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Smaller and Isolated Grassland Fragments Are Exposed to Stronger Seed and Insect Predation in Habitat Edges

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Abstract: Habitat fragmentation threatens terrestrial arthropod biodiversity, and thereby also leads to alterations of ecosystem functioning and stability. Predation on insects and seeds by arthropods are two very important ecological functions because of their community-structuring effects. We addressed the effect of fragment connectivity, fragment size, and edge effect on insect and seed predation of arthropods. We studied 60 natural fragments of two grassland ecosystems in the same region (Hungarian Great Plain), 30 forest-steppes, and 30 burial mounds (kurgans). The size of fragments were in the range of 0.16–6.88 ha for forest-steppe and 0.01–0.44 ha for kurgan. 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. Our study emphasizes the important role of landscape and fragment-scale factors interacting with edge effect in shaping ecosystem functions in natural grassland fragments of modified landscapes. Managing functional landscapes to optimize the assessment of ecosystem functions and services needs a multispatial scale approach.

Keywords: arthropod predation; connectivity; dummy caterpillar; ecosystem function; edge effect; forest-steppe; fragment size; kurgan; landscape-scale; seed predation

1. Introduction

Habitat loss and fragmentation are among the most relevant threats to arthropod biodiversity [1]. Agricultural expansion, afforestation with exotic tree species, and urbanization are the primary drivers of loss of natural or seminatural habitats and their insect communities [2], leading to small habitat fragments and decreased connectivity between them [3]. Classical island biogeography theory attempted to explain the effect of island size and distance from mainland sources on the diversity of species [4]. This concept was applied for terrestrial habitat fragments and the differences between oceanic islands, and isolated habitat fragments are now well-recognized [5,6]. The predictive power of habitat area was also demonstrated for arthropods of terrestrial islands [7,8].

The effect of decreasing connectivity on arthropods is highly taxon-specific. Habitat generalists and highly mobile species may cover large distances in a strongly modified landscape matrix [3]. The spatial proximity of suitable habitat fragments is more important for arthropods that are habitat specialists and have low mobility; thus, they may form isolated populations [9]. Furthermore, the conversion of a continuous habitat into disjunct

habitat fragments usually increases the length of the edges between fragments and the surrounding matrix, which may significantly change the characteristics of edges, and the plant and animal diversity of communities [10,11].

Spillover is the movement of organisms across habitat edges [12]. Its effect is more pronounced near edges than in the central part of the habitat [13]. Most of the studies focused on how the influx of predators from seminatural habitats relates to the pest control services in agricultural fields [14–16]. Only a few studies found spillover from natural habitats [17,18]. For example, Madeira et al. [19] argue that spillover from adjacent crop habitats shapes carabid, rove beetle, and spider assemblages in fragmented seminatural grasslands.

Small habitat fragments are important biodiversity refuges [20] and may harbour a large proportion of the regional species pool in arable landscapes [21]. Species richness and density of arthropods in small fragments can be as high as in large ones [22,23]. However, there are some species that are disadvantaged in small habitats [24]. Changes in species richness and community composition can lead to alterations of ecosystem functioning and stability [25,26]; consequently, habitat fragmentation may broadly affect species interactions [27–29]. Furthermore, the effect of fragmentation on different ecosystem functions depends on the specific function and species identity [30]. Species of certain functional groups, such as larger body size or higher trophic level, may be more vulnerable to habitat loss, and this may have an effect on ecosystem functioning, resulting in a weaker top down effect in food webs [31]. However, the net effect of fragmentation remains controversial [32]. Large variation exists in how plant and animal species and species interactions respond to fragmentation. For example, Tong et al. [33] found that seed predation of acorn weevils (*Curculio glandium* Marsham) was high in large, less isolated fragments. In contrast, Elzinga et al. [34] found higher rates of seed predation on white campion (*Silene latifolia* Poir.) by the specialist moth lychnis (*Hadena bicruris* Hufnagel) in small fragments.

Insect and seed predation are important ecological functions because of the associated community-structuring effects [35,36]. Measuring species interactions such as insect and seed predation is challenging. Instead of measuring the function itself, studies often use densities of predators as a proxy [37], which can be misleading [38,39]. Here, we aimed to study the effects of fragmentation (i.e., increasing isolation, decreasing fragment size, and edge effect) directly on predation in two grassland ecosystems.

