The role of small habitat patches and secondary habitats in conserving diversity

Final report

1. Introduction

Natural ecosystems worldwide, including Eurasian steppe grasslands and forest-steppes, underwent dramatic habitat loss and fragmentation during the last two centuries. Land-use changes, such as the abandonment of historical land-use practices like extensive grazing, forest plantation, agricultural expansion, and intensification, deterioration of habitat quality, result in a negative effect on biodiversity. The loss of suitable habitat areas is usually associated with habitat fragmentation; fragmented landscapes hold a few to many habitat patches generally reduced in their size (Fahrig, 2017). The community composition of small patches may differ from that of large patches as species have widely varying area, resource, and environmental requirements (Didham, 2010).

Landscape spatial heterogeneity is an important driver of diversity, which is a combination of compositional and configurational heterogeneity. Landscape composition can be measured as the variety and abundance of different cover types. In contrast, configuration refers to the spatial arrangement, size and position of landscape elements or the cumulative length of edges (Fahrig et al. 2011). A landscape matrix is an extensive land cover that has undergone intense anthropogenic perturbation around the focal habitat. Most fragmentation studies focus on habitat fragments vs. landscape matrix as a black-and-white dichotomy, with habitat fragments being the only suitable area for the organisms. However, many organisms may benefit from resources outside the habitat fragments. Therefore, the landscape matrix is a crucial determinant of patterns of diversity. Matrix quality is the degree to which natural conditions are altered in the matrix. A high-quality matrix, which contains many secondary habitats and is structurally similar to the natural habitats, may allow certain rates of dispersal and mitigate the effect of habitat loss (Fisher and Lindenmayer 2007). Linear landscape elements such as road verges can enhance the configurational heterogeneity of the landscape. They may provide shelter, suitable habitat structure, food sources and a favourable microclimate. These linear habitats can act as dispersal corridors for many grassland specialist species and reduce the effect of habitat fragmentation (Schirmal et al. 2016). Besides agricultural expansion and intensification, the land cover of tree plantations is increasing in Europe, replacing natural forests. These secondary forests include native and non-native tree plantations. Although they are usually under intensive forestry management, forest plantations may also harbour a significant part of the original biota (Gallé et al. 2017).

Invasive plants establish populations in nearly all types of secondary habitats. They may form dense stands and outcompete native flora by altering microclimate, nutrient and water availability. The changes in vegetation have bottom-up effects on higher trophic levels, and modify biotic interactions (Litt et al. 2014). In Central Europe, milkweed (*Asclepias syriaca*) causes serious conservation problems by invading large natural areas and secondary habitats, such as old fields and forest plantations (Gallé et al. 2015).

Recently, there has been an obvious shift from species-based approaches toward a trait-based concept in community ecology. The trait-based functional diversity concept includes biologically essential information directly into statistical models, thereby enhancing the generalization of results. These results may also be used as a proxy for ecosystem functions and services, such as predation and herbivory (Gallé & Batáry, 2019).

Here, we summarize the main findings of 12 published articles where the PI is either first or last author (cumulative impact factor: 31.752) and three other manuscripts submitted or under preparation. Hardeep Kaur and Kapilkumar Nivrutti Inge PhD students graduated under the co-supervision of the PI and Attila Torma (participant) at the University of Szeged, and Kitti Révész started her PhD (under the supervision of the PI) at MATE University from the topic of our project.

We specifically focused on the following research questions:

(1) How does the habitat properties of native and exotic forest plantations relate to natural forest patches and do plantation forests serve as a secondary habitat for forest-steppe vegetation and arthropods, or is it a matrix with low permeability?

(2) Does unpaved road verges serve as habitats for invertebrates and plant species and does the configuration of landscape elements affect vegetation and arthropods of verges?

(3) How is the arthropod and plant diversity pattern of small forest-steppe patches related to that of the extensive patches, and how does landscape structure affect the forest steppe biota?

