechus meridionalis*). However, canals, especially grassland canals, can provide good support for saline marshland vegetation (Molnár *et al*., 2008) and accompanied true bug communities. Bearing in mind that the wetland area in Kiskunság is constantly decreasing and all kinds of marshlands are disappearing from the region (Biró *et al*., 2007), it is important to think that canals could be crucial in sustaining local populations of wetland arthropod species. Yet, the dispersal abilities of individual species could dictate their success in reaching potential canal habitats and their existence in the region. Seibold *et al*. (2019) showed that the number of weak dispersers among grassland plant-dwelling arthropods decreases if the surrounding cover of arable land increases. This could be a serious threat to common marshland species of A-cluster, like those from genera *Agramma* and *Dimorphopterus*. These species by definition are weak dispersers, small in size, and often brachypterous, thus, they were mostly linked to grassland canals. In contrast, *Antheminia varicornis* is a larger species with good flying abilities and the one that reached and established in an isolated agricultural saline canal.

Canals of Kiskunság have great potential for true bug conservation, but some of these habitats are not self-sustainable and certain human interventions are needed from time to time. Maintenance of woody vegetation and reeds is needed to sustain a rich herb layer (Blomqvist *et al*., 2003). Dredging and vegetation removal from the canal slopes, as well as, filling of canals should be carefully planned because they directly destroy habitat and its conservation value could decrease if the important species and accompanied microhabitats disappear (Twisk *et al*., 2000, 2003). Also, further drop in ground-water level in the region can contribute to the absence of natural fluctuations of water and salt migrations in the soil or even leaching the salts from canals (Molnár & Borhidi, 2003; Šefferová-Stanová *et al*., 2008) which can potentially cause disappearing of saline vegetation and associated true bug species. Saline habitats are very resilient to invasions if the water-salt dynamics is preserved (Török *et al*., 2011). Salinity is already a strong stressor in saline grasslands and invasive plants cannot compete with native halophytes and salt-tolerant species (Kelemen *et al*., 2013); this extreme environment is not welcoming to invasive true bugs as well. Removal of excessive biomass in agricultural canals can be managed by cutting, whereas grassland canals are occasionally grazed all together with nearby grasslands.

The type of landscape matrix in which a canal is embedded came up as the most influential factor in defining the conservation character of canals for true bugs. Grassland canals are better secondary habitats for saline habitat specialists, but agricultural canals accommodated more species and diversified local true bug fauna. Canals serve as shelters and overwintering places, but they also concentrate species by providing fresh food for herbivores (Herzon & Helenius, 2008); this is especially important in the summer months when surrounding semi-natural grasslands are dry and not very welcoming places to live in.

6. CONCLUSIONS

A manageable number of species and ecological diversity of true bugs are cornerstones of their applicability in biodiversity and habitat assessments in European farmland, whereas grasslands are perfect model systems to study biology, ecology and functional roles of true bugs in detail. These insects are highly responsive to vegetation change (natural or human-induced) by modifying the species and functional composition of their communities. However, any conservation planning requires substantial knowledge of fauna and the distribution of species of conservation interest.

The study on true bugs from saline grasslands in Vojvodina fills the gap in knowledge on biodiversity from the southernmost part of the Pannonian Region. Now we know what species are currently present in northern Serbia, how frequent and spatially distributed they are, and finally, what species should be prioritized in conservation. Serbia is on the borderline of ranges of some saline habitat specialists; marginal populations and habitat patches merit exclusive treatment in conservation because of the higher risk of extinction. However, true bug communities in saline grasslands are highly nested, which is positively correlated with the robustness of communities (i.e. tolerance to species' extinction) (Neff *et al.*, 2021). The core of well-nested true bug communities is not the most numerous group of specialized grass-feeders, but a set of 'generalists' (in its broadest sense) of low abundance. Every one of these 'generalists' is ecologically finely tuned and unique, thus, the incorporation of every new species increases the functional diversity and stability of the community.

Knowledge of the taxonomic and functional diversity of saline grassland true bugs was also used to measure variations in the response of these insects to different causes of habitat change. Results show that sub-communities of different habitat strata were not influenced in the same way by a habitat change. This is important information for management planning, which aims to improve habitat quality for all residents of saline grasslands. But, well-preserved saline grasslands are not enough to sustain rich and healthy populations of true bugs, grassy elements of green and blue infrastructure are very important in supporting communities in a mainly agricultural landscape. In that sense, the drainage canals of the Pannonian Region seem to have great potential to support saline habitat specialists, especially species related to saline marshlands. Moreover, canals significantly enrich true bug diversity in farmland.

7. ACKNOWLEDGEMENT

I am grateful for the opportunity to join the Department of Ecology in Szeged where I met wonderful people, learned a lot and hopefully produced something valuable during my stay here. There is a long list of people I would like to thank, but I hope those I forgot will forgive me.

I would like to thank my supervisor Attila Torma, who has been a great support during my studies, as a mentor and as a friend. His guidelines have been crucial in every step of the realization of this thesis. I found our professional and relaxed discussions to be the most valuable which shaped me to become a better ecologist. The biggest support to my Rufford projects in Serbia was delivered by a dear friend and colleague Bojana Nadažnin, without whose help the realization of my projects would have been questionable. Bojana has been a great companion in our fieldwork sessions, and her perfect organization skills have made my life much easier. Friends and colleagues from Serbia who also helped me with preparation, fieldwork, organization and logistics for my projects are Nikola Milić, David Grabovac, Miloš Popović, Tanja Tomić, Ranko Perić, Mirjana Ćuk, Ivan Tot, Milovan Ilić, Anita Sučić and Klara Sabadoš. Hungarian colleagues and new friends who made my work in the lab and in the field enjoyable are Róbert Gallé, Zoltán Bátori, Csaba Tölgyesi, István Elek Maák and lovely Anna Nagy. I would also like to thank the reviewers for their well-intentioned suggestions to improve this manuscript. Last but not least, I want to thank my cutie Vaishali Rani who is always ready to help me with my English writings.

Many people led me and helped me on this journey including family members, friends, and colleagues from Serbia, Hungary, and all around the world. It has been a pleasure to meet, work and party with all of them and I hope our friendships and collaborations will last for many years.

8. REFERENCES

Achtziger, R., Frieß, T., Rabitsch, W. (2007): True bugs (Insecta: Heteroptera) as suitable indicators for nature conservation. *Insecta* 10: 93–127.

Almeida-Neto, M., Guimarães, P., Guimarães Jr, P.R., Loyola, R.D., Ulrich, W. (2008): A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos* 117(8): 1227–1239. DOI: 10.1111/j.0030-1299.2008.16644.x

Almeida-Neto, M., Ulrich, W. (2011): A straightforward computational approach for measuring nestedness using quantitative matrices. *Environmental Modelling and Software* 26(2): 173–178. DOI: 10.1016/j.envsoft.2010.08.003

Atmar, W., Patterson, B.D. (1993): The measure of order and disorder in the distribution of species in fragmented habitat. *Oecologia* 96(3):373–382. DOI: 10.1007/BF00317508

Balbuena, J.A., Monlleó-Borrull, C., Llopis-Belenguer, C., Blasco-Costa, I., Sarabeev, V.L., Morand, S. (2021a): Fuzzy quantification of common and rare species in ecological communities (FuzzyQ). *Methods in Ecology and Evolution* 12(6): 1070–1079. DOI: 10.1111/2041-210X.13588

Balbuena, J.A., Monlleó-Borrull, C., Llopis-Belenguer, C., Blasco-Costa, I., Sarabeev, V.L., Morand, S. (2021b): *Code for fuzzy quantification of common and rare species in ecological communities* (version v1.0). Zenodo. DOI: 10.5281/zenodo.4469291

Batáry, P., Báldi, A., Ekroos, J., Gallé, R., Grass, I., Tscharntke, T. (2020): Biologia Futura: landscape perspectives on farmland biodiversity conservation. *Biologia Futura* 71: 9–18. DOI: 10.1007/s42977-020-00015-7

Bates, D., Mächler, M., Bolker, B., Walker, S. (2015): Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software* 67(1): 1–48. DOI: 10.18637/jss.v067.i01

Beckett, S.J., Boulton, C.A., Williams, H.T.P. (2014): FALCON: a software package for analysis of nestedness in bipartite networks [v1; ref status: indexed, http://f1000r.es/3z8]. *F1000 Research* 3: 185. DOI: 10.12688/f1000research.4831.1

Bengtsson, J., Bullock, J.M., Egoh, B., Everson, C., Everson, T., O'Connor, T., O'Farrell, P.J., Smith, H.G., Lindborg, R. (2019): Grasslands—more important for ecosystem services than you might think. *Ecosphere* 10(2): e02582. DOI: 10.1002/ecs2.2582

Berglund, H., Jonsson, B.G. (2003): Nested plant and fungal communities; the importance of area and habitat quality in maximizing species capture in boreal old-growth forests. *Biological Conservation* 112(3): 319–328. DOI: 10.1016/S0006-3207(02)00329-4

Biró, M., Révész, A., Molnár, Zs., Horváth, F. (2007): Regional habitat pattern of the Danube-Tisza Interfluve in Hungary, I: The landscape structure and habitat pattern; the fen and alkali vegetation. *Acta Botanica Hungarica* 49(3–4): 267–303. DOI: 10.1556/ABot.49.2007.3-4.4

Biró, M., Révész, A., Molnár, Zs., Horváth, F., Czúcz, B. (2008): Regional habitat pattern of the Danube-Tisza Interfluve in Hungary II: The sand, the steppe and the riverine vegetation, degraded and regenerating habitats, regional habitat destruction. *Acta Botanica Hungarica* 50(1–2): 19–60. DOI: 10.1556/ABot.50.2008.1–2.2

Blomqvist, M.M., Vos, P., Klinkhamer, P.G.L., ter Keurs, W.J. (2003): Declining plant species richness of grassland ditch banks—A problem of colonisation or extinction. *Biological Conservation* 109: 391–406. DOI: 10.1016/S0006 -3207(02)00165 -9

Blomqvist, M.M., Tamis, W.L.M., de Snoo, G.R. (2009): No improvement of plant biodiversity in ditch banks after a decade of agri-environment schemes. *Basic and Applied Ecology* 10: 368–378. DOI: 10.1016/j.baae.2008.08.007

Boch, S. , Becker, T., Deák, B., Dengler, J., Klaus, V.H. (2021): Grasslands of temperate Europe in a changing world – Editorial to the 16th EDGG Special Feature in Tuexenia. *Tuexenia* 41: 351–359. DOI: 10.14471/2021.41.020

Bölöni, J., Molnár, Zs., Horváth, F., Illyés, E. (2008): Naturalness-based habitat quality of the Hungarian (semi-)natural habitats. *Acta Botanica Hungarica* 50: 149–159. DOI: 10.1556/ABot.50.2008.Suppl.7

Braby, M.F., Williams, M.R. (2016): Biosystematics and conservation biology: critical scientific disciplines for the management of insect biological diversity. *Austral Entomology* 55: 1–17. DOI:10.1111/aen.12158

Brändle, M., Stadler, J., Brandl, R. (2000): Body size and host range in European Heteroptera. *Ecography* 23: 139–147.

Braun-Blanquet, J. (1928): *Pflanzensoziologie. Grundzüge der Vegetationskunde*. Springer, Berlin.

Braun-Blanquet, J. (1964): *Pflanzensoziologie*. Grundzüge der Vegetationskunde 3. Springer, Wien—New York.

Cardoso, P., Borges, P.A.V., Triantis, K.A., Ferrández, M.A., Martín, J.L. (2011a): Adapting the IUCN Red List criteria for invertebrates. *Biological Conservation* 144(10): 2432–2440. DOI: 10.1016/j.biocon.2011.06.020

Cardoso, P., Erwin, T.L., Borges, P.A.V., New, T.R. (2011b): The seven impediments in invertebrate conservation and how to overcome them. *Biological Conservation* 144(11): 2647–2655. DOI: 10.1016/j.biocon.2011.07.024

Clavel, J., Julliard, R., Devictor, V., (2011): Worldwide decline of specialist species: toward a global functional homogenization? *Frontiers in Ecology and the Environment* 9(4): 222–228. DOI: 10.1890/080216

Council Directive 2009/147/EC on the conservation of wild birds, codified version of Directive 79/409/EEC.

Council Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora.

Császár, P., Torma A., Gallé-Szpisjak N., Tölgyesi C., Gallé R. (2018): Efficiency of pitfall traps with funnels and/or roofs in capturing ground-dwelling arthropods. *European Journal of Entomology* 115: 15–24. DOI: 10.14411/eje.2018.003

Cutler, A.H. (1994): Nested biotas and biological conservation: metrics, mechanisms, and meaning of nestedness. *Landscape and Urban Planning* 28(1): 73–82. DOI: 10.1016/0169-2046(94)90045-0

De Cáceres, M., Legendre, P. (2009): Associations between species and groups of sites: indices and statistical inference. *Ecology* 90(12): 3566–3574. DOI: 10.1890/08-1823.1

Deák, B., Valkó, O., Alexander, C., Mücke,W., Kania, A., Tamás, J., Heilmeier, H. (2014b): Fine-scale vertical position as an indicator of vegetation in alkaligrasslands – Case study based on remotely sensed data. *Flora* 209(12): 693–697. DOI: 10.1016/j.flora.2014.09.005

Deák, B., Valkó, O., Tóthmérész, B., Török, P. (2014a): Alkali marshes of Central Europe: Ecology, management and nature conservation. *In*: Shao, H.B. (Ed.): *Salt Marshes*. Nova Science Publishers, Inc. ISBN: 978-1-63321-325-8

Dengler, J., Janišová, M., Török, P., Wellstein, C. (2014): Biodiversity of Palaearctic grasslands: a synthesis. *Agriculture, Ecosystems and Environment* 182: 1–14. DOI: 10.1016/j.agee.2013.12.015

Di Giulio, M., Edwards, P.J., Meister, E. (2001): Enhancing insect diversity in agricultural grasslands: the roles of management and landscape structure. *Journal of Applied Ecology* 38: 310–319. DOI: 10.1046/j.1365-2664.2001.00605.x

Dítě, D., Eliáš, P. jun., Melečková, Z. (2013): *Artemisia santonicum* subsp. *patens* in Slovakia: The sad story of obligate halophyte on the northern edge of its distribution range. *Hacquetia* 12(2): 5–16. DOI: 10.2478/HACQ-2013-0009

Dítětová, Z., Dítě, D., Eliáš, P. jun., Galvánek, D. (2016): The impact of grazing absence in inland saline vegetation – a case study from Slovakia. *Biologia* 71(9): 980–988. DOI: 10.1515/biolog-2016-0125

Dray, S., Choler, Ph., Dolédec, S., Peres-Neto, P.R., Thuiller, W., Pavoine, S., ter Braak, C.J.F. (2014): Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. *Ecology* 95(1): 14–21. DOI: 10.1890/13-0196.1

Dray, S., Dufour, A. (2007): The ade4 Package: Implementing the Duality Diagram for Ecologists. *Journal of Statistical Software* 22(4): 1–20. DOI: 10.18637/jss.v022.i04.