We chose forest-steppes and kurgans due to their intense exposure to fragmentation and their special role in nature conservation in the steppe zone [40]. Both types of steppe fragments have the potential to preserve the natural flora, fauna, and act as local biodiversity hotspots [40,41]. Forest-steppes are mosaics of grassland and forest fragments at the contact zone between closed-canopy temperate forests and steppe grasslands. They are among the most complex ecosystems in Eurasia, and their elements play a key role in landscape dynamics [41]. Kurgans (burial mounds) are artificial formations and were developed for burial purposes by steppic people (mainly in the range of IV–I millennia BC) by piling soil on the grave of an important person. The height of the kurgans ranges between half and a few meters, with the diameter between a few meters and 100 m [42]. These relatively small landscape elements represent important refuges for Eurasian steppe wildlife [43]. Both ecosystems are of high natural conservation value, harbouring numerous rare and protected plant and animal species. The fragment size and landscape structure of the two ecosystems are in different scales: small-scale landscape structure and relatively large fragment size in the case of forest-steppes, and large-scale landscape and small fragment size for kurgans. However, the landscape matrix between fragments was relatively homogeneous and highly modified for both ecosystems. Our aim was to compare the two systems, and we expected different responses to the local and landscape factors.

We expected all studied fragmentation effects to be important determinants of insect and seed predation; however, the magnitude and relative importance of these effects, as well as their interaction, is not known. We tested the following hypotheses: (1) Predation

rates are higher when connectivity decreases in the landscape, because isolation can enhance the spillover of generalist predators from the matrix. (2) Predation rates are higher in the edges than in the centres of a fragment, as a consequence of the edge effect. (3) Predation rates are lower in small than in large fragments, as functional groups of higher trophic levels are expected to be more sensitive to area loss. We aimed to reveal the similarities and differences of these questions in the two investigated fragmented grassland ecosystems of the same region using standardized methods.

2. Materials and Methods

2.1. Study Region and Sampling Design

We conducted our study on 60 natural grassland fragments in two different regions of the Hungarian Great Plain. We sampled 30 forest-steppe fragments in the central part of the Kiskunság region and 30 kurgans in southern Hungary. The investigated fragments were scattered around four settlements (Dévaványa, Kunágota, Makó, and Szentes) in the case of kurgans, and around three villages (Pirtó, Bócsa, and Kunfehértó) in the case of forest-steppes (Supplementary Material Figure S1). We established two transects of sentinel prey, and two trays of seeds in each centre and edge of every fragment (Figure 1B). Both areas are characterized by a continental climate with 500 to 550 mm mean annual precipitation, and 9.5 and 10 °C mean temperature, respectively [40,44]. Forest-steppes comprise extensive dry grasslands dominated by *Festuca vaginata* Waldst. and Kit ex Willd., *Stipa borysthenica* Klokov ex Prokudin, and relatively small forest fragments of poplar (*Populus alba* L.) and hawthorn (*Crataegus monogyna* Jacq.) [41]. Our study focused on dry steppic grasslands. The potential vegetation of kurgans consists of pannonic loess steppic grasslands [40] dominated by crested wheatgrass (*Agropyron cristatum* (L.) Gaertn.) and forage kochia *(Kochia prostrata* (L.) Schrad.) [45].
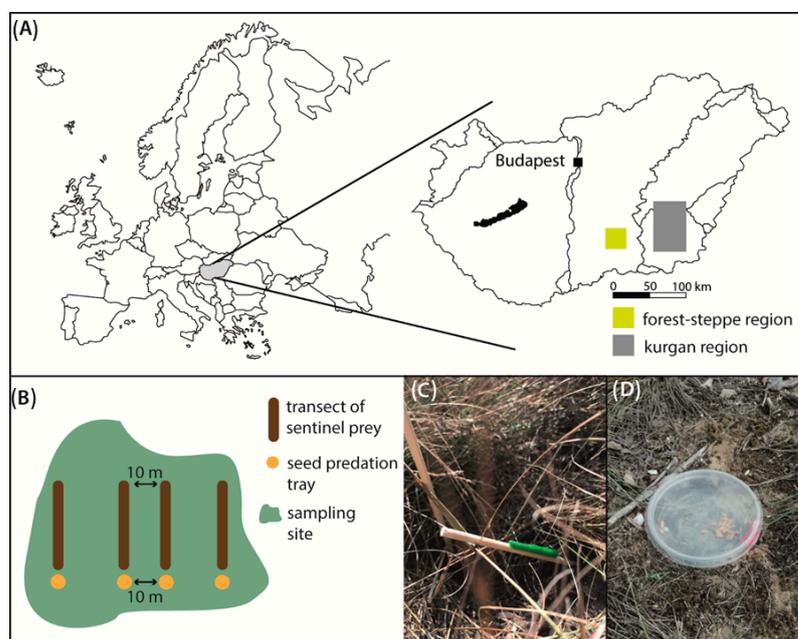
Figure 1. (**A**) Location of study regions in Hungary, Europe. (**B**) Sampling design. Light green represents the area of grassland fragment. Transects of sentinel preys and seed predation trays were minimum of 10 m away from each other, even in same transect position. (**C**) Sentinel prey. (**D**) Seed predation tray.