2. Results of case studies

2.1. Methodological and framework considerations

2.1.1. Our methodological study assessed the efficiency of pitfall traps with funnels and roofs, a widely used sampling method in capturing ground-dwelling arthropods. Several factors affect the pitfall traps' sampling efficiency, e.g. material, size and modification of parts and by the accumulation of plant litter in the traps, rainfall and by-catches of small vertebrates. This may cause a bias in the catch by obstructing traps or attracting certain insects. A roof that prevents rain and plant litter from entering a trap prevents dilution of the preservative and escape of arthropods. Our main goal was to compare the effect of four types of differently combined funnel and roof pitfall traps on the capture efficiency of epigeal arthropods. We found that a funnel and/or a roof had no effect on spider catches. Total abundance of large carabids and thus the total abundance of ground beetles was lower in funnel pitfall traps without a roof than in other types of traps. However, funnel pitfall traps with roofs collected significantly more carabid beetles, especially individuals of those species that are large or good fliers. We conclude that funnel pitfall traps with roofs have no negative effects on capture efficiency of ground beetles and spiders; therefore, we recommended the application of this sampling technique (Császár et al. 2019).

2.1.2. In our forum article we argued that the use of trait-based information in ecology goes back to the early decades of 20th century, i.e. to the dawn of this scientific field – for example Elton in the 1920's years, emphasized the functional role of species in a community. Later, Balogh's "syntrophium" Root's "guild" and the "functional group concept" by Cummins were the foundations of the recently used feeding traits. The use of trait-based information has grown exponentially over the last twenty years, which improves our understanding of ecosystem processes. The trait-based concept is ready for use with numerous well-established indices and procedures available to quantify functional diversity. However, databases of functionally important traits, especially of less studied invertebrate taxa, are scarce and usually incomplete

(Moretti et al. 2017). Besides theoretical improvement and formation of new hypotheses, a great progress would be the development of such trait databases according to standardized protocols across taxa (Gallé and Batáry 2019).

2.2. Habitat properties affecting arthropod diversity

Most natural forest steppes in Central-Europe were converted to forest plantations, a significant part of plantations are composed of exotic pine trees. This brings dramatic changes in habitat structure. The formerly open-canopy forest patches and grasslands became closed-canopy forests and key habitat factors were altered, such as microhabitat diversity, plant species composition, microclimate, and amount of dead organic matter. Due to altered habitat factors, forest plantations are prone to invasion by exotic herbaceous plant species.

2.2.1. We studied the difference in spider species richness, assemblage composition, and functional diversity of native forest steppes, exotic pine plantations, their edges, and adjacent grasslands. We selected ten native forest patches and ten pine plantations in commercial maturity, all plantations had a direct interface with extensive forest steppe areas. We sampled spiders in forests, forest edges, and adjacent steppe grasslands, resulting in 60 sampling plots. We found different species composition in natural forest patches and pine plantations; however, forest edges and grasslands near forest edges did not differ significantly. Spiders with preferences for shaded and humid habitats were associated with forests. Web builders were associated with pine plantations and their edges, large vegetation dwelling spiders had preferences for grasslands and native forest edge, and ballooning spiders were associated with grasslands and edges. Pine forest belts around natural forest steppe patches, besides being low quality secondary habitats for forest steppe spiders, also hamper effective dispersal; the high density of trees and the lower wind speed may act as barriers for effective ballooning (Gallé et al. 2018).