Duelli, P., Obrist, M.K. (1998): In search of the best correlates for local organismal biodiversity in cultivated areas. *Biodiversity and Conservation* 7(3): 297–309. DOI: 10.1023/A:1008873510817

Duelli, P., Obrist, M.K. (2003): Biodiversity indicators: the choice of values and measures. *Agriculture, Ecosystems and Environment* 98: 87–98. DOI: 10.1016/S0167-8809(03)00072-0

Dufrêne, M., Legendre, P. (1997): Species Assemblages and Indicator Species: The Need for a Flexible Asymmetrical Approach. *Ecological Monographs* 67(3): 345–366. DOI: 10.1890/0012-9615(1997)067[0345:SAAIST]2.0.CO;2

Dunn, R. (2005): Modern Insect Extinctions, the Neglected Majority. *Conservation Biology* 19(4): 1030–1036. DOI: 10.1111/j.1523-1739.2005.00078.x

Eliáš, P., Dítě, D., Dítě, Z. (2020): Halophytic Vegetation in the Pannonian Basin: Origin, Syntaxonomy, Threat, and Conservation. *In*: Grigore, M.N. (Ed.): *Handbook of Halophytes*. Springer Nature, Switzerland. DOI: 10.1007/978-3-030-17854-3_11-1

European Commission (2008): *LIFE and Europe´s grasslands. Restoring a forgotten habitat*. Office for Official Publications of the European Communities, Luxembourg. DOI: 10.2779/23028

European Commission (2018): *Farming for Natura 2000. Guidance on how to support Natura 2000 farming systems to achieve conservation objectives, based on Member States good practice experiences*. Publications Office of the European Union. Luxembourg.

European Commission (2020): *EU Biodiversity Strategy for 2030. Bringing nature back into our lives*. COM(2020) 380 final. Brussels, 20.5.2020.

European Environment Agency (2002): The Pannonian region - the remains of the Pannonian Sea. *In*: *Europe's biodiversity - biogeographical regions and seas*. European Environment Agency, Technical report, Copenhagen.

Evans, D. (2012): Building the European Union's Natura 2000 network. *Nature Conservation* 1: 11–26. DOI: 10.3897/natureconservation.1.1808

Faber-Langendoen, D., Josse, C. (2010): *World Grasslands and Biodiversity Patterns. A Report to IUCN Ecosystem Management Programme*. NatureServe, Arlington, Virginia.

Fischer, J., Lindenmayer, D.B. (2005): Nestedness in fragmented landscapes: a case study on birds, arboreal marsupials and lizards. *Journal of Biogeography* 32(10): 1737–1750. DOI: 10.1111/j.1365-2699.2005.01319.x

Fischer, M., Bossdorf, O., Gockel, S., Hänsel, F., Hemp, A., Hessenmöller, D., Korte, G., Nieschulze, J., Pfeiffer, S., Prati, D., Renner, S., Schöning, I., Schumacher, U., Wells, K., Buscot, F., Kalko, E.K.V., Linsenmair, K.E., Schulze, E.D., Weisser, W.W. (2010): Implementing largescale and longterm functional biodiversity research: The Biodiversity Exploratories. *Basic and Applied Ecology* 11: 473–485. DOI: 10.1016/j.baae.2010.07.009

Fleishman, E., Murphy, D.D. (1999): Patterns and processes of nestedness in a Great Basin butterfly community. *Oecologia* 119(1): 133–139. DOI: 10.1007/s004420050769

Fox, J., Weisberg, S. (2019): *An R Companion to Applied Regression*, Third edition. Sage, Thousand Oaks CA.

Friess, N., Gossner, M.M., Weisser, W.W., Brandl, R., Brändle, M. (2017): Habitat availability drives the distribution–abundance relationship in phytophagous true bugs in managed grasslands. *Ecology* 98(10): 2561–2573. DOI: 10.1002/ecy.1947

Gallé, L., Györffy, Gy., Hornung, E., Körmöczi, L. (1988): Indication of environmental heteromorphy and habitat fragmentation by invertebrate communities in grasslands. *In*: Bohac, J., Ruzicka, V. (Eds.): *Proc. Vth Int. Conf. Bioindicatores Deteriorisationis Regionis*, Inst. Landscape Ecology CAS, Ceské Budéjovice. 167 p.

Gámez-Virués, S., Perović, D.J., Gossner, M.M., Börschig, C., Blüthgen, N., de Jong, H., Simons, N.K., Klein, A.M., Krauss, J., Maier, G., Scherber, Ch., Steckel, J., Rothenwöhrer, Ch., Steffan-Dewenter, I., Weiner, Ch.N., Weisser, W., Werner, M., Tscharntke, T., Westphal, C. (2015): Landscape simplification filters species traits and drives biotic homogenization. *Nature Communications* 6: 8568. DOI: 10.1038/ncomms9568

Gossner, M.M., Heckmann, R., Moretti, M. (2018): From the South and from the North? – *Quilnus marcosi* Heiss & Baena and *Aradus angularis* J. Sahlberg, two flat bug species new for Central Europe (Hemiptera, Heteroptera, Aradidae). *Alpine Entomology* 2: 7–14. DOI: 10.3897/alpento.2.21801

Gossner, M.M., Simons, N.K., Achtziger, R., Blick, Th., Dorow, W.H.O., Dziock, F., Köhler, F., Rabitsch, W., Weisser, W.W. (2015a): A summary of eight traits of Coleoptera, Hemiptera, Orthoptera and Araneae, occurring in grasslands in Germany. *Scientific Data* 2: 150013. DOI: 10.1038/sdata.2015.13

Gossner, M.M., Simons, N.K., Höck, L., Weisser, W.W. (2015b): Morphometric measures of Heteroptera sampled in grasslands across three regions of Germany. *Ecology* 96(4): 1154. DOI: 10.1890/14-2159.1

Harper, J.L., Hawksworth, D.L. (1994): Biodiversity: measurement and estimation. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 345: 5–12. DOI:10.1098/rstb.1994.0081

Harvey, J.A., Heinen, R., Armbrecht, I., Basset, Y., Baxter-Gilbert, J.H., Bezemer, T.M., Böhm, M., Bommarco, R., Borges, P.A.V., Cardoso, P., Clausnitzer, V., Cornelisse, T., Crone, E.E., Dicke, M., Dijkstra, K.D.B., Dyer, L., Ellers, J., Fartmann, T., Forister, M.L.,… de Kroon, H. (2020): International scientists formulate a roadmap for insect conservation and recovery. *Nature Ecology & Evolution* 4: 174–176. DOI: 10.1038/s41559-019-1079-8

Heiss, E., Péricart, J. (1983): Revision of Palaearctic Piesmatidae. *Mitteilungen der Münchner Entomologischen Gesellschaft* 73: 61–171.

Herzon, I., Helenius, J. (2008) Agricultural drainage ditches, their biological importance and functioning. *Biological Conservation* 141(5) : 1171–1183. DOI: 10.1016/j.biocon.2008.03.005

Hochkirch, A., Samways, M.J., Gerlach, J., Böhm, M., Williams, P., Cardoso, P., Cumberlidge, N., Stephenson, P.J., Seddon, M.B., Clausnitzer, V., Borges, P.A.V., Mueller, G.M., Pearce-Kelly, P., Raimondo, D.C., Danielczak, A., Dijkstra, K.D.B. (2020): A strategy for the next decade to address data deficiency in neglected biodiversity. *Conservation Biology* 35(2): 502–509. DOI: 10.1111/cobi.13589

Horvat, I., Horvatić, S., Gračanin, M., Tomažić, G., Em., H., Maksić, B. (1950): *Priručnik za tipološko istraživanje i kartiranje vegetacije*. Nakladni zavod Hrvatske, Zagreb.

Horváth, G. (1897): Ordo Hemiptera. *In*: Paszlavszky, J. (Ed.): *A Magyar Birodalom Állatvilága (Fauna Regni Hungariae), III. (Arthropoda)*. A K. M. Természetudományi Társulat, Budapest, 72 pp. [in Hungarian and Latin]

Hughes, J.B., Daily, G.C., Ehrlich, P.R. (2000): Conservation of Insect Diversity: a Habitat Approach. *Conservation Biology* 14(6): 1788–1797.

Hylander, K., Nilsson, C., Jonsson, B.G., Göthner, T. (2005): Differences in habitat quality explain nestedness in a land snail meta-community. *Oikos* 108(2): 351–361. DOI: 10.1111/j.0030-1299.2005.13400.x

IPBES (2018): *Report of the Plenary of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services on the work of its sixth session*. IPBES/6/15/Add.5. Medellin, Colombia, 18–24 March 2018.

IPBES (2019): *Report of the Plenary of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services on the work of its seventh session*. IPBES/7/10/Add.1. Paris, 29 April–4 May 2019.

IUCN (2021): *The IUCN Red List of Threatened Species. Version 2021-3*. https://www.iucnredlist.org. Accessed on [13 February 2022].

Josse, J., Husson, F. (2016): missMDA: A Package for Handling Missing Values in Multivariate Data Analysis. *Journal of Statistical Software* 70(1): 1–31. DOI: 10.18637/jss.v070.i01.

Kaur, H., Torma, A., Gallé-Szpisjak, N., Šeat, J., Lőrinczi, G., Módra, G., Gallé, R. (2019): Road verges are important secondary habitats for grassland arthropods. *Journal of Insect Conservation* 23: 899–907. DOI: 10.1007/s10841-019-00171-9

Kelemen, A., Török, P., Valkó, O., Miglécz, T., Tóthmérész, B. (2013): Mechanisms shaping plant biomass and species richness: Plant strategies and litter effect in alkali and loess grasslands. *Journal of Vegetation Science* 24: 1195–1203. DOI: 10.1111/jvs.12027

Kis, B. (1984): Heteroptera. Partea generală şi suprafamilia Pentatomoidea. *In*: *Fauna Republicii Socialiste România*, Vol. 8. Editura Academiei Republicii Socialiste România, Bucureşti, 213 pp. [in Romanian]

Kleyer, M., Dray, S., de Bello, F., Lepš, J., Pakeman, R.J., Strauss, B., Thuiller, W., Lavorel, S. (2012): Assessing species and community functional responses to environmental gradients: which multivariate methods? *Journal of Vegetation Science* 23(5): 805–821. DOI: 10.1111/j.1654-1103.2012.01402.x

Kment, P., Hradil, K., Straka, M., Sychra, J. (2017): Heteroptera (ploštice). *In*: Hejda, R., Farkač, J., Chobot, K. (Eds.): Red list of threatened species in the Czech Republic. Invertebrates. *Příroda Praha* 36: 137–147.

Kőrösi, Á., Batáry, P., Orosz, A., Rédei, D., Báldi, A. (2012): Effects of grazing, vegetation structure and landscape complexity on grassland leafhoppers (Hemiptera: Auchenorrhyncha) and true bugs (Hemiptera: Heteroptera) in Hungary. *Insect Conservation and Diversity* 5: 57–66. DOI: 10.1111/j.1752-4598.2011.00153.x

Kradin, N.N. (2002): Nomadism, Evolution and World-Systems: Pastoral Societies in Theories of Historical Development. *Journal of World-Systems Research* 8(3): 368–388. DOI: 10.5195/jwsr.2002.266

Kremen, C., Colwell, R.K., Erwin, T.L., Murphy, D.D., Noss, R.F., Sanjayan, M.A. (1993): Terrestrial Arthropod Assemblages: Their Use in Conservation Planning. *Conservation Biology* 7(4): 796–808.

Lakušić, D., Blaženčić, J., Ranđelović, V., Butorac, B., Vukojičić, S., Zlatković, B., Jovanović, S., Šinžar-Sekulić, J., Žukovec, D., Ćalić, I., Pavićević, D. (2005): *Staništa Srbije—Priručnik sa opisima i osnovnim podacima*. Biološki fakultet, Univerzitet u Beogradu, 684 pp. [in Serbian]

Laliberté, E., Legendre, P. (2010): A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91: 299–305. DOI: 10.1890/08-2244.1

Lehr, P.A. (Ed.) (1988): *Keys to the insects of the Far East of the USSR*, Vol. 2. Homoptera and Heteroptera. Nauka Publishing House, Leningrad, 211 pp.

Lenth, R. (2020): *emmeans: Estimated Marginal Means, aka Least-Squares Means*. R package version 1.5.0.

Li, X., Wang, Sh., Prather, Ch., Wan, H.Y., Zhu, H., Nummi, P., Inbar, M., Gao, Q., Wang, D., Zhong, Zh. (2021): Large herbivores facilitate an insect herbivore by modifying plant community composition in a temperate grassland. *Ecology and Evolution* 11(22): 16314–16326. DOI: 10.1002/ece3.8327

Lindenmayer, D.B., Fischer, J. (2006): Chapter 13—Nestedness and Community Assembly. *In*: *Habitat fragmentation and landscape change: an ecological and conservation synthesis*. Island Press, Washington, 133–141 pp.

Lis, B., Stroiński, A., Lis, J.A. (2008): *Coreoidea—Alydidae, Coreidae, Rhopalidae, Stenocephalidae. Heteroptera Poloniae,* Vol. 1. Centrum Studiów nad Bioroznorodoscia (CesStuBio), Katedra Biosystematiki UO, Opole, 157 pp. [in Polish]

Lis, J.A., Lis, B., Ziaja, D. (2012): *Pentatomoidea—Plataspidae, Thyreocoridae, Cydnidae, Acanthosomatidae, Scutelleridae. Heteroptera Poloniae,* Vol. *2.* Centrum Studiów nad Bioroznorodoscia (CesStuBio), Katedra Biosystematiki UO, Opole, 144 pp. [in Polish]

Löffler, F., Poniatowski, D., Fartmann, T. (2020): Extinction debt across three taxa in well-connected calcareous grasslands. *Biological Conservation* 246: 108588. DOI: 10.1016/j.biocon.2020.108588

López-Pintor, A., Sal, A.G., Benayas, J.M.R. (2006): Shrubs as a source of spatial heterogeneity—The case of *Retama sphaerocarpa* in Mediterranean pastures of central Spain. *Acta Oecologica* 29: 247–255. DOI: 10.1016/j.actao.2005.11.001

Lőrinczi, G., Bozsó, M., Duma, I., Petrescu, M., Gallé, R., Torma, A. (2011): Preliminary results on the invertebrate fauna (Araneae, Orthoptera, Heteroptera and Hymenoptera: Formicidae) of alkaline grasslands of the Hungarian-Romanian border. *In*: Körmöczi, L. (Ed.): Ecological and socio-economic relations in the valleys of river Körös/Cris and river Maros/Mures. *Tiscia Monograph Series* 9: 159–173.

Magurran, A.E. (2004): *Measuring Biological Diversity*. Blackwell Science Ltd. ISBN: 0-632-05633-9

Manojlović, M. (2014): *Popravka halomorfnih zemljišta*. Univerzitet u Novom Sadu, Poljoprivredni fakultet, Novi Sad. ISBN 978-86-7520-292-9 [in Serbian]

Martinez Arbizu, P. (2020): *pairwiseAdonis: Pairwise multilevel comparison using adonis*. R package version 0.4

Matocq, A. (2004): Review of the species assigned to the genus *Megalocoleus* Reuter, 1890 (Heteroptera : Miridae). *Annales de la Société entomologique de France (N.S.)* 40 (1): 69–101. DOI: 10.1080/00379271.2004.10697407

Matocq, A., Pluot-Sigwalt, D. (2012): Revision of the genus *Amblytylus* and an attempt to improve our understanding of the genera *Amblytylus* and *Megalocoleus* (Heteroptera: Miridae: Phylinae). *Annales de la Société entomologique de France (N.S.)* 48 (1–2): 123–154. DOI: 10.1080/00379271.2012.10697760

Matthews, T.J., Cottee-Jones, H.E.W., Whittaker, R.J. (2015): Quantifying and interpreting nestedness in habitat islands: a synthetic analysis of multiple datasets. *Diversity and Distributions* 21(4): 1–13. DOI: 10.1111/ddi.12298

McGeoch, M.A. (2007): The selection, testing and application of terrestrial insects as bioindicators. *Biological Reviews* 73(2): 181–201. DOI: 10.1111/j.1469-185X.1997.tb00029.x

McGeoch, M.A., Van Rensburg, B.J., Botes, A. (2002): The verification and application of bioindicators: a case study of dung beetles in a savanna ecosystem. *Journal of Applied Ecology* 39(4): 661–672. DOI: 10.1046/j.1365-2664.2002.00743.x

Menezes, J.F.S., Fernandez, F.A.S. (2013): Nestedness in forest mammals is dependent on area but not on matrix type and sample size: an analysis on different fragmented landscapes. *Brazilian Journal of Biology* 73(3): 465–470. DOI: 10.1590/S1519-69842013000300002

Millennium Ecosystem Assessment (2005): *Ecosystems and Human Well-being: Synthesis*. World Resources Institute. Island Press, Washington, DC.