We selected the study sites on the basis of the size of the fragments and along a landscape configuration gradient by performing preliminary field visits and GIS calculations. We calculated Hanski's connectivity index [46] and hostile matrix percentage to quantify landscape configuration and composition using Google aerial photographs (captured in

2019), the basic ecosystem map of Hungary, and Quantum GIS 3.6.1 software [47]. Since kurgans and forest-steppes had two different spatial resolutions (i.e., kurgans were situated in large-scale agricultural landscapes and forest-steppe fragments were in a matrix of relatively small-scale forest plantations), we performed GIS calculations within a 1000 m radius buffer around the kurgans, and within a 500 m radius buffer around the forest-steppes. For connectivity calculations, we considered all habitat fragments (other forest-steppe fragments and open-sand grasslands for forest-steppes, closed and alkali grasslands for kurgans) that were located around the focal fragment. As we applied the connectivity index to entire predator communities containing many taxa, scaling parameters α and β were set to the value of 0.5 [48]. For hostile matrix calculations, we considered all nonhabitat fragments (coniferous and deciduous plantations, clear-cut areas, young afforestation for forest-steppes, and arable lands for kurgans) and calculated their pooled percentage cover in a buffer around each site. As we found significant correlations between hostile matrix percentage and connectivity in both habitat regions (forest-steppes: Pearson $r = -0.64$, $p < 0.001$; kurgans: Pearson $r = -0.95$, $p < 0.001$; i.e., proportion of hostile matrix significantly decreased with increasing connectivity), we used only connectivity as landscape-level variable in further analyses. Lastly, we selected 15 small (0.16–0.48 ha for forest-steppe; 0.01–0.10 ha for kurgan) and 15 large (0.93–6.88 ha for forest-steppe; 0.20–0.44 ha for kurgan) grassland fragments. Connectivity values of the selected fragments ranged from 0 (isolated) to 2637 (connected) for kurgans (mean = 689) and 24 to 811 for forest-steppes (mean = 394).

2.2. Sentinel Prey

We assessed the predatory activity of carnivorous insects with dummy green caterpillars of moths made of plasticine, exposed for seven days. This method of sentinel prey is easy to use and appropriate to assess in situ predation pressure [39,49]. Dummy caterpillars were 25 mm long and 5 mm in diameter, and made from light green nontoxic modelling plasticine (Fimo Soft®, Staedtler Mars GmbH & Co. KG, Nuremberg, Germany). All caterpillars were covered by PlastiDip® (PlastiDip International, Blaine, MN, USA) silicon spray to avoid drying and eliminate the smell of plasticine [50]. We fixed all caterpillars to 5 cm long wooden sticks with superglue for easier handling.

We attached them to the ground by pushing the end of the stick into the soil. We placed dummy caterpillars in transects, 1 m distance from each other. We used 2400 sentinel preys altogether (2 regions × 30 study sites × 2 transect positions × 2 transects × 10 caterpillars; Figure 1). The transects of sentinel preys were at a minimum of 10 m away from each other even in the same transect position. We installed dummy caterpillars on 21–27 June and collected them from 28 June to 4 July 2019. Potential predators were identified by the attack marks that they left on dummy caterpillars. We inspected the marks by using magnifying glasses and microscopes in the laboratory, following the methods described by Low et al. [51]. Multiple attack marks by the same predator group were assumed to originate from the same predator. Signs by different predator types were considered independent attacks.