2.2.2. We compared the milkweed invasion's direct and indirect effects on plant and arthropod diversity in forest-steppe fragments. We focused on organisms with different ecological roles: plants as primary producers, bees and hoverflies as pollinators (2538 individuals of 56 species), true bugs as herbivores (2812 individuals of 74 species), and the predatory group of spiders (1272 spiders of 66 species). The temperature and soil moisture were lower in invaded sites than in non-invaded areas. The invasion had a positive effect on plant species richness and flower abundance. We found exclusively indirect impacts of invasion on pollinator, herbivore, and predator arthropods by altering physical habitat characteristics and food resources. Pollinators were positively affected by the abundance of native flowers. The species richness of true bugs increased with increasing plant species richness. Spiders were positively affected by vegetation structure and soil moisture. Furthermore, the mean temperature had a negative effect on the species richness of spiders. Fragment size had a strong negative effect on spider species richness of invaded sites; however, fragment size had no effect on control sites. We did not identify strong negative effects of milkweed on the native biota (Gallé et al 2022a).

2.2.3. We established 40 sampling sites in 10 plantation forests. Sites were selected according to tree species (native poplar forests and exotic pine plantations) and common milkweed density (invaded and non-invaded sites) in a full factorial design. We collected spiders with pitfall traps (1621 adult spiders from 53 species). We found a significant effect of milkweed invasion on spider functional diversity (Rao's quadratic entropy), with invaded sites having a lower functional diversity than non-invaded sites. A stronger effect of invasion on the RaoQ of spiders was observed in pine compared to poplar plantations. Spider species were larger, and web-building spiders were more frequent in poplar forests than in pine plantations. We found no effect of milkweed invasion on species richness or abundance of spiders. The species composition of spider assemblages in the two forest types was clearly separated according to non-metric multidimensional scaling. We identified seven species associated with pine plantations and six species associated with poplar plantations (Ingle et al. 2019).

2.2.4. We investigated the effect of tree species on the winter active spider fauna of non-native pine and native poplar plantations. We established 40 sampling sites in five non-native pine and five poplar plantations and collected spiders with pitfall traps for two winters in the same plantation forests as in study 2.2.3. We assessed the average height of vegetation and percentage cover of leaf litter, mosses, herbaceous vegetation, and shrubs to characterize habitat structure. We found higher species richness and activity density of spiders in the non-native compared to the native plantations, presumably due to the more temperate microclimate in pine than in poplar plantations. However, there was no significant effect of habitat structure and its interaction with forest type on species richness and activity density of spiders. The species composition of non-native and native plantation forests differed significantly. Furthermore, we identified six characteristic spider species of non-native plantations with a preference for relatively moist habitat conditions. The single characteristic species for the native plantations preferred dry and partly shaded habitats (Ingle et al. 2020).

2.2.5. The ground-dwelling spider *Pardosa alacris* is a common species in Central-European native and plantation forests. Habitat type and prey availability may play important roles in their overwintering. The effect of overwintering on the body condition and behaviour of spiders in semi-natural and non-native habitats is relatively unknown. Here we assess the effects of winter on spiders from native poplar and non-native pine plantations. We determined the sex of the collected individuals and assessed the locomotory behaviour (distance covered and speed) and body condition (body size and total fat content) of spiders. Forest type and sex had significant effects on body length. Fat content was significantly higher in the spring than in autumn, and spiders covered larger distances and were faster in autumn than in spring. Fat content had a significant negative effect on average speed. Spiders in native forests were smaller but grew more during the winter than in non-native plantations, possibly due to higher prey availability in native forests. Visually-hunting predators may significantly affect spiders. Fat spiders with better body condition moved less, and were thus less detectable by predators. However, the low movement rate may result in a low rate of encountering prey items, thus lowering feeding efficiency (Ingle et al. 2018).

2.2.6. We studied the spillover of spiders and carabids between hay meadows and natural forests after mowing and tested whether leaving unmown buffer strips in the edges can mitigate undesirable aspects of mowing-induced spillover. We found that mowing affected the assemblages both in the meadows and forests and, interestingly, changes were more profound in the forests. Mowing reduced the spillover of forest assemblages into meadows. Mowing also led to the retraction of forest assemblages from the peripheral zones of forests but did not trigger an influx of meadow assemblages into the forests. Wide (10 m) unmown buffers attenuated or completely offset most of these effects. Leaving narrow (5 m) buffers had unexpected consequences, as they did not function only as buffers but as facilitators of forest-ward spillover from meadows, potentially compromising ecological interactions such as predation or competition in forests (Tölgyesi 2018).