Molnár Á., Molnár Zs., Kotymán L., Balogh G. (2016): A Csanádi puszták növényzete és növényzeti változásai az elmúlt 10 évben. *Crisicum* 9: 37–63.

Molnár, Zs, Borhidi, A. (2003): Hungarian alkali vegetation: Origins, landscape history, syntaxonomy, conservation. *Phytocoenologia* 33(2–3): 377–408. DOI: 10.1127/0340-269X/2003/0033-0377

Molnár, Zs., Biró, M., Bölöni, J., Horváth, F. (2008): Distribution of the (semi-)natural habitats in Hungary I. Marshes and grasslands. *Acta Botanica Hungarica* 50(Suppl.): 59–105. DOI: 10.1556/ABot.50.2008.Suppl.5

Neff, F., Blüthgen, N., Christé, M.N., Simons, N.K., Steckel, J., Weisser, W.W., Westphal, C., Pellisser, L., Gossner, M.M. (2019): Cross-scale effects of land use on the functional composition of herbivorous insect communities. *Landscape Ecology* 34(8): 2001–2015. DOI: 10.1007/s10980-019-00872-1

Neff, F., Brändle, M., Ambarlı, D., Ammer, Ch., Bauhus, J., Boch, S., Hölzel, N., Klaus, V.H., Kleinebecker, T., Prati, D., Schall, P., Schäfer, D., Schulze, E.D., Seibold, S., Simons, N.K., Weisser, W.W., Pellisser, L., Gossner, M.M. (2021): Changes in plant-herbivore network structure robustness along land-use intensity gradients in grasslands and forests. *Science Advances* 7(20): eabf3985. DOI: 10.1126/sciadv.abf3985

Neff, F., Resch, M.C., Marty, A., Rolley, J.D., Schütz, M., Risch, A.C., Gossner, M.M. (2020): Long-term restoration success of insect herbivore communities in seminatural grasslands: a functional approach. *Ecological Applications* 30(6): e02133. DOI: 10.1002/eap.2133

New, T.R. (1999): Entomology and nature conservation. *European Journal of Entomology* 96: 11–17.

Nielsen, A., Bascompte, J. (2007): Ecological networks, nestedness and sampling effort. *Journal of Ecology* 95(5): 1134–1141. DOI: 10.1111/j.1365-2745.2007.01271.x

Official Gazette of Slovenia (2010): Annex 19: Red list of true bugs (Heteroptera). *In*: *Rules on the inclusion of endangered plant and animal species in the Red List*, Official Gazette of the Republic of Slovenia No. 82/02 and 42/10, Ljubljana. (Priloga 19: Rdeči seznam stenic (Heteroptera). Pravilnik o uvrstitvi ogroženih rastlinskih in živalskih vrst v rdeči seznam. Uradni list RS, št. 82/02 in 42/10, Ljubljana.) [in Slovenian]

Oksanen, F.J., Blanchet, G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Henry, M., Stevens, H., Szoecs, E., Wagne, H., (2017): *Vegan: Community Ecology Package*. R package Version 2.4-3.

Pásztor, L., Laborczi, A., Bakacsi, Zs., Szabó, J., Illés, G. (2018): Compilation of a national soil-type map for Hungary by sequential classification methods. *Geoderma* 311: 93–108. DOI: 10.1016/j.geoderma.2017.04.018

Patterson, B.D., Atmar, W. (1986): Nested subsets and the structure of insular mammalian faunas and archipelagos. *Biological Journal of the Linnean Society* 28 (1–2): 65–82. DOI: 10.1111/j.1095-8312.1986.tb01749.x

Patterson, B.D., Brown, J.H. (1991): Regionally nested patterns of species composition in granivorous rodent assemblages. *Journal of Biogeography* 18(4): 395–402. DOI: 10.2307/2845481

Peart, B. (Ed.) (2008): *Life in a Working Landscape: Towards a Conservation Strategy for the World's Temperate Grasslands*. The World Temperate Grasslands Conservation Initiative Workshop. Hohhot, China, June 28-29, 2008.

Peintinger, M., Bergamini, A., Schmid, B. (2003): Species-area relationships and nestedness of four taxonomic groups in fragmented wetlands. *Basic and Applied Ecology* 4(5): 385–394. DOI: 10.1078/1439-1791-00181

Péricart, J. (1972): Hémiptères. Anthocoridae, Cimicidae at Microphysidae de l'Ouest-Paléarctique. *Fauna de l'Europe et du Bassin Méditerranéen*, Vol. 7. Paris, 402 pp.

Péricart, J. (1983): Hémiptères. Tingidae euro-méditerranéens. *Fauna de France* 69. Fédération Française des Sociétés de Sciences Naturelles, Paris, 619 pp.

Péricart, J. (1984): Hémiptères. Berytidae euro-méditerranéens. *Fauna de France* 70. Fédération Française des Sociétés de Sciences Naturelles, Paris, 165 pp.

Péricart, J. (1987): Hémiptères. Nabidae d'Europe occidentale et du Maghreb. *Fauna de France* 71. Fédération Française des Sociétés de Sciences Naturelles, Paris, 185 pp.

Péricart, J. (1998): Hémiptères. Lygaeidae euro-méditerranéens. *Fauna de France* 84 A, B, C. Fédération Française des Sociétés de Sciences Naturelles, Paris, Vol. 1, 468 pp; Vol. 2, 453 pp; Vol. 3, 487 pp.

Pongrácz, R., Bartholy, J., Miklós, E. (2011): Analysis of projected climate change for Hungary using ENSEMBLES simulations. *Applied Ecology and Environmental Research* 9(4): 387–398. DOI: 10.15666/ aeer/0904_387398

Poniatowski, D., Fartmann, T. (2010): What determines the distribution of a flightless bush-cricket (Metrioptera brachyptera) in a fragmented landscape? *Journal of Insect Conservation* 14: 637–645. DOI: 10.1007/s10841-010-9293-3

Protić, Lj. (1998): *Catalogue of the Heteroptera fauna of Yugoslav countries*. *Part one*. Special issue 38. Natural History Museum, Belgrade, 215 pp.

Protić, Lj. (2001): *Catalogue of the Heteroptera fauna of Yugoslav countries. Part two*. Special issue 39. Natural History Museum, Belgrade, 272 pp.

Protić, Lj. (2011a): Genus *Geocoris* Fallén (Heteroptera: Lygaeidae) in Serbia and adjacent regions. *Acta entomologica serbica* 16(1–2): 25–33.

Protić, Lj. (2011b): *Heteroptera*. Special issues 43. Natural History Museum, Belgrade, 259 pp. [in Serbian with English summary]

Putshkov, V.G. (1986): *Poluzhestkokrylye semeystva Rhopalidae (Heteroptera) fauny SSSR*. [True bugs of the family Rhopalidae (Heteroptera) of the fauna of Soviet Union.] Nauka, Leningrad, 132 pp. [in Russian]

QGIS Development Team (2020): *QGIS Geographic Information System*. Open Source Geospatial Foundation Project. http://qgis.osgeo.org

R Core Team (2020): *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org

Rabitsch, W. (2008): Notes on the True bugs (Insecta, Heteroptera) in the National Park Lake Neusiedl–Seewinkel and comments about their suitability as indicators for a habitat management (Austria). *Abh. Zool.-Bot. Ges. Österreich* 37: 155–172.

Rabitsch, W. (2012): Checklist and red list of true bugs of Burgenland (Insecta, Heteroptera). *Wissenschaftliche Mitteilungen Niederösterreichisches Landesmuseum* 23: 161–306.

Rabitsch, W., Deckert, J. (2007): Die Ritterwanze *Lygaeus equestris* LINNAEUS, 1758 (Heteroptera: Lygaeidae)—das Insekt des Jahres 2007. *Beitrage zur Entomofaunistik* 8: 212–218.

Roberge, J.M., Angelstam, P. (2003): Usefulness of the Umbrella Species Concept as a Conservation Tool. *Conservation Biology* 18(1):76–85. DOI: 10.1111/j.1523-1739.2004.00450.x

Robin, L. (2011): The rise of the idea of biodiversity: crises, responses and expertise. *Quaderni* 76: 25–37. DOI: 10.4000/quaderni.92

Samways, M.J. (2005): *Insect Diversity Conservation*. Cambridge University Press, UK. ISBN-13 978-0-511-08027-2

Samways, M.J., Barton, P.S., Birkhofer, K., Chichorro, F., Deacon, C., Fartmann, T., Fukushima, C.S., Gaigher, R., Habel, J.C., Hallmann, C.A., Hill, M.J., Hochkirch, A., Kaila, L., Kwak, M.L., Maes, D., Mammola, S., Noriega, J.A., Orfinger, A.B., Pedraza, F.,… Cardoso, P. (2020): Solutions for humanity on how to conserve insects. *Biological Conservation* 242: 108427. DOI: 10.1016/j.biocon.2020.108427

Schouten, M.A., Verweij, P.A., Barendregt, A., Kleukers, R.J.M., de Ruiter, P.C. (2007): Nested assemblages of Orthoptera species in the Netherlands: the importance of habitat features and life-history traits. *Journal of Biogeography* 34(11): 1938–1946. DOI: 10.1111/j.1365-2699.2007.01742.x

Schuh, R.T., Lindskog, P., Kerzhner, I.M. (1995): *Europiella* Reuter (Heteroptera: Miridae): recognition as a Holarctic group, notes on synonymy, and description of a new species, *Europiella carvalhoi*, from North America. *Proceedings of the Entomological Society of Washington* 97 (2): 379–395.

Šeat, J., Nadaždin, B., Cvetković, M., Jovanov, A., Tot, I. (2016): Providing a base for conservation of true bugs (Insecta, Heteroptera) and their saline habitats in Vojvodina (northern Serbia). *Hyla herpetological bulletin* 2016(1): 19–23.

Šeat, J., Torma, A. (2018): Seasonal changes of Heteroptera assemblages in Pannonian salt grasslands of Serbia. *8th European Hemiptera Congress*, 24–29 Jun 2018, Zawiercie, Poland. Book of Abstracts, 120 p.

Šefferová-Stanová, V., Janák, M., Ripka, J. (2008): *Management of Natura 2000 habitats. 1530 *Pannonic salt steppes and salt marshes*. European Commission. ISBN 978-92-79-08316-7

Seibold, S., Gossner, M.M., Simons, N.K., Blüthgen, N., Müller, J., Ambarlı, D., Ammer, Ch., Bauhus, J., Fischer, M., Habel, J.C., Linsenmair, K.E., Nauss, Th., Penone, C., Prati, D., Schall, P., Schulze, E.D., Vogt, J., Wöllauer, S., Weisser, W.W. (2019): Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature* 574: 671–674. DOI: 10.1038/s41586-019-1684-3

Shinohara, N., Yoshida, T. (2021): Temporal changes of local and regional processes in the assembly of herbivorous insect communities. *Oikos* 130(10): 1626–1635. DOI: 10.1111/oik.08350

Simons, N.K., Gossner, M.M., Lewinsohn, T.M., Boch, S., Lange, M., Müller, J., Pašalić, E., Socher, S.A., Türke, M., Fischer, M., Weisser, W.W. (2014b): Resource-mediated indirect effects of grassland management on arthropod diversity. *PLoS ONE* 9(9): e107033. DOI:10.1371/journal.pone.0107033

Simons, N.K., Gossner, M.M., Lewinsohn, T.M., Lange, M., Türke, M., Weisser, W.W. (2014a): Effects of land-use intensity on arthropod species abundance distributions in grasslands. *Journal of Animal Ecology* 84: 143–154. DOI: 10.1111/1365-2656.12278

Simons, N.K., Weisser, W.W., Gossner, M.M. (2016): Multi-taxa approach shows consistent shifts in arthropod functional traits along grassland land-use intensity gradient. *Ecology* 97(3): 754–764. DOI: 10.1890/15-0616.1

Sodhi, N.S., Ehrlich, P.R. (2010): *Conservation Biology for All*. Oxford University Press Inc., New York. ISBN: 978–0–19–955423–2 (Hbk.)

Španović, T. (1948): Šume na slatinama. *Šumarski list* 9–10: 296–304. [in Serbian]

Staniczenko, P.P.A., Kopp, J.C., Allesina, S. (2013): The ghost of nestedness in ecological networks. *Nature Communications* 4: 1391. DOI: 10.1038/ncomms2422

Stein, A., Gerstner, K., Kreft, H. (2014): Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters* 17: 866–880. DOI: 10.1111/ele.12277

Štepanovičová, O., Bianchi, Z. (2001): Red (Ecosozological) List of Heteroptera of Slovakia. *In*: Balaž, D., Marhold, K., Urban, P. (Eds.): *Red List of plants and animals of Slovakia Nature Conservation*. Ochrana Prírody 20 (Suppl.): 105–106. [in Slovak with English abstrakt]

Suttie, J.M., Reynolds, S.G., Batello, C. (Eds.) (2005): *Grasslands Of The World*. Food and Agriculture Organization of the United Nations. Plant Production and Protection Series, No. 34. https://www.fao.org/3/y8344e/y8344e00.htm

Tölgyesi, C., Török, P., Hábenczyus, A.A., Bátori, Z., Valkó, O., Deák, B., Tóthmérész, B., Erdős, L., Kelemen, A. (2020): Underground deserts below fertility islands? Woody species desiccate lower soil layers in sandy drylands. *Ecography* 43(6): 848–859. DOI: 10.1111/ecog.04906

Torma, A. (2012): Further data on the true bug fauna (Insecta: Heteroptera) of alkaline grasslands in the Hungarian-Romanian border region. *In*: Körmöczi, L. (Ed.): Landscape-scale connections between the land use, habitat quality and ecosystem goods and services in the Mures/Maros valley. *Tiscia Monograph Series* 10: 45–66.