2.3. Seed Predation

We exposed seeds in transparent, plastic trays to assess seed predation. Placing the seeds in shallow containers in the ground is a simple and established way for assessing seed predation [52,53]. We placed 10 seeds of *Triticum spelta* L. as large, and 10 seeds of *Festuca rubra* L. as small seeds in each tray. We used the different sizes to increase attractiveness for a wider range of seed predator arthropods. The trays were round plastic containers, 10 cm in diameter (Figure 1D). We fixed the container to the ground by attaching a plastic stick to the container and dug it into the soil. We excluded birds and rodents by closing the containers with transparent lids and creating 1 × 1 cm openings on their sides (only for arthropods). Altogether, we had 2 regions × 30 study sites × 2 transect positions × 2 trays, resulting in a total of 240 seed predation trays (Figure 1). The containers were a minimum

of 10 m away from each other. We installed trays from 31 May to 6 June and collected them from 7 to 13 June 2019. Thus, all trays were exposed for 7 days. Seed predators were assumed to be responsible for missing seeds. We counted the remaining seeds in each tray and inspected them for further predation marks in the laboratory. We considered multiple attack marks on the same seed as one predation event. Several oligo- and monophagous specialist seed predator insects were present on our study sites, but their seed-predation effect was not included in our data.

2.4. Statistical Analysis

Insect predation rates were calculated as the number of sentinel prey items showing signs of predation per total number exposed per transect. Seed predation rates were calculated as the number of missing seeds and remaining seeds with predation marks per total seed number exposed per transect. To test whether connectivity, fragment size, transect position, and their second-order interactions (fixed factors) had a significant effect on insect and seed predation rates, we used generalized linear mixed-effects models with the model averaging method. Models were fitted with binomial distribution. Connectivity ranged between 0 and 1. We used lmer (lme4) [54] models with fragment ID within village as a nested random-effect term. We used seed size as an offset variable in models of seed predation rates. We calculated Akaike's information criteria corrected for small sample sizes (AICc) to rank candidate models. The models with <6 ΔAICc of the best model (i.e., the model with the lowest AICc) were used for model averaging [55,56] with the R package MuMIn [57].

3. Results

3.1. Sentinel Prey

Overall, 72.13% (1731/2400) of the dummy caterpillars were attacked. On the basis of the identification of attack marks, 87.52% of the predators were ants, 7.93% beetles, 5.21% reptiles, 3.40% wasps, 3.17% birds, 1.25% mammals, and 0.79% were bees. The effect of landscape and local variables was not unequivocal for the two ecosystems. Fragment size, transect position, and their interaction had the highest relative importance for insect predation in forest-steppes (Table 1). We detected higher predation rates in edges in the central transects of small forest-steppes; however, we detected the opposite pattern in large fragments (Figure 2A). We found no interaction effect between fragment size and transect position in kurgans (Table 1, Figure 2B). Variables that best explained insect predation in kurgans were connectivity, transect position, and their interaction according to relative importance values (Table 1). Increasing connectivity had a negative effect on the predation rates of edges but not in kurgan centres (Figure 2D).

Table 1. Summary table for GLMM results after multimodel averaging of the best candidate models showing relative importance of each explanatory variable (fragment size: large (L) vs. small (S), transect position: centre (C) vs. edge (E), and connectivity), and their interactions on insect and seed predation rates in forest-steppes (FS) and kurgans (KU).

Model [a]	Variable	Relative Importance (%) [b]	Multimodel Estimate ± 95% [c]	
Insect predation (FS)	Fragment size (L/S)	100	−0.215	±0.538
	Transect (C/E)	100	−0.449	±0.427 *
	Fragment size × transect	100	0.895	±0.538 **
	Connectivity	36	0.050	±0.928
	Connectivity × transect	8	0.300	±1.140
	Connectivity × fragment size	7	0.251	±1.689
Insect predation (KU)	Connectivity	67	−0.418	±1.887
	Transect (C/E)	62	0.405	±0.651
	Connectivity × Transect	49	−1.303	±1.014 *
	Fragment size (L/S)	33	−0.258	±1.087
	Fragment size × transect	4	−0.077	±0.573
	Connectivity × Fragment size	4	−0.425	±3.402

Table 1. *Cont.*

Model [a]	Variable	Relative Importance (%) [b]	Multimodel Estimate ± 95% [c]	
Seed predation (FS)	Fragment size (L/S)	100	−0.521	±0.651
	Transect (C/E)	100	0.208	±0.313
	Fragment size × Transect	100	0.635	±0.387 **
	Connectivity	38	0.071	±1.203
	Connectivity × transect	8	0.164	±0.827
	Connectivity × fragment size	8	−0.380	±2.125
Seed predation (KU)	Connectivity	100	1.281	±1.589
	Transect (C/E)	100	0.098	±0.439
	Connectivity × transect	100	−1.731	±0.872 ***
	Fragment size (L/S)	42	0.064	±1.037
	Fragment size × transect	15	0.227	±0.469
	Connectivity × Fragment size	11	−0.547	±2.797