2.3. Road verges support arthropod diversity

The role of linear landscape elements in biodiversity conservation has long been recognized. Such landscape elements may counteract the negative effect of agricultural intensification and forestry management on a landscape scale on biodiversity by increasing habitat connectivity and providing source habitats and overwintering sites for several predatory invertebrate species.

2.3.1. Our first study focused on the spider, ant and true bug fauna and functional diversity (FD) of fragmented forest steppe patches, moderately grazed pastures and road verges embedded in a matrix of forest plantations in Hungary, Central Europe. We established 30 sampling sites, 10 in each of the grassland components of forest steppes, pastures and road verges near pine plantation forests. We collected arthropods with pitfall and sweep-net techniques. We observed higher species richness in road verges for spiders (6983 spiders of 72 species) and ants (16 425 ants of 27 species), but it did not affect true bugs (5534 individuals of 147 species). We also found higher FD values for spiders and different trait compositions for all taxa in road verges compared with forest steppes and pastures. Species composition suggests that road verges do not serve as a habitat for several forest-steppe and grassland species, in spite of the fact that numerous specialist species were found in the road verges. We show that forest steppes have a higher species richness of spiders than pastures, and there are differences in species assemblage composition of the two habitat types for all taxa (Kaur et al. 2019).

2.3.2. Our second study assessed the effect of landscape composition and configuration on the overwintering arthropod fauna of grassy field margins and hedgerows. We sampled ground-dwelling arthropods at field edges of different types (grassy field margin and hedgerows). Sampled landscapes differed in composition (diverse and simple) and configuration (mosaic and large-scale agricultural landscapes). We focused on spiders (2502 adult spiders belonging to 72 species) and carabids (3004 beetles of 66 species). We detected larger spiders in hedgerows than in grassy field margins and in complex landscapes rather than in simple landscapes. We found a significant effect of interaction between landscape composition and edge type on the ballooning propensity of spiders. Agrobiont carabids were abundant in field edges of compositionally simple and large-scale agricultural landscapes. Furthermore, we showed an effect of interaction between landscape composition and edge type on agrobiont spiders. We collected larger carabids in grassy field margins than in hedgerows, and carabids were smaller in simple landscapes than in diverse landscapes. The spider community was affected by edge type, and landscape composition significantly affected the carabid community structure (Gallé et al. 2018).

2.4. Landscape-scale effects on forest steppes

The surrounding landscape matrix's quality often determines the habitat fragments' biodiversity pattern. Dispersal of organisms depends mostly on species traits related to mobility and the contrast between the habitat fragment and the matrix. Therefore, variation in species richness and composition among fragments, i.e. beta-diversity, can also be affected by matrix quality. Furthermore, habitat fragmentation and landscape structure may lead to ecosystem functioning and stability alterations.

2.4.1. We focused on forest steppe fragments to reveal the effects of fragment size and matrix quality. We investigated 18 forest steppe fragments along a gradient ranging in size from 0.2 to 6 ha, and embedded in a gradient of changing matrix quality. We collected data on plants (164 species), spiders (5595 adult spiders of 111 species) and ants (8773 ants belonging to 32 species) in three different habitat types: natural forest and steppe parts of the forest steppe fragments and in the directly neighbouring dominant element of the landscape matrix, being pine plantations (54 sampling sites). Species turnover (beta diversity) was higher for steppes than for forests indicating a higher degree of isolation for steppes. Increasing matrix quality decreased plant species richness in small fragments. The low dispersal between fragments prevents the displacement of poor competitors by stronger competitors and promotes the coexistence of species. Matrix quality positively affected spider richness independently of fragment size, but had no effect on ants (Gallé et al. 2022b).