Torma, A., Bozsó, M., Gallé, R. (2018): Secondary habitats are important in biodiversity conservation: a case study on orthopterans along ditch banks. *Animal Biodiversity and Conservation* 41(1): 97–108. DOI: 10.32800/abc.2018.41.0097

Torma, A., Bozsó, M., Tölgyes, Cs., Gallé, R. (2017): Relationship of different feeding groups of true bugs (Hemiptera: Heteroptera) with habitat and landscape features in Pannonic salt grasslands. *Journal of Insect Conservation* 21(4): 645–656. DOI: 10.1007/s10841-017-0007-y

Torma, A., Császár, P. (2013): Species richness and composition patterns across trophic levels of true bugs (Heteroptera) in the agricultural landscape of the lower reach of the Tisza River Basin. *Journal of Insect Conservation* 17(1): 35–51. DOI: 10.1007/s10841-012-9484-1

Torma, A., Császár, P., Bozsó, M., Deák, B., Valkó, O., Kiss, O., Gallé, R. (2019): Species and functional diversity of arthropod assemblages (Araneae, Carabidae, Heteroptera and Orthoptera) in grazed and mown salt grasslands. *Agriculture, Ecosystems and Environment* 273: 70–79. DOI: 10.1016/j.agee.2018.12.004

Torma, A., Gallé, R., Bozsó, M. (2014): Effects of habitat and landscape characteristics on the arthropod assemblages (Araneae, Orthoptera, Heteroptera) of sand grassland remnants in Southern Hungary. *Agriculture, Ecosystems and Environment* 196: 42–50. DOI: 10.1016/j.agee.2014.06.021

Torma, A., Varga, Cs., Varga, M. (2010): Spatial Pattern of True Bugs (Heteroptera) in Heterogeneous Grassland – Preliminary Results. *Acta Phytopathologica et Entomologica Hungarica* 45(1): 81–87. DOI: 10.1556/APhyt.45.2010.1.5

Török, P., Janišová, M., Kuzemko, A., Rūsiņa, S., Dajić-Stevanović, Z. (2018): Grasslands, their Threats and Management in Eastern Europe. *In*: Squires, V.R., Dengler, J., Hua, L., Feng, H. (Eds.): *Grasslands of the World: Diversity, Management and Conservation*. CRC Press, Boca Raton, US. ISBN: 9781498796262

Török, P., Kapocsi, I., Deák, B. (2011): Conservation and management of alkali grassland biodiversity in Central-Europe. *In*: Zhang, W.J. (Ed.): *Grasslands: Types, Biodiversity and Impacts*. Nova Science Publishers, Inc. ISBN: 978-1-61470-555-0

Török, P., Penksza, K., Tóth, E., Kelemen, A., Sonkoly, J., Tóthmérész, B. (2018): Vegetation type and grazing intensity jointly shape grazing effects on grassland biodiversity. *Ecology and Evolution* 8(20): 10326–10335. DOI: 10.1002/ece3.4508

Tóth T. (2010): Medium-term vegetation dynamics and their association with edaphic conditions in two Hungarian saline grassland communities. *Grassland Science* 56: 13–18. DOI: 10.1111/j.1744-697X.2009.00167.x

Tscharntke, T., Greiler, H.J. (1995): Insect communities, grasses, and grasslands. *Annual Review of Entomology* 40: 535–558. DOI: 10.1146/annurev.en.40.010195.002535

Twisk, W., Noordervliet, M.A.W., ter Keurs, W.J. (2000): Effects of ditch management on caddisfly, dragonfly and amphibian larvae in intensively farmed peat areas. *Aquatic Ecology* 34(4): 397–411. DOI: 10.1023/A:1011430831180

Twisk, W., Noordervliet, M.A.W., ter Keurs, W.J. (2003): The nature value of the ditch vegetation in peat areas in relation to farm management. *Aquatic Ecology* 37(2): 191–209. DOI: 10.1023/A:1023944028022

UkrBIN (2017): Heteroptera. Dataset ID #705. *In*: *UkrBIN, Database on Biodiversity Information*. Available from: http://www.ukrbin.com Accessed on [13 February 2022] [in Ukrainian]

Ulrich, W., Almeida-Neto, M., Gotelli, N.J. (2009): A consumer's guide to nestedness analysis. *Oikos* 118(1): 3–17. DOI: 10.1111/j.1600-0706.2008.17053.x

Ulricha, W., Gotelli, N.J. (2012): A null model algorithm for presence–absence matrices based on proportional resampling. *Ecological Modelling* 244: 20–27. DOI: 10.1016/j.ecolmodel.2012.06.030

van Dijk, W.F.A., Schaffers, A.P., Leewis, L., Barendse, F. (2013): Temporal effects of agri-environmental schemes on ditch bank plant species. *Basic and Applied Ecology* 14(3): 289–297. DOI: 10.1016/j.biocon.2014.01.006

van Klink, R., Rickert, C., Vermeulen, R., Vorst, O., WallisDeVries, M.F., Bakker, J.P. (2013): Grazed vegetation mosaics do not maximize arthropod diversity: Evidence from salt marshes. *Biological Conservation* 164: 150–157. DOI: 10.1016/j.biocon.2013.04.023

van Klink, R., Ruifrok, J.L., Smit, Ch. (2016): Rewilding with large herbivores: Direct effects and edge effects of grazing refuges on plant and invertebrate communities. *Agriculture, Ecosystems & Environment* 234: 81–97. DOI: 10.1016/j.agee.2016.01.050

van Klink, R., van der Plas, F., van Noordwijk, C.G.E., WallisDeVries, M.F., Olff, H. (2014): Effects of large herbivores on grassland arthropod diversity. *Biological Reviews* 90(2): 347–366. DOI: 10.1111/brv.12113

Verschuuren, J.M. (2002): Implementation of the Convention on Biodiversity in Europe: 10 Years of Experience with the Habitats Directive. *Journal of International Wildlife Law and Policy* 5: 251–267. DOI: 10.1080/13880290209354013

Wachmann, E., Melber, A., Deckert, J. (2004): Wanzen, Vol. 2. *Tierw. Deutschlds*. 75: 1–294 pp.

Wachmann, E., Melber, A., Deckert, J. (2006): Wanzen, Vol. 1. *Tierw. Deutschlds*. 77: 1–263 pp.

Wachmann, E., Melber, A., Deckert, J. (2007): Wanzen, Vol. 3. *Tierw. Deutschlds*. 78: 1–272 pp.

Wachmann, E., Melber, A., Deckert, J. (2008): Wanzen, Vol. 4. *Tierw. Deutschlds*. 81: 1–230 pp.

Wagner, D.L., Grames, E.M., Forister, M.L., Berenbaum, M.R., Stopak, D. (2021): Insect decline in the Anthropocene: Death by a thousand cuts. *PNAS* 118(2): e2023989118. DOI: 10.1073/pnas.2023989118

Wagner, E. (1965): Über einige bemerkenswerte Heteropteren aus dem Gebiet des Neusiedlersees. *Wissenschaftliche Arbeiten Burgenland* 32: 116–124.

Wagner, E., Weber, H.H. (1964): Hétéroptères. Miridae. *Fauna de France* 67. Fédération Française des Sociétés de Sciences Naturelles, Paris, 590 pp.

Ward, D.F., Larivière, M.C. (2004): Terrestrial invertebrate surveys and rapid biodiversity assessment in New Zealand: lessons from Australia. *New Zealand Journal of Ecology* 28(1): 151–159.

Watling, J.I., Donnelly, M.A. (2006): Fragments as Islands: a Synthesis of Faunal Responses to Habitat Patchiness. *Conservation Biology* 20(4): 1016–1025. DOI: 10.1111/j.1523-1739.2006.00482.x

Weisser, W.W., Siemann, E. (2008): The Various Effects of Insects on Ecosystem Functioning. *In*: Weisser, W.W., Siemann, E (Eds.): *Insects and Ecosystem Function*. Ecological Studies (Analysis and Synthesis), vol. 173. Springer, Berlin, Heidelberg. 3–24 pp. DOI: 10.1007/978-3-540-74004-9_1

Wesche, K., Ambarlı, D., Kamp, J., Török, P., Treiber, J., Dengler, J. (2016): The Palaearctic steppe biome: a new synthesis. *Biodivers Conserv* 25: 2197–2231. DOI: 10.1007/s10531-016-1214-7

Woodcock, B.A., Potts, S.G., Westbury, D.B., Ramsay, A.J., Lambert, M., Harris, S.J., Brown, V.K. (2007): The importance of sward architectural complexity in structuring predatory and phytophagous invertebrate assemblages. *Ecological Entomology* 32: 302–311. DOI: 10.1111/j.1365-2311.2007.00869.x

Worthen, W.B. (1996): Community composition and nested-subset analyses: basic descriptors for community ecology. *Oikos* 76(3): 417–426. DOI: 10.2307/3546335

Wright, D.H., Patterson, B.D., Mikkelson, G.M., Cutler, A., Atmar, W. (1998): A comparative analysis of nested subset patterns of species composition. *Oecologia* 113(1): 1–20. DOI: 10.1007/s004420050348

Zahn, A., Englmaier, I., Drobny, M. (2010): Food availability for insectivores in grasslands - arthropod abundance in pastures, meadows and fallow land. *Applied Ecology and Environmental Research* 8(2): 87–100.

Zhu, H., Wang, D., Wang, L., Bai, Y., Fang, J., Liu, J. (2012): The effects of large herbivore grazing on meadow steppe plant and insect diversity. *Journal of Applied Ecology* 49(5): 1075–1083. DOI: 10.1111/j.1365-2664.2012.02195.x

Živković, B., Nejgebauer, V., Tanasijević, Đ., Miljković, N., Stojković, L., Drezgić, P. (1972): *Zemljišta Vojvodine* (*Soils of Voyvodina*). Institut za poljoprivredna istraživanja, Novi Sad. 439–495 pp. [in Serbian]

Zobel, M., van der Maarel, E., Dupré, C. (1998): Species pool: The concept, its determination and significance for community restoration. *Applied Vegetation Science* 1(1): 55–66. DOI: 10.2307/1479085

Zulka, K.P., Abensperg-Traun, M., Milasowszky, N., Bieringer, G., Gereben-Krenn, B.A., Holzinger, W., Hölzler, G., Rabitsch, W., Reischütz, A., Querner, P., Sauberer, N., Schmitzberger, I., Willner, W., Wrbka, T., Zechmeister, H. (2014): Species richness in dry grassland patches of eastern Austria: A multi-taxon study on the role of local, landscape and habitat quality variables. *Agriculture, Ecosystems & Environment* 182: 25–36. DOI: 10.1016/j.agee.2013.11.016

Zurbrügg, C., Frank, T. (2006): Factors influencing bug diversity (Insecta: Heteroptera) in semi-natural habitats. *Biodiversity and Conservation* 15(1): 275–294. DOI: 10.1007/978-1-4020-5204-0_17

9. SUMMARY

Saline habitats of the Pannonian Region form the most continuous inland salt-affected landscape in Europe. They are listed in Annex I of the Habitats Directive (1530 *Pannonic salt steppes and salt marshes) as areas of high conservation importance due to their restricted geographic distribution and characteristic taxa that cannot be found anywhere else in Europe. The uniqueness of saline grasslands is the fine-scale zonation of vegetation with around 50 distinct plant communities. Compositional mosaicism of vegetation in saline grasslands is driven by microtopography, seasonal changes in astatic groundwater and salt content in the soil.

In the last two decades, terrestrial true bugs have been highly used as model organisms and bioindicators in ecological studies. Most of these experiments have been studying the effects of grassland management, landscape heterogeneity and habitat quality on true bugs as surrogates of local biodiversity. Terrestrial true bugs are predominantly phytophagous with remarkable species richness in grasslands and other open grassy habitats. The herbivory of true bugs (with different degrees of specialization) makes them sensitive to any change in vegetation composition, structure or quality. True bugs are considered as good indicators in assessments related to nature conservation because they have a high indicator value and comparatively low processing effort.

True bugs have a good potential to become a staple group in all kinds of biodiversity and habitat assessments of the European mainland where the true bug fauna is well-known. The recognition of rare, endemic and endangered true bugs can raise the value of protected sites or assign conservation significance to unprotected ones. Their numerous species have vast ecological functions and responses to environmental changes which can help to create fine-tuned and specific management according to local needs. The following aims of this thesis were addressed by using true bugs as bioindicators: (i) Assessing the conservation status of saline grasslands at the edge of the Pannonian Region and identifying the key elements of true bug community structure in saline grasslands (Study 1), (ii) Assessing the effects of grazing as the most applied management type on biodiversity of saline grasslands (Study 2), and (iii) Assessing the importance of drainage canals as secondary habitats in biodiversity conservation of saline grasslands (Study 3).

Study 1: The study was conducted in the northern Serbian province of Vojvodina where 138 locations were visited, covering a variety of saline habitats and vegetation types, but *Artemisia*

salt steppes were the focus of the study. True bugs were sampled by standard sweep-netting method and various sampling procedures (total inventory, rapid assessment, targeted search for certain species, transects varying in length and number per sampling site). In total 210 true bug species were identified in saline grasslands of northern Serbia. The most important records of new species for Serbian fauna are: *Agramma ruficorne*, *Chlamydatus saltitans*, *Solenoxyphus fuscovenosus*, *Lygaeosoma anatolicum*, *Emblethis brachynotus*, *Geotomus punctulatus* and *Phimodera flori*. Species strongly connected to salt-affected areas are of special interest in conservation and can be divided into three groups: (i) Trophic specialists (*Solenoxyphus fuscovenosus*, *Antheminia varicornis*) always appear in combination with a host plant specialized to salty soil, i.e. halophytes, (ii) Habitat specialists (*Conostethus hungaricus*, *Henestaris halophilus*) do not have a preference for a single host plant or the host is not known and typically are present in *Artemisia* steppe vegetation, (iii) The last group consists of species that are highly associated with saline grasslands in the Pannonian Region (*Lygaeosoma anatolicum*, *Peritrechus meridionalis*, *Crypsinus angustatus*). Regardless of their exclusivity and prioritization in conservation, saline specialists can be highly frequent and even dominant at a certain part of a season (e.g. *Conostethus hungaricus*) or in a certain vegetation type (e.g. *Solenoxyphus fuscovenosus*, *Antheminia varicornis*). On the other hand, 10 species recorded in saline grasslands in Serbia had in total three records, altogether with historical and new data. Rare species deserve a special place in red lists and conservation planning; species in the data deficient category should be treated as threatened following the precautionary principle.

In addition, seventeen *Artemisia* alkali steppe fragments among the above-mentioned sites in Vojvodina were selected to study nested patterns of true bug communities. Three different sampling procedures varying in sampling effort and methodology were applied: (i) sweep-netting along a single 20 m long transect, (ii) sweep-netting along three parallel 30 m long transects, and (iii) the total inventory of true bugs. Datasets were analyzed for nestedness in the form of both binary and weighted matrices (except total inventory data). To analyze binary matrices, NODF and spectral radius metrics were used to measure the degree of nestedness, and on weighted ones, WNODF and spectral radius were applied. Spearman's rank correlation method was applied to test possible correlations between the site ordering in a matrix and assessed true bug data, vegetation data and landscape features of sampling sites. Three sampling procedures varying in intensity of sampling showed that even the minimal sampling effort (i.e. 20 m long transect) resulted in detectable significant nestedness. Grass-feeders are the most abundant and the most represented in saline grasslands, they are the core of a true bug community. However, true bug communities without grass-feeders continued to be nested, which means grass-feeders were not responsible for this structural pattern, but less numerous polyphagous generalists were. This study also confirmed that a higher number of species (matrix size) and more frequent species occurrences in different sites (matrix fill) provided higher values of nestedness and a more steady pattern. The results of this study showed no correlation between grassland patch size and site ranking in nested matrices, which confirmes that nestedness is not necessarily affected by the habitat area. In the case of invertebrates who use space at a fine scale, nestedness is most probably caused by habitat nestedness as a result of a gradient in habitat quality or diversity of microhabitats.

Study 2: The study was conducted in the Csanádi puszták in southern Hungary, where the original vegetation of saline grasslands, wet (alkali meadows) and dry (*Artemisia* salt steppes) patches is still preserved. Sampling was conducted in 50 m × 100 m fenced areas (i.e. experimental plots) with an inner ungrazed area and the extensively grazed grassland outside the fence. In total 12 sampling sites were surveyed, 6 in each saline grassland type (wet and dry grasslands). Each experimental plot was divided into two equal sub-plots (50 m × 50 m) to implement two different collecting methods for true bugs (sweep-netting and pitfall-trapping). The sampling of true bugs was conducted in four different regimes: (i) in the centre of an experimental plot, (ii) at the inner sides of a plot, (iii) at the outer sides of a plot, and (iv) at the distance of 25 m from a plot. To detect the response of true bugs to grazing, vegetation type and edge effect, generalized linear mixed models were applied. Species richness, abundance and community weighted mean trait values of true bugs were used as response variables. As a result, the season had the strongest effect on true bug communities in different saline grasslands and greatly influenced the effects of grazing, but the edge effect showed a minor impact on true bugs. Removal of grass biomass by spring grazing was the most influential for the plant-dwellers in more productive wet saline grasslands causing a shift in community composition to more drought-tolerant and smaller size species. In summer, the effects of vegetation type dominated in shaping communities. Plant-dwelling true bugs of dry saline grasslands were on average represented by bigger and more polyphagous species. All aforementioned habitat changes in saline grasslands greatly influenced communities of plant-dwellers. On the contrary, ground-dwellers showed minor sensitivity to changes in vegetation cover caused by management or seasonal dynamics. Communities of plant-dwelling nymphs more or less mirrored patterns of plant-dwelling adults. Indicator species analysis showed the dominance of grass-feeders in both dry and wet saline grasslands. Recorded grass-feeding species appeared to have a preference to a certain grassland type and many of them were indicators of ungrazed parts as well.