[a] Models fitted with binomial distribution (number of candidate models, ΔAIC < 6). [b] Each variable's importance within the best candidate models (ΔAIC < 6). [c] Significance levels: *: <0.05, **: <0.01, ***: <0.001.
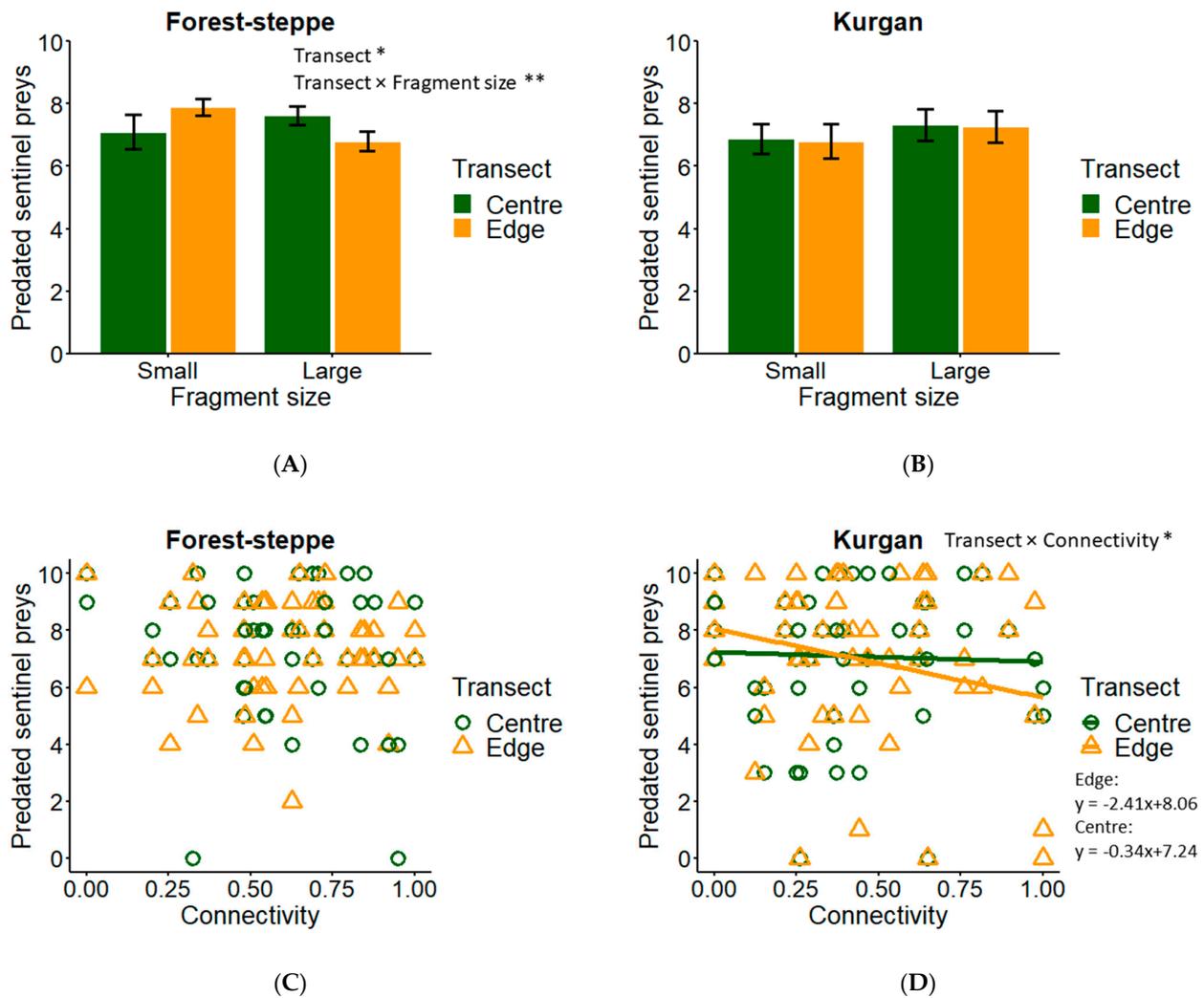