2.4.2. We assessed the landscape scale effects in Hungary's largest forest steppe areas. The high number of natural forest fragments in extensive forest steppes and the relatively homogenous grassland matrix between them offer the opportunity to disentangle the effects of habitat size and landscape structure (both landscape composition and landscape configuration). We selected 40 forest fragments: 20 forest fragments in an extensive, dry, sandy forest-steppe region and 20 fragments in a mesic forest-steppe region of Hungary (Turjánvidék). We classified the detected plants (169 plant species), spiders (11323 adult spiders belonging to 125 species) and carabids (8249 carabid beetles of 73 species) according to their habitat association as forest specialist species or open habitat species. We then tested the effect of fragment size, landscape composition, and landscape configuration on their species richness and abundance. We found that increasing forest fragment size, forest habitat amount, and edge length had in general positive effects on forest spider abundance, but negative on open-habitat arthropod abundances and plant species richness, varying a little among the studied taxa. Most interestingly, the effects of fragment size were often moderated by both landscape composition and landscape configuration, as well as habitat association of species. The fragment size effect was more pronounced in landscapes with low forest habitat amount having positive effects on forest spiders and negative effects on open-habitat plants (Gallé et al 2022c).

2.4.3. We assessed how habitat and landscape-scale heterogeneity, such as variation in fragment size (small vs large) and landscape configuration (measured as connectivity index), affect diversity. We focused on plants (377 species) and arthropods with different feeding behaviour and mobility: spiders (predators, moderate dispersal; 6204 adult spiders of 193 species), true bugs (mainly herbivores and omnivores with moderate dispersal; 8139 individuals of 206 species), wild bees (pollinators with good dispersal abilities; 112 species, 2934 individuals), and wasps (pollinators, omnivores with good dispersal abilities; 83 species and 872 individuals). We studied 60 dry grassland fragments in the same region (Hungarian Great Plain); 30 fragments were represented by the grassland component of forest-steppe stands, and 30 were situated on burial mounds (kurgans). The size of fragments ranged between 0.16–6.88 ha (small: 0.16–0.48 ha, large: 0.93–6.88 ha) for forest-steppes and 0.01–0.44 ha (small: 0.01–0.10 ha and large: 0.20–0.44 ha) for kurgans. Fragments also represented an isolation gradient from almost cleared and homogenous landscapes, to landscapes with relatively high compositional heterogeneity. Fragment size, connectivity, and their interaction affected specialist and generalist species abundances of forest-steppes and kurgans. Large fragments had higher species richness of ground-dwelling spiders, and the effect of connectivity was stronger positive for specialist arthropods and stronger negative for generalists in large than in small fragments. We also found a strong positive impact of connectivity for generalist plants in small kurgans in contrast to larger ones (Gallé et al 2022d).

2.4.4. We addressed the effect of fragment connectivity, fragment size, and edge effect on two ecosystem functions, insect and seed predation of arthropods. Predation on insects and seeds by arthropods are two important ecological functions because of their community-structuring effects. In this study, we used the sampling design of the former (2.4.3.) study. We used 2400 sentinel arthropod preys (dummy caterpillars) and 4800 seeds in trays for the measurements. Attack marks on dummy caterpillars were used for predator identification and calculation of insect predation rates. In the case of seeds, predation rates were calculated as the number of missing or damaged seeds per total number of exposed seeds. Increasing connectivity played a role only in generally small kurgans, with a negative effect on insect and seed predation rates in the edges. In contrast, fragment size moderated edge effects on insect and seed predation rates in generally large forest-steppes. The difference between edges and centres was more pronounced in small than in large fragments (Kuli-Révész et al. 2021).