Study 3: The study area covered a part of the Danube-Tisza interfluve of central Hungary. The substrate here is diverse and certain zonality of the soils can be recognized. According to dominant soil types, the main open habitats present here are fen, sandy and saline grasslands and marshlands. The sampling sites were 200 m long sections of agricultural (bordering cropland) and grassland (bordering grassland) drainage canals. In total, 60 canals were surveyed, 30 of each surrounding landscape matrix type and 20 of each habitat type (fen, saline habitat and sandy habitat). Sampling was also done in 5 m × 200 m transects in reference semi-natural grasslands parallel to every grassland canal. Standardization of the species richness scores of canals to habitat-specific average reference species richness scores was performed. The result of standardization was ‘species excess’ (expressed in %), a value that represented proportional excess or deficit of species richness compared to habitat-specific reference averages. Linear mixed-effects models were applied to evaluate how landscape matrix, habitat type, canal size, season, the abundance of reeds and woody vegetation in canals determine the true bug species richness (i.e. species excesses) as the response variable. Permutational multivariate analysis of variance was applied to detect dissimilarity in true bug community composition of different habitats. RLQ and fourth-corner analyses assessed environmental factors that shape true bug community composition and habitat attributes associated with certain traits of true bugs. To separate functional groups (i.e. trait syndromes) of true bugs, hierarchical cluster analysis was applied. Landscape matrix, season and habitat (i.e. substrate) end up being the most influential factors in shaping the community composition of true bugs in drainage canals, whereas other attributes of canals had a negligible effect. Agrarian saline canals had the highest number of species among saline habitats with many singletons. Grassland canals were more similar in species richness to corresponding reference saline grasslands, but their community composition was distinctive. Based on functional and life-history traits of true bugs, three trait syndromes were recognized which separated species from saline habitats in three species clusters. Species of A- and B-clusters were associated with open grassland-like habitats. A-cluster contained species of low dispersive abilities with preference for humid grasslands and saline marshlands, whereas B-cluster comprised highly mobile species of dry saline grasslands. C-cluster species were associated with agricultural canals and mostly consisted of bigger size habitat generalists with good dispersal abilities. Rare species in the study were mostly associated with reference saline grasslands and most saline habitat specialists were associated with the same habitats as well. In general, grassland canals are better secondary habitats for saline habitat specialists, but agricultural canals accommodated more species and diversified local true bug fauna.

10. ÖSSZEFOGLALÁS

A Pannon szikesek kiemelt természetvédelmi jelentőségűek.

Az ökorégió peremén lévő szikes gyepek állapotának vizsgálata során a közösségek erős beágyazottságot mutattak, mely a domináns fajok kizárásával is maradt, arra utalva, hogy nem ezek, hanem a ritkább fajok felelősek a beágyazott mintázatért. A beágyazottságot nem befolyásolta az élőhely területe, inkább azok minőségében, a mikroélőhelyek diverzitásában lévő különbségek eredményezték, melyek a gyephasználat során változhatnak.

A legelés-kizárásos vizsgálatunk alapján, a szikeseken az időszak és a vegetáció típusa befolyásolta a legeltetés poloskaközösségekre kifejtett hatását. A tavaszi legeltetéskor történő biomassza-redukció a produktívabb, nedves szikes gyepek poloskaközösségeire hat, a közösség összetételének eltolódását okozva a szárazságtűrőbb és kisebb méretű fajok felé. Nyáron a növényzet típusa a meghatározó: száraz szikesekben átlagosan nagyobb, polifág fajok voltak. A változások a növényzeten mozgó poloskákat érintette szemben a talajszinten mozgó poloskákkal; a lárvák közösség-dinamikája tükrözte az imágókét.

A másodlagos élőhelyek vizsgálata alapján a tájmátrix, az időszak és az élőhely típusa szignifikáns tényezők a csatornákban található poloskaközösségek szempontjából. A mezőgazdasági csatornákban volt a legtöbb faj; a gyepi csatornák poloskaközösségei jobban hasonlítottak a referenciagyepekéhez. A poloskák jellegeit tekintve három jelleg-kompozíciós mintázatot azonosítottunk (A, B és C klaszter). Az A alacsony diszperziós képességű, nedves területeket preferáló fajokat tartalmazott, a B a száraz szikes gyepek erősen mozgékony fajait. A C mezőgazdasági csatornákhoz kapcsolódott, és többnyire nagyobb méretű, jó terjedőképességű élőhely generalista fajokból állt. A gyepi csatornák általában jobb másodlagos élőhelyek a szikes élőhelyek specialistái számára, míg a mezőgazdasági csatornák több – főleg generalista, jó diszperziós képességű – fajnak nyújtanak életteret, és változatosabbá teszik a lokális táj poloskafaunáját.

A poloskák környezeti változásokra adott válaszaik elősegíthetik a helyi igényeknek megfelelő finomhangolt és specifikus természetvédelmi vonatkozású kezelések kidolgozását.

11. APPENDIX

11.1. List of sampling sites in Serbia

Sampling sites in saline grassland fragments are named by the nearest toponym; related information on latitude, longitude and elevation for the locations are given too. The coordinates of sampling sites are given in decimal degrees following the WGS 84 reference system.

Banatska Dubica 973: 45.2670ºN 20.8120ºE, 76 m; Banatska Dubica 974: 45.2654ºN 20.8017ºE, 74m; Banatsko Aranđelovo 800: 46.0750ºN 20.2228ºE, 75 m; Banatsko Aranđelovo 801: 46.0681ºN 20.1972ºE, 75 m; Banatsko Aranđelovo 802: 46.1008ºN 20.1923ºE, 74 m; Banatsko Aranđelovo 803: 46.1166ºN 20.1784ºE, 74 m; Bezdan 833: 45.8462ºN 18.9706ºE, 83 m; Bezdan 834: 45.8303ºN 18.9697ºE, 82 m; Bočar 939: 45.7863ºN 20.2729ºE, 72 m; Bočar 940: 45.7834ºN 20.2156ºE, 72 m; Bočar 941: 45.7746ºN 20.2110ºE, 74 m; Bočar 942: 45.7579ºN 20.2845ºE, 74 m; Boka 985: 45.3474ºN 20.8088ºE, 71 m; Botoš 966: 45.2933ºN 20.6427ºE, 71 m; Botoš 967: 45.3201ºN 20.6372ºE, 74 m; Čoka 867: 45.9507ºN 20.1825ºE, 77 m; Čoka 869: 45.9418ºN 20.1247ºE, 76 m; Čonoplja 924: 45.8030ºN 19.2244ºE, 84 m; Čonoplja 925: 45.7976ºN 19.2135ºE, 84 m; Crna Bara 799: 45.9691ºN 20.3066ºE, 73 m; Dobrica 972: 45.2142ºN 20.8397ºE, 73 m; Elemir 947: 45.4424ºN 20.2488ºE, 73 m; Hajdukovo (Ludaš Lake): 46.1036ºN 19.8220ºE, 95 m; Horgoš (Galamboš): 46.1069ºN 19.9130ºE, 85 m; Horgoš (Galamboš) 2: 46.1156ºN 19.92006ºE, 84 m; Horgoš (Kilapoš): 46.1336ºN 19.9085ºE, 84 m; Horgoš (Lofej): 46.1463ºN 19.8688ºE, 94 m; Horgoš (Stočni pašnjak): 46.1368ºN 19.9335ºE, 81 m; Horgoš (Volujski pašnjak) 1: 46.1624ºN 19.9271ºE, 84 m; Horgoš (Volujski pašnjak) 2: 46.1495ºN 19.9378ºE, 83 m; Horgoš 837: 46.1562ºN 19.9358ºE, 84 m; Horgoš 841: 46.1415ºN 19.9658ºE, 79 m; Horgoš 847: 46.1422ºN 19.95651ºE, 80 m; Idvor: 45.1788ºN 20.5220ºE, 71 m; Ilandža 969: 45.1447ºN 20.9201ºE, 75 m; Ilandža 970: 45.1756ºN 20.9237ºE, 75 m; Ilandža 971: 45.1878ºN 20.8919ºE, 76 m; Jankov Most 948 I: 45.4897ºN 20.4289ºE, 74 m; Jaša Tomić 978: 45.4350ºN 20.8408ºE, 73 m; Jaša Tomić 980: 45.4522ºN 20.8373ºE, 72 m; Jazovo: 45.9051ºN 20.2466ºE, 75 m; Jazovo 804: 45.9252ºN 20.2364ºE, 75 m; Jazovo 805: 45.9052ºN 20.2610ºE, 75 m; Jazovo 809: 45.9199ºN 20.3015ºE, 73 m; Jazovo 810: 45.9058ºN 20.3002ºE, 74 m; Jazovo 811: 45.8964ºN 20.3032ºE, 73 m; Jazovo 872: 45.9066ºN 20.2094ºE, 73 m; Kanjiža 858: 46.0523ºN 19.9933ºE, 79 m; Kanjiža 859: 46.0578ºN 19.9895ºE, 79 m; Kanjiža 860: 46.0584ºN 20.0034ºE, 78 m; Kapetanski rit 2: 46.0182ºN 19.9302ºE, 82 m; Kapetanski rit 3: 46.0140ºN 19.9506ºE, 81 m; Karavukovo: 45.5129ºN 19.1787ºE, 78 m; Konak: 45.3063ºN 20.9136ºE, 75 m; Kruševlje 1: 45.9314ºN 19.1286ºE, 85 m; Kruševlje 2: 45.9230ºN 19.1068ºE, 84 m; Kruševlje 3: 45.9360ºN 19.1129ºE, 85 m; Kruševlje 918: 45.9459ºN 19.1131ºE, 86 m; Kruševlje 919: 45.9466ºN 19.1277ºE, 86 m; Kruševlje 920: 45.9388ºN 19.1263ºE, 86 m; Kruševlje 923: 45.9231ºN 19.1182ºE, 85 m; Kruševlje Lake: 45.9460ºN 19.0907ºE, 82 m; Kumane 930: 45.5349ºN 20.2724ºE, 74 m; Kumane 932: 45.5479ºN 20.2611ºE, 73 m; Kumane 933: 45.5887ºN 20.2782ºE, 75 m; Kumane 934: 45.5267ºN 20.2201ºE, 74 m; Lukino Selo 960: 45.2947ºN 20.4300ºE, 71 m; Mali Pesak 849: 46.0906ºN 19.9755ºE, 80 m; Mali Pesak 850: 46.0839ºN 20.0016ºE, 80 m; Mali Pesak 851: 46.0887ºN 20.0251ºE, 78 m; Mali Radanovac: 46.1183ºN 19.7076ºE, 106 m; Margita: 45.2153ºN 21.1875ºE, 75 m; Margita 981: 45.2221ºN 21.1822ºE, 77 m; Mokrin 808: 45.9185ºN, 20.3670ºE, 72 m; Mokrin 812: 45.9205ºN 20.3341ºE, 72 m; Mužlja 956 II: 45.3314ºN 20.3867ºE, 71 m; Mužlja 957: 45.3306ºN 20.3717ºE, 72 m; Mužlja 958: 45.3283ºN 20.3663ºE, 73 m; Mužlja 959: 45.3293ºN 20.4111ºE, 72 m; Neuzina 975: 45.3130ºN 20.7476ºE, 74 m; Neuzina 976: 45.3442ºN 20.7040ºE, 69 m; Neuzina 977: 45.3473ºN 20.7241ºE, 75 m; Novo Miloševo 938: 45.7329ºN 20.2944ºE, 74 m; Novo Miloševo 944: 45.7023ºN 20.2750ºE, 75 m; Obzir 953: 45.8259ºN 19.1468ºE, 81 m; Obzir 954: 45.8327ºN 19.1408ºE, 80 m; Obzir 955: 45.8349ºN 19.1276ºE, 83 m; Okanj: 45.4584ºN 20.2762ºE, 70 m; Okanj 946: 45.4638ºN 20.2705ºE, 74 m; Padej 873: 45.8609ºN 20.1666ºE, 77 m; Padej 874: 45.8590ºN 20.1642ºE, 78 m; Padej 875: 45.8421ºN 20.1657ºE, 76 m; Padej 876: 45.8318ºN 20.1504ºE, 76 m; Padej 877: 45.8258ºN 20.1481ºE, 74 m; Padej 878: 45.8337ºN 20.1890ºE, 75 m; Padej 879: 45.8394ºN 20.2010ºE, 74 m; Podlokanj 797: 46.0434ºN 20.3242ºE, 73 m; Podlokanj 798: 46.0411ºN 20.3226ºE, 75 m; Rančevo: 45.8566ºN 19.0886ºE, 82 m; Rančevo 956 I: 45.8586ºN 19.1216ºE, 83 m; Riđica (Medura Lake): 45.9916ºN 19.1318ºE, 91 m; Riđica 921: 45.9691ºN 19.1276ºE, 87 m; Rusanda: 45.5323ºN 20.2576ºE, 74 m; Sajan 794: 45.8657ºN 20.2953ºE, 74 m; Sajan 795: 45.8701ºN 20.3024ºE, 74 m; Sajan 796: 45.8823ºN 20.3265ºE, 73 m; Sajan 806: 45.8622ºN 20.2730ºE, 73 m; Sajan 807: 45.8685ºN 20.2845ºE, 74 m; Sajan 880: 45.8303ºN 20.2808ºE, 73 m; Sanad 870: 45.9870ºN 20.1102ºE, 78 m; Sanad 871: 45.9735ºN 20.1119ºE, 78 m; Sečanj: 45.3481ºN 20.7789ºE, 73 m; Slano Kopovo: 45.6328ºN 20.1876ºE, 73 m; Slano Kopovo 936: 45.6019ºN 20.2251ºE, 75 m; Srpski Miletić 1: 45.5488ºN 19.1782ºE, 79 m; Srpski Miletić 2: 45.5438ºN 19.1823ºE, 79 m; Stanišić 922: 45.9257ºN 19.1482ºE, 85 m; Stanišić 948 II: 45.9053ºN 19.1537ºE, 85 m; Stanišić 949: 45.8903ºN 19.1632ºE, 84 m; Stanišić 951: 45.8783ºN 19.1694ºE, 83 m; Šurjan 982: 45.3688ºN 20.9000ºE, 74 m; Šurjan 983: 45.3729ºN 20.9022ºE, 74 m; Šurjan 984: 45.4110ºN 20.8773ºE, 76 m; Sutjeska 968: 45.3768ºN 20.6737ºE, 74 m; Svetozar Miletić 952: 45.8479ºN 19.1676ºE, 83 m; Svilojevo 928: 45.6643ºN 19.0422ºE, 82 m; Svilojevo 929: 45.6383ºN 19.0814ºE, 81 m; Tomaševac 964: 45.2449ºN 20.6047ºE, 72 m; Tomaševac 965: 45.2839ºN 20.6368ºE, 71 m; Trešnjevac 856: 45.9859ºN 19.9996ºE, 77 m; Trešnjevac 857: 45.9707ºN 20.0133ºE, 79 m; Vlajkovac: 45.0801ºN 21.1862ºE, 77 m; Vojvoda Zimonjić 852: 46.0261ºN 19.9844ºE, 79 m; Vojvoda Zimonjić 853: 46.0389ºN 19.9638ºE, 80 m; Vojvoda Zimonjić 854: 46.0299ºN 19.9708ºE, 80 m; Vojvoda Zimonjić 855: 46.0262ºN 19.9740ºE, 80 m; Žabalj 1: 45.3654ºN 20.0965ºE, 76 m; Žabalj 2: 45.3759ºN 20.1336ºE, 75m.

11.2. List of true bug species recorded in saline grasslands of Serbia

New species from Serbian fauna are marked with an asterisk (*). Species with a maximum of three records or a maximum of three known locations in Serbia are marked as 'rare' (^{R}). Names of **saline specialists** are boldfaced.

Categories of species conservation status: critically endangered (CR), endangered (EN/E), vulnerable (VU/V), near threatened (NT), least concern (LC), data deficient (DD), rare (R), regionally extinct (RE).

CIMICOMORPHA

Tingidae

Acalypta gracilis (Fieber, 1844)

^{R} *Acalypta marginata* (Wolff, 1804)

Agramma (*Agramma*) *atricapillum* (Spinola, 1837)
Conservation status: Austria (Burgenland) NT, Slovenia V.

Agramma (*Agramma*) *confusum* (Puton, 1879)
Conservation status: Czech Republic CR.

Agramma (*Agramma*) *minutum* Horváth, 1874
Conservation status: Czech Republic CR.

*, ^{R} *Agramma* (*Agramma*) *ruficorne* (Germar, 1835)
Conservation status: Austria (Burgenland) EN, Czech Republic CR, Slovenia E.

Catoplatus carthusianus (Goeze, 1778)

Catoplatus horvathi (Puton, 1878)
Conservation status: Czech Republic VU.

Corythucha arcuata (Say, 1832)

Dictyla humuli (Fabricius, 1794)

Kalama tricornis (Schrank, 1801)

Lasiacantha capucina (Germar, 1837)

Lasiacantha gracilis (Herrich-Schaeffer, 1830)
Conservation status: Austria (Burgenland) NT.

Oncochila scapularis (Fieber, 1844)

Tingis (*Tingis*) *auriculata* (Costa, 1847)
Conservation status: Austria (Burgenland) NT.

Tingis (*Tingis*) *cardui* (Linnaeus, 1758)

Tingis (*Tropidocheila*) *reticulata* Herrich-Schaeffer, 1835

Miridae

Acetropis (*Acetropis*) *carinata* (Herrich-Schaeffer, 1841)

Acetropis (*Acetropis*) *longirostris* Puton, 1875

Adelphocoris lineolatus (Goeze, 1778)

Adelphocoris seticornis (Fabricius, 1775)

Amblytylus concolor Jakovlev, 1877
Conservation status: Austria (Burgenland) DD.

Amblytylus nasutus (Kirschbaum, 1856)

Apolygus spinolae (Meyer-Dür, 1841)

^{R} *Atomoscelis onusta* (Fieber, 1861)

Brachycoleus decolor Reuter, 1887
Conservation status: Czech Republic VU, Slovenia V.

Capsodes gothicus (Linnaeus, 1758)

Capsus ater (Linnaeus, 1758)

Charagochilus (*Charagochilus*) *gyllenhalii* (Fallén, 1807)

$^{*, R}$ *Chlamydatus* (*Chlamydatus*) *saltitans* (Fallén, 1807)

Chlamydatus (*Euattus*) *pullus* (Reuter, 1870)

Closterotomus norwegicus (Gmelin, 1790)

Compsidolon (*Apsinthophylus*) *pumilum* (Jakovlev, 1876)
Conservation status: Austria (Burgenland) DD.

***Conostethus hungaricus* Wagner, 1941**

Conservation status: Austria (Burgenland) EN, Slovakia CR.

Remarks: Horváth mentioned this species as *Conostethus salinus* Sahlb. This saline specialist is usually associated with *Lepidium cartilagineum* Thell (syn. *L. crassifolium*) which is present in Hungary and Austria (Torma *et al*., 2010; Rabitsch, 2012); however, the distribution of this plant is limited to the northernmost part of Serbia (Lakušić *et al*., 2005). Interestingly, *C. hungaricus* is distributed further on the south, too. Species from Poaceae family are most likely host plants of *C. hungaricus* in Serbia, as Wachmann *et al*. (2004) noted.

^{R} *Criocoris nigricornis* Reuter, 1894

Conservation status: Austria (Burgenland) DD, Czech Republic VU.

Criocoris sulcicornis (Kirschbaum, 1856)

Conservation status: Czech Republic EN.

Deraeocoris (*Camptobrochis*) *serenus* (Douglas & Scott, 1868)

Deraeocoris (*Deraeocoris*) *ruber* (Linnaeus, 1758)

Deraeocoris (*Deraeocoris*) *ventralis* Reuter, 1904

Dicyphus (*Brachyceroea*) *globulifer* (Fallén, 1829)

Europiella artemisiae (Becker, 1864)

Globiceps (*Kelidocoris*) *flavomaculatus* (Fabricius, 1794)

Halticus apterus (Linnaeus, 1758)

Heterocapillus tigripes (Mulsant & Rey, 1852)

Conservation status: Czech Republic VU.

Heterocordylus (*Heterocordylus*) *genistae* (Scopoli, 1763)

Leptopterna dolabrata (Linnaeus, 1758)

Leptopterna ferrugata (Fallén, 1807)

Lygus gemellatus (Herrich-Schaeffer, 1835)

Lygus pratensis (Linnaeus, 1758)

Lygus punctatus (Zetterstedt, 1838)

Conservation status: Czech Republic CR.

Lygus rugulipennis Poppius, 1911

^{R} *Macrotylus* (*Alloeonycha*) *atricapillus* (Scott, 1872)

Macrotylus (*Alloeonycha*) *horvathi* (Reuter, 1876)

Macrotylus (*Macrotylus*) *herrichi* (Reuter, 1873)

Megaloceroea recticornis (Geoffroy, 1785)

Megalocoleus molliculus (Fallén, 1807)

Megalocoleus naso (Reuter, 1879)

Melanotrichus flavosparsus (Sahlberg, 1842)

Myrmecoris gracilis (Sahlberg, 1848)

Notostira elongata (Geoffroy, 1785)

Notostira erratica (Linnaeus, 1758)

Omphalonotus quadriguttatus (Kirschbaum, 1856)
Conservation status: Austria (Burgenland) LC, Czech RepublicVU.

Orthocephalus saltator (Hahn, 1835)
Conservation status: Austria (Burgenland) DD.

Orthops (*Orthops*) *kalmii* (Linnaeus, 1758)

Plagiognathus (*Plagiognathus*) *arbustorum* (Fabricius, 1794)

Plagiognathus (*Plagiognathus*) *chrysanthemi* (Wolff, 1804)

Polymerus (*Poeciloscytus*) *brevicornis* (Reuter, 1879)

Polymerus (*Poeciloscytus*) *cognatus* (Fieber, 1858)

Polymerus (*Poeciloscytus*) *unifasciatus* (Fabricius, 1794)

Polymerus (*Poeciloscytus*) *vulneratus* (Panzer, 1806)

Polymerus (*Polymerus*) *nigrita* (Fallén, 1807)

* ***Solenoxyphus fuscovenosus* (Fieber, 1864)**
Conservation status: Austria (Burgenland) CR, Slovakia CR.
Remarks: We published the first records on saline specialist *S. fuscovenosus* from Serbia after our first project in 2015 (Šeat *et al*., 2016). Back then, only two locations were known for the species; however, a targeted search showed that *S. fuscovenosus* almost always occupies bare solonchak patches where the host plant *Camphorosma annua* Pall. (Amaranthaceae) is present.

Stenodema (*Brachystira*) *calcarata* (Fallén, 1807)

Stenotus binotatus (Fabricius, 1794)

Systellonotus triguttatus (Linnaeus, 1767)

Trigonotylus caelestialium (Kirkaldy, 1902)

Trigonotylus pulchellus (Hahn, 1834)
Conservation status: Austria (Burgenland) CR, Czech Republic CR.

Nabidae

Nabis (*Nabis*) *pseudoferus* Remane, 1949

Nabis (*Nabis*) *punctatus* Costa, 1847

Anthocoridae

Orius (*Heterorius*) *majusculus* (Reuter, 1879)

Orius (*Orius*) *niger* (Wolff, 1811)

Reduviidae

Coranus (*Coranus*) *griseus* (Rossi, 1790)

Rhynocoris (*Rhynocoris*) *iracundus* (Poda, 1761)

PENTATOMORPHA

Alydidae

Alydus calcaratus (Linnaeus, 1758)

Camptopus lateralis (Germar, 1817)
Conservation status: Austria (Burgenland) DD.

Coreidae

Bathysolen nubilus (Fallén, 1807)

Ceraleptus gracilicornis (Herrich-Schaeffer, 1835)
Conservation status: Czech Republic EN.

Coreus marginatus (Linnaeus, 1758)

Coriomeris denticulatus (Scopoli, 1763)

Spathocera lobata (Herrich-Schaeffer, 1840)
Conservation status: Austria (Burgenland) CR.

Syromastus rhombeus (Linnaeus, 1767)

Rhopalidae

Brachycarenus tigrinus (Schilling, 1829)

Chorosoma schillingii (Schilling, 1829)
Conservation status: Czech Republic NT.

Corizus hyoscyami (Linnaeus, 1758)

Liorhyssus hyalinus (Fabricius, 1794)
Conservation status: Austria (Burgenland) DD.

Maccevethus caucasicus (Kolenati, 1845)
Conservation status: Slovakia EN (= *Maccevethus errans caucasicus* (Kolenati, 1845)).

Myrmus miriformis (Fallén, 1807)

Rhopalus (*Rhopalus*) *conspersus* (Fieber, 1837)

Rhopalus (*Rhopalus*) *distinctus* (Signoret, 1859)
Conservation status: Czech Republic EN.

Rhopalus (*Rhopalus*) *parumpunctatus* Schilling, 1829

Rhopalus (*Rhopalus*) *subrufus* (Gmelin, 1790)

Stictopleurus abutilon (Rossi, 1790)

Stictopleurus crassicornis (Linnaeus, 1758)

Stictopleurus pictus (Fieber, 1861)
Conservation status: Austria (Burgenland) DD.

Stictopleurus punctatonervosus (Goeze, 1778)

Stenocephalidae

Dicranocephalus albipes (Fabricius, 1781)
Conservation status: Czech Republic CR.

Artheneidae

Holcocranum saturejae (Kolenati, 1845)

Berytidae

Berytinus (*Berytinus*) *clavipes* (Fabricius, 1775)

Berytinus (*Lizinus*) *geniculatus* (Horváth, 1885)
Conservation status: Austria (Burgenland) NT, Czech Republic EN, Slovenia R.

Berytinus (*Lizinus*) *montivagus* (Meyer-Dür, 1841)
Conservation status: Austria (Burgenland) NT, Czech Republic NT.

Gampsocoris punctipes (Germar, 1822)
Conservation status: Czech Republic CR.

Neides tipularius (Linnaeus, 1758)
Conservation status: Slovenia E.

Blissidae

Dimorphopterus blissoides (Baerensprung, 1859)
Conservation status: Slovenia V.

Dimorphopterus doriae (Ferrari, 1874)

Dimorphopterus spinolae (Signoret, 1857)

Ischnodemus sabuleti (Fallén, 1826)

Cymidae

Cymus claviculus (Fallén, 1807)

Cymus glandicolor Hahn, 1832

Cymus melanocephalus Fieber, 1861

Geocoridae

Geocoris (*Geocoris*) *ater* (Fabricius, 1787)
Conservation status: Czech Republic NT.

R *Geocoris* (*Geocoris*) *grylloides* (Linnaeus, 1761)

Geocoris (*Piocoris*) *erythrocephalus* (Lepeletier & Serville, 1825)
Conservation status: Austria (Burgenland) DD.

***Henestaris halophilus* (Burmeister, 1835)**
Conservation status: Austria (Burgenland) EN, Czech Republic CR, Slovakia VU, Slovenia V.
Remarks: Horváth (1897) mentioned *H. halophilus* as '*passim frequens*' (randomly frequent) in the *Regio banatica* (today's northern Serbia), but without any information on localities. This species is the most common saline specialist in various salt-affected grasslands in northern Serbia.

Heterogastridae

Heterogaster artemisiae Schilling, 1829

Heterogaster urticae (Fabricius, 1775)

Platyplax salviae (Schilling, 1829)

Lygaeidae

Kleidocerys resedae (Panzer, 1797)

* ***Lygaeosoma anatolicum* Seidenstücker, 1960**
Remarks: *L. anatolicum* in Serbia and Hungary (see Lőrinczi *et al.*, 2011; Torma, 2012; Torma *et al.*, 2017) is highly associated with saline grasslands.

Lygaeus equestris (Linnaeus, 1758)

Lygaeus simulans Deckert, 1985

Nysius cymoides (Spinola, 1837)
Conservation status: Czech Republic CR.

Nysius ericae (Schilling, 1829)

Nysius helveticus (Herrich-Schaeffer, 1850)
Conservation status: Slovenia R.

Nysius senecionis (Schilling, 1829)

Nysius thymi (Wolff, 1804)

Ortholomus punctipennis (Herrich-Schaeffer, 1838)

Oxycarenidae

Camptotelus lineolatus (Schilling, 1829)
Conservation status: Austria (Burgenland) EN, Czech Republic VU.

Metopoplax origani (Kolenati, 1845)
Conservation status: Slovenia R.

Microplax interrupta (Fieber, 1837)
Conservation status: Austria (Burgenland) CR, Czech Republic EN, Slovenia R.

Oxycarenus (*Euoxycarenus*) *pallens* (Herrich-Schaeffer, 1850)

Piesmatidae

Parapiesma kochiae (Becker, 1867)

Parapiesma quadratum (Fieber, 1844)
Conservation status: Austria (Burgenland) EN, Slovenia V (= Piesma quadratum).

Piesma maculatum (Laporte, 1833)

Rhyparochromidae

Aoploscelis bivirgata (Costa, 1853)

Beosus maritimus (Scopoli, 1763)

Beosus quadripunctatus (Müller, 1766)

*, R *Emblethis brachynotus* Horváth, 1897
Conservation status: Czech Republic RE.

Emblethis denticollis Horváth, 1878
Conservation status: Slovenia R.

Emblethis griseus (Wolff, 1802)

R *Megalonotus antennatus* (Schilling, 1829)
Conservation status: Czech Republic VU.

Megalonotus chiragra (Fabricius, 1794)

Megalonotus praetextatus (Herrich-Schaeffer, 1835)
Conservation status: Czech Republic VU.

Megalonotus sabulicola (Thomson, 1870)

Pachybrachius fracticollis (Schilling, 1829)
Conservation status: Austria (Burgenland) NT.

Peritrechus geniculatus (Hahn, 1832)

Peritrechus gracilicornis Puton, 1877
Conservation status: Czech Republic EN.

***Peritrechus meridionalis* Puton, 1877**
Conservation status: Austria (Burgenland) CR.
Remarks: *P. meridionalis* in Serbia and Austria (see Rabitsch, 2012) is highly associated with saline grasslands.

Peritrechus nubilus (Fallén, 1807)
Conservation status: Czech Republic NT.

Plinthisus (*Plinthisomus*) *pusillus* (Scholtz, 1847)
Conservation status: Czech Republic NT.