2.4.5. We investigated the effects of habitat type and landscape heterogeneity on species richness, functional diversity and species composition of spiders. The ground-dwelling spiders were sampled in the grasslands, forest edges and forest interiors along a gradient of landscape composition (forest amount) and configuration (edge length) within 18 landscapes. We selected one sampling site per habitat in each landscape. We recorded 22550 adult spiders belonging to 153 species. The three habitats of forest-steppes had a distinct assemblage composition with a characteristic set of species traits. Xerothermic species of web-building spiders were mostly found in grasslands, whereas spiders with a preference for moisture habitats in the forests. The forest edges had higher species richness than forest interiors and the highest proportion of ballooning species. The functional diversity was the highest in grassland, while lowest in the forest patches. We found a significant effect of interaction between landscape composition and habitat type. Increasing landscape composition positively affected species richness in grasslands; however, we observed the opposite pattern for forest edges and interiors. Web builders were positively affected by increasing landscape composition at the edges but negatively in the grasslands. The landscape configuration did not affect spider assemblages (Hamřík et al. 2022).

Conclusions

We found a profound effect of habitat structure and microclimate on arthropod species composition and functional diversity. In pine plantation forests, we found higher functional diversity than in natural forest steppe forests. The hot and dry microclimate of natural forest steppes favours some trait states (e.g., drought-tolerant, preferences for open habitats), which may lead to convergence in trait values and a lower functional diversity of forest steppe spider assemblages than that of assemblages in pine plantations. Furthermore, we found that microclimatic differences and prey availability presumably override habitat structure's effect on winter-active spiders.

Milkweed causes serious conservation problems in Central Europe by invading large natural, semi-natural and agricultural areas. The invasion of milkweed affected native (poplar) and non-native (pine) plantation forests and forest-steppe grasslands. The similar species richness and the higher functional diversity of non-invaded sites suggested that functionally different species were present. In contrast, the invaded sites had lower functional diversities and thus more uniform trait state compositions, suggesting that environmental filtering played an important role in species sorting, making invaded plantations low-quality secondary habitats for the original spider fauna. Furthermore, our study on grassland biota emphasizes that revealing the indirect effects of invasions is essential for understanding the invasion mechanisms and would support active restoration efforts.

We detected a high species richness and numerous specialist and rare species on natural and semi-natural forest steppes. Our results further indicate that the components of forest steppe mosaic form distinct plant and arthropod communities. Therefore, the effort should be made to conserve each component of the natural Eurasian forest-grassland mosaic.

Our findings concerning the effect of habitat structure could be integrated in forest edge management plans, and using wide buffers can be recommended to refine standard management practices in hay meadow–forest mosaics. Narrow buffers should be applied with great caution and should generally be avoided if the forest-specific assemblages are of conservation interest.

Road verges should be considered as an essential refuge for grassland specialist arthropods, as they provide secondary linear habitats for many arthropod species. We would suggest the maintenance of these grassy strips in order to preserve arthropod biodiversity. Small-scale agricultural landscapes with a high density of road verges and grassy margins may have higher overall densities of ground-dwelling spiders and carabids than large-scale landscapes due to the higher quantity of available overwintering sites

Our project highlight the complexity of landscape scale effects, and calls for a situation-specific optimization of landscape management in nature conservation. For our particular situation, besides the well-known effect of enhancing habitat quality, the findings provide evidence that improving matrix quality would support diversity. Increasing connectivity between fragments by restoring natural and semi-natural habitat patches would help preserve the threatened forest steppe biota and grassland biodiversity. Furthermore, an effective conservation strategy should consider not only the presence of forest fragments, but also the size and configuration as well as the connectivity of forest fragments to maximize the diversity benefits of forest patches.

We emphasize the important role of landscape-scale factors interacting with habitat properties and edge effects in shaping diversity and ecosystem functions in modified landscapes. Managing functional landscapes to support diversity, conserve specialist species and optimize ecosystem functions and services need a multiscale approach.

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Articles closely connected to our project are marked with asterisk

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