Pterotmetus staphyliniformis (Schilling, 1829)

Raglius alboacuminatus (Goeze, 1778)

Raglius confusus (Reuter, 1886)
Conservation status: Austria (Burgenland) NT, Czech Republic NT.

Scolopostethus decoratus (Hahn, 1833)

Sphragisticus nebulosus (Fallén, 1807)
Conservation status: Slovenia R.

Trapezonotus (*Trapezonotus*) *arenarius* (Linnaeus, 1758)

Tropistethus holosericus (Scholtz, 1846)

Xanthochilus quadratus (Fabricius, 1798)
Conservation status: Czech Republic NT.

Cydnidae

Canthophorus melanopterus (Herrich-Schaeffer, 1835)
Conservation status: Czech Republic EN.

*, R *Geotomus punctulatus* (Costa, 1847)

Legnotus limbosus (Geoffroy, 1785)

Legnotus picipes (Fallén, 1807)

Tritomegas bicolor (Linnaeus, 1758)

Plataspidae

Coptosoma scutellatum (Geoffroy, 1785)

Scutelleridae

Eurygaster maura (Linnaeus, 1758)

Eurygaster testudinaria (Geoffroy, 1785)

Odontoscelis (*Odontoscelis*) *fuliginosa* (Linnaeus, 1761)

Odontotarsus purpureolineatus (Rossi, 1790)
Conservation status: Czech Republic NT.

* *Phimodera flori* Fieber, 1863
Conservation status: Czech Republic CR.

Pentatomidae

Aelia acuminata (Linnaeus, 1758)

Aelia rostrata Boheman, 1852
Conservation status: Austria (Burgenland) VU.

Ancyrosoma leucogrammes (Gmelin, 1790)
Conservation status: Slovakia EN.

Antheminia lunulata (Goeze, 1778)
Conservation status: Austria (Burgenland) VU, Czech Republic NT.

***Antheminia varicornis* (Jakovlev, 1874)**
Conservation status: Austria (Burgenland) EN.
Remarks: *A. varicornis* is a saline specialist related to saline marshlands and its host plant *Bolboschoenus maritimus* (L.) Palla (Cyperaceae).

Carpocoris (*Carpocoris*) *fuscispinus* (Boheman, 1850)

Carpocoris (*Carpocoris*) *purpureipennis* (Degeer, 1773)

***Crypsinus angustatus* (Baerensprung, 1859)**
Conservation status: Austria (Burgenland) DD, Slovakia CR.
Remarks: Targeted search showed that *C. angustatus* frequently occupies salt-affected grassland patches where the host plant *Lepidium ruderale* L. (Brassicaceae) is present.

Derula flavoguttata Mulsant & Rey, 1856
Conservation status: Austria (Burgenland) DD.

Dolycoris baccarum (Linnaeus, 1758)

Eurydema (*Eurydema*) *oleracea* (Linnaeus, 1758)

Eurydema (*Eurydema*) *ornata* (Linnaeus, 1758)
Conservation status: Czech Republic VU.

Eysarcoris aeneus (Scopoli, 1763)

Eysarcoris ventralis (Westwood, 1837)
Conservation status: Austria (Burgenland) DD.

Graphosoma italicum (Müller, 1766)

Jalla dumosa (Linnaeus, 1758)

Neottiglossa (*Neottiglossa*) *leporina* (Herrich-Schaeffer, 1830)

Neottiglossa (*Neottiglossa*) *pusilla* (Gmelin, 1790)

Nezara viridula (Linnaeus, 1758)

Peribalus (*Peribalus*) *strictus* (Fabricius, 1803)

Piezodorus lituratus (Fabricius, 1794)

Podops (*Opocrates*) *rectidens* Horváth, 1883

Podops (*Podops*) *inunctus* (Fabricius, 1775)

Rubiconia intermedia (Wolff, 1811)
Conservation status: Czech Republic NT.

Sciocoris (*Aposciocoris*) *microphthalmus* Flor, 1860

Sciocoris (*Sciocoris*) *cursitans* (Fabricius, 1794)

Sciocoris (*Sciocoris*) *distinctus* Fieber, 1851
Conservation status: Czech Republic EN.

Sciocoris (*Sciocoris*) *sulcatus* Fieber, 1851
Conservation status: Austria (Burgenland) NT, Czech Republic CR.

Vilpianus galii (Wolff, 1802)
Conservation status: Austria (Burgenland) NT, Czech Republic VU.

Zicrona caerulea (Linnaeus, 1758)

Pyrrhocoridae

Pyrrhocoris apterus (Linnaeus, 1758)

Pyrrhocoris marginatus (Kolenati, 1845)
Conservation status: Czech Republic NT, Slovenia R.

11.3. Effects of sampling location (edge *vs*. centre) on saline grassland true bugs communities

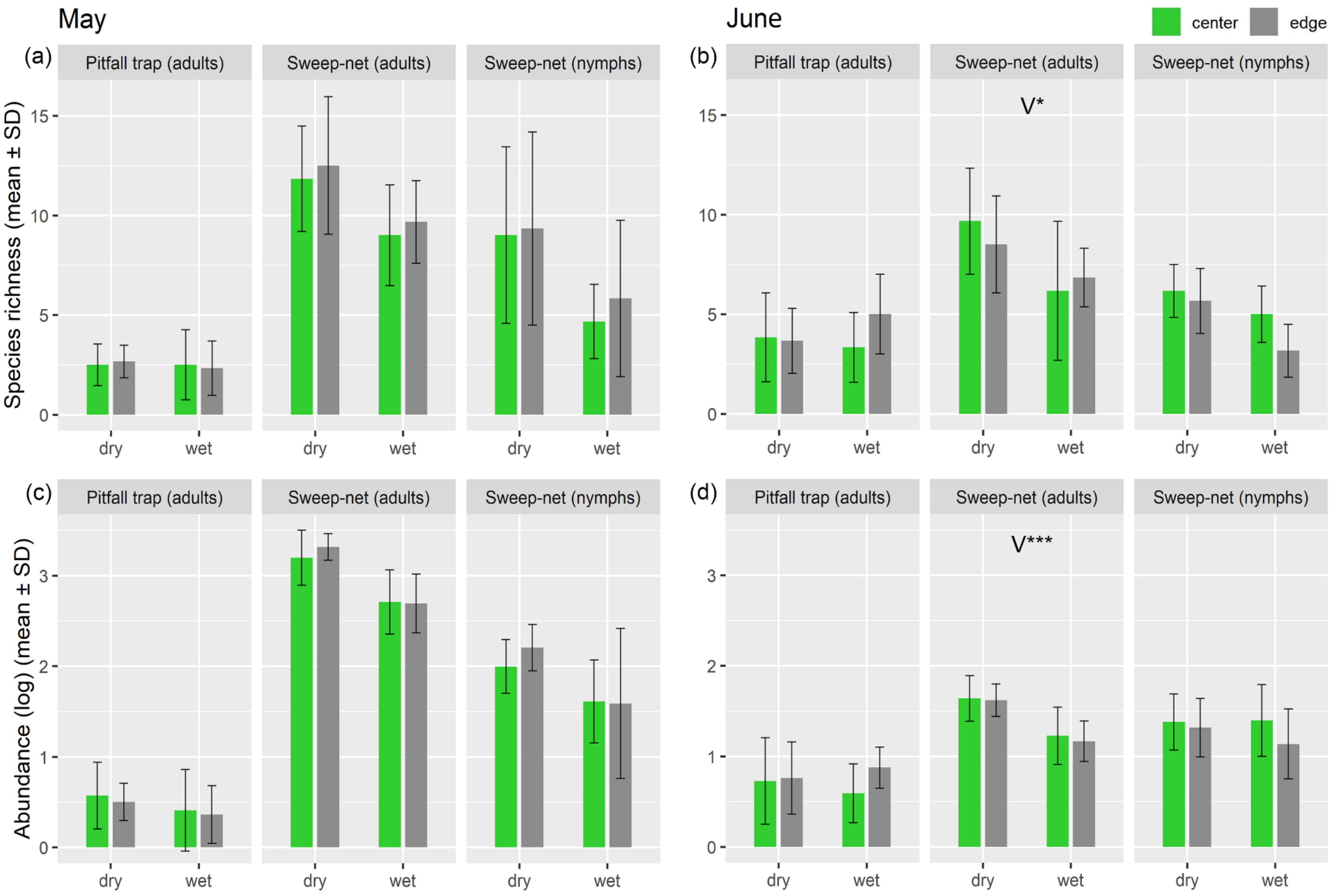

Figure 18. Effects of sampling location (centre *vs*. edge) and vegetation type (dry *vs*. wet) on species richness and abundance of true bugs in saline grasslands according to GLMMs. Significant results are marked with asterisks (*** $p \leq 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$). Abbreviations: V–vegetation type, L– location of a sample.

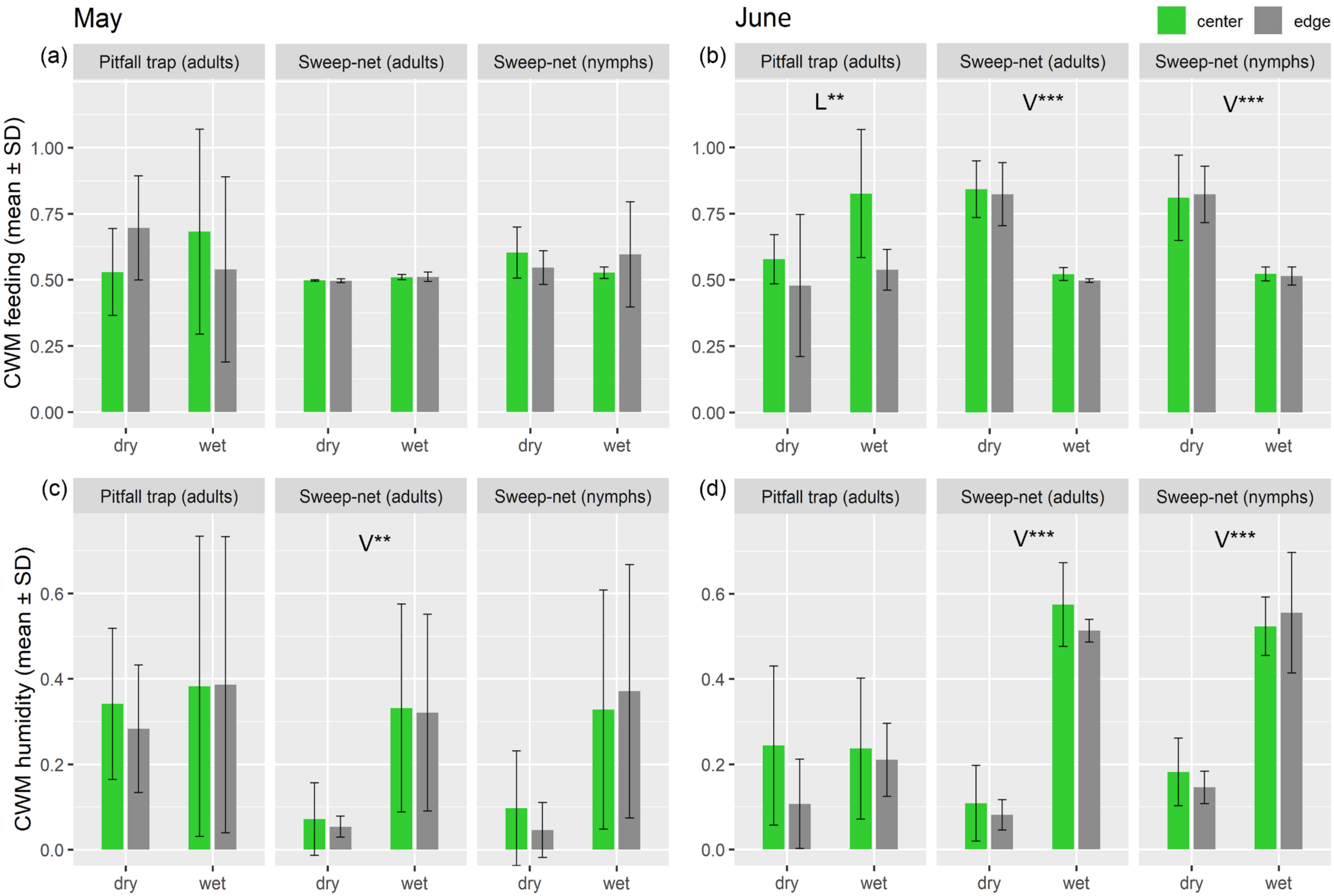

Figure 19. Effects of sampling location (centre *vs*. edge) and vegetation type (dry *vs*. wet) on feeding specialization and humidity preference of true bugs in saline grasslands according to GLMMs. Significant results are marked with asterisks (*** $p \leq 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$). Abbreviations: V–vegetation type, L–location of a sample.

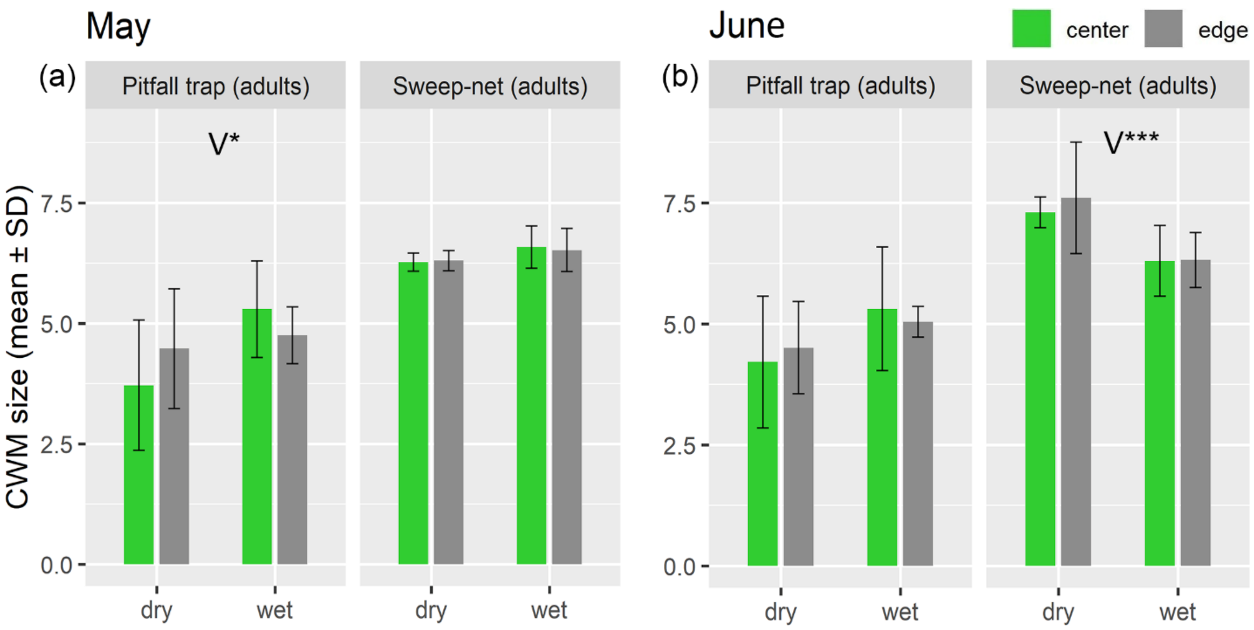

Figure 20. Effects of sampling location (centre *vs*. edge) and vegetation type (dry *vs*. wet) on body size of true bugs in saline grasslands according to GLMMs. Significant results are marked with asterisks (*** p ≤ 0.001, ** p ≤ 0.01, * p ≤ 0.05). Abbreviations: V–vegetation type, L–location of a sample.

11.4. Additional graphs from RLQ and fourth-corner analyses

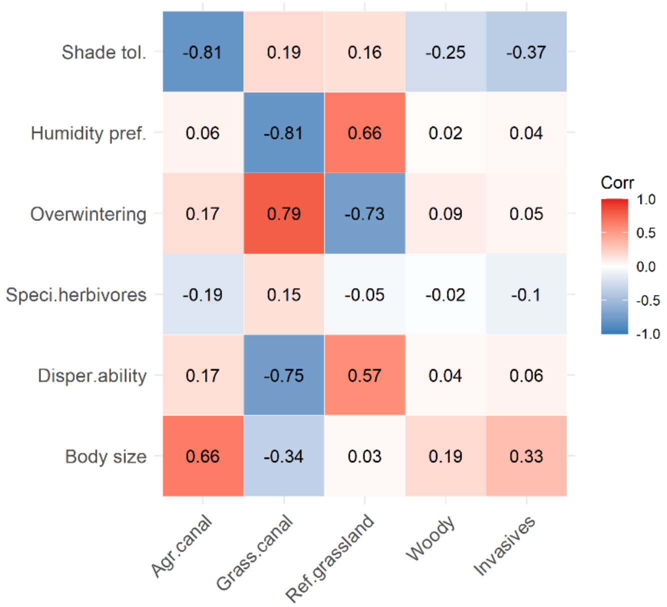

Figure 21. The result of RLQ analysis gives true bugs' trait–environment attributes correlation matrix. Red coloured cells indicate positively associated attributes, blue cells indicate negatively associated attributes and white cells indicate the absence of association between attributes.

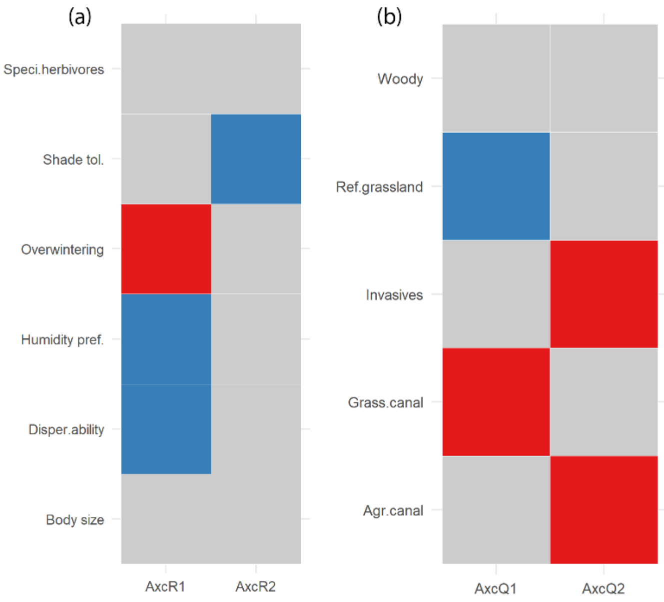

Figure 22. Results of fourth-corner analysis represent direct links between (a) true bugs' traits and (b) environment attributes and RLQ ordination axes. Positive correlations are given in red, and negative correlations are represented as blue cells.

11.5. Analysis of true bug rarity and commonness

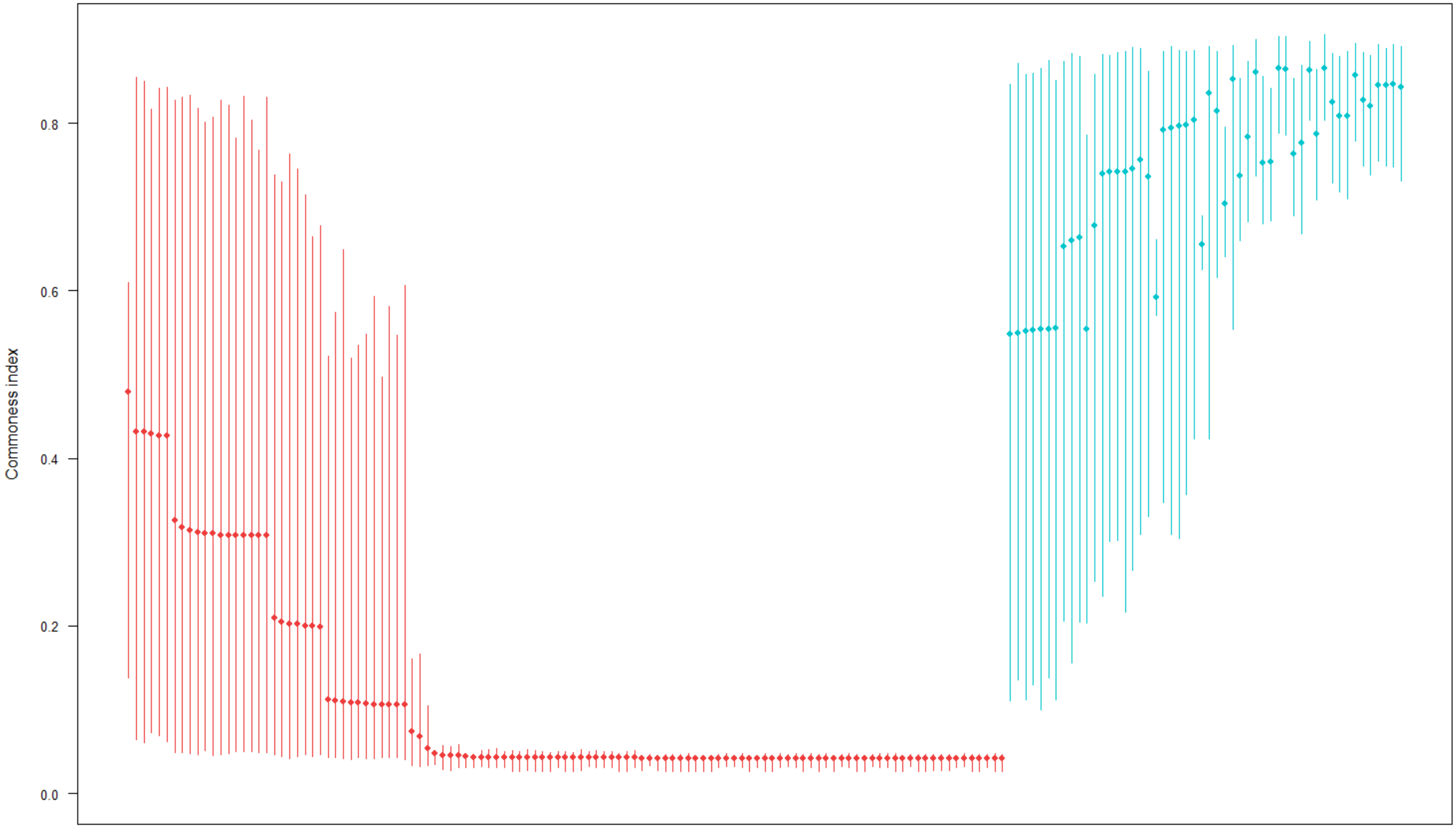

Figure 23. Commonness indices of true bug species in saline habitats of Kiskunság. Red dots represent commonness index values of rare species and turquoise dots represent index values of common species. Error bars refer to 95% confidence intervals computed with 1,000 bootstrap samples.

12. LIST OF PUBLICATIONS

MTMT Author ID: 30796299

Publications related to the PhD thesis:

Tölgyesi, C., Torma, A., Bátori, Z., Šeat, J., Popović, M., Gallé, R., Gallé-Szpisjak, N., Erdős, L., Vinkó, T., Kelemen, A.; Török, P. (2022): Turning old foes into new allies—Harnessing drainage canals for biodiversity conservation in a desiccated European lowland region. *Journal of Applied Ecology* 59(1): 89–102. DOI: 10.1111/1365-2664.14030 [**IF: 6.530**, **Scimago: D1**, number of independent citations: (MTMT): 0]

Šeat, J., Nadaždin B., Milić N., Ćuk M., Torma A. (2021): How steady is the nested pattern in saline grassland true bug communities? Effects of sampling effort and data completeness on nestedness. *Acta Oecologica* 110: 103670. DOI: 10.1016/j.actao.2020.103670 [**IF: 1.674, Scimago: Q2**, number of independent citations: (MTMT): 0]

Šeat, J., Nadaždin, B. (2021): True bugs (Heteroptera) of the Pannonic salt steppes and salt marshes in Serbia and their conservation status in the Pannonian countries. *Annales de la Société entomologique de France (N.S.)* 57(2). DOI: 10.1080/00379271.2021.1888155 [**IF: 1.111, Scimago: Q2**, number of independent citations: (MTMT): 0]

Other publications:

Panjković, B., Rat, M., Mihajlović, S., Galambos, L., Kiš, A., Puzović, S., Nadaždin, B., Šeat, J., Vukajlović, F., Tot, I., Đapić, M. (2021): Invasive Alien Species in the Balkan Peninsula. *In*: Pullaiah, T., Ielmini, M.R. (Eds.): *Invasive Alien Species: Observations and Issues from Around the World. Volume 3: Issues and Invasions in Europe*. John Wiley & Sons Ltd. 42–87 pp. DOI: 10.1002/9781119607045.ch27

Šeat J., Nadaždin B., Šćiban M. (2020): *Acrosternum heegeri* (Heteroptera: Pentatomidae) in Serbia. *Acta entomologica serbica* 25(1): 77–81. DOI: 10.5281/zenodo.3871640

Šeat J., Vujić M., Nadaždin B. (2019): New faunal data on true bugs (Heteroptera) in Serbia. *Acta entomologica serbica* 24(1): 95–99. DOI: 10.5281/zenodo.2648459

Šeat, J., Nadaždin, B. (2019): The true bugs (Insecta, Heteroptera) of the Ovčar-Kablar Gorge. *Beležnik Ovčarsko-kablarske klisure* 8(3): 8–16.

Kaur, H., Torma, A., Gallé-Szpisjak, N., Šeat, J., Lőrinczi, G., Módra, G., Gallé, R. (2019): Road verges are important secondary habitats for grassland arthropods. *Journal of Insect Conservation* 23: 899-907. DOI: 10.1007/s10841-019-00171-9 [**IF: 1.553, Scimago: Q1**, number of independent citations: (MTMT): 2]

Šeat, J. (2018): Contribution to the knowledge on true bugs (Insecta: Heteroptera) of Vlasina. *Zastita Prirode* 67(1–2):43–54. DOI: 10.5937/ZasPri1702043S

Vaselek, S., Popović, M., Šeat, J., Ćurić, A. (Eds.) (2018): Explore and protect the natural beauty of Balkans. *International Rufford Small Grants Conference*. 27th–28th September 2018, Silver Lake, Serbia, 1–54 pp.

Šeat J., Nadaždin B., Cvetković M., Jovanov A., Tot I. (2017): Providing a base for conservation of true bugs (Insecta, Heteroptera) and their saline habitats in Vojvodina (northern Serbia). *Hyla herpetological bulletin* 2016 (1): 19–23.

Popović, M., Šašić, M., Medenica, I., Šeat J., Đurđević, A., Crnobrnja-Isailović, J. (2017): Living on the edge: population ecology of Phengaris teleius in Serbia. *Journal of Insect Conservation* 21: 401-409. DOI: 10.1007/s10841-016-9922-6 [**IF: 1.562, Scimago: Q1**, number of independent citations: (MTMT): 0]

Protić, Lj., Šćiban, M., Šeat, J., Stanković, M. (2017): True bug fauna (Insecta: Heteroptera) of the Zasavica Special Nature Reserve. *Naučno-stručni skup o biodiverzitetu i drugim vrednostima rezervata Zasavica "Zasavica 2017"*, Sremska Mitrovica, Srbija, 117–127 pp.

Protić, Lj., Šeat, J. (2016): First records of the alien sycamore seed bug *Belonochilus numenius* in Serbia (Heteroptera: Lygaeidae). *Acta entomologica serbica* 21: 13–19. DOI: 10.5281/zenodo.198280

Šeat, J. (2015): *Halyomorpha halys* (Stål, 1855) (Heteroptera: Pentatomidae) a new invasive species in Serbia. *Acta entomologica serbica* 20: 167–171. DOI: 10.5281/zenodo.45391

Šeat, J., Nadaždin, B. (2015): Overview of the true bug (Heteroptera) fauna of the Ovčar–Kablar Gorge. *Beležnik Ovčarsko-kablarske klisure* 6(1): 38–47.

Šeat, J. (2013): True Bugs (Heteroptera) of the Stara planina Mountain (Serbia). *Acta entomologica serbica* 18(1–2): 17–41.

Popović, M., Šeat, J., Ilić, N., Đurić, M. (2013): New findings of *Theophilea subcylindricollis* (Coleoptera: Cerambycidae) in Serbia. *Acta entomologica serbica* 18(1–2): 237–240.

Šeat, J. (2011): True Bugs (Heteroptera) of Pčinja Valley (Serbia). *Acta entomologica serbica* 16(1–2): 9–24.

Cumulative impact factor (IF): 12.430

Conferences:

Šeat, J., Torma, A. (2019): Uloga stenica (Heteroptera) u brzoj proceni kvaliteta slatinskih pašnjaka u Vojvodini. *XII Symposium of entomologist of Serbia*, 25–29 September 2019, Niš, Serbia, 31 p.

Nadaždin, B., Šeat, J. (2019): Prilog poznavanju faune stenica (Insecta: Heteroptera) Pčinjskog kraja. *XII Symposium of entomologist of Serbia*, 25–29 September 2019, Niš, Serbia, 30–31 pp.

Šeat, J., Torma, A. (2019): Role of landscape composition and management in shaping true bug communities of Serbian saline grasslands. *Student Conference on Conservation Science*, 27–31 August 2019, Tihany, Hungary.

Šeat, J. (2018): True Bugs (Heteroptera) of Saline Grasslands in Serbian Banat. *3rd Rufford Small Grants Conference–Explore and protect the natural beauty of Balkans*, 27–28 September, Srebrno jezero, Serbia, 18 p.

Šeat, J., Kaur, H., Gallé, R., Torma, A. (2018): The role of road verges as secondary linear habitats for forest-steppe Heteroptera. *8th European Hemiptera Congress*, 24–29 Jun 2018, Zawiercie, Poland, 61 p.

Šeat, J., Torma, A. (2018): Seasonal changes of Heteroptera assemblages in Pannonian salt grasslands of Serbia. *8th European Hemiptera Congress*, 24–29 Jun 2018, Zawiercie, Poland, 120 p.

Šeat, J., (2017): Invasive true bugs in the “Alciphron” database of insects of Serbia. *XI Symposium of entomologist of Serbia* 2017, 17–21 September, Goč, Serbia, 112–113 pp.

Nadaždin, B., Šeat, J. (2017): Fauna of true bugs (Heteroptera) of the steppe and saline habitats in the Special Nature Reserve “Selevenjske pustare”. *XI Symposium of entomologist of Serbia* 2017, 17–21 September, Goč, Serbia, 97–98 pp.

Šeat, J. (2016): True Bugs (Heteroptera) of Halophytic Habitats in Vojvodina. *Nature knows no boundaries–Rufford Small Grants Conference*, 21–22 March, Banja Luka, Bosnia and Herzegovina, 31 p.

Šeat, J., Nadaždin, B., Tot, I. (2015): True bugs (Heteroptera) of Saline Habitats in Vojvodina Province – Preliminary results. *X Symposium of entomologist of Serbia* 2015, 23–27 September, Kladovo, Serbia, 11 p.

Šeat, J. (2013): True bugs (Heteroptera) in the Alciphron database. *IX Symposium of entomologists of Serbia* 2013, 18–22 September, Tara, Serbia, 36 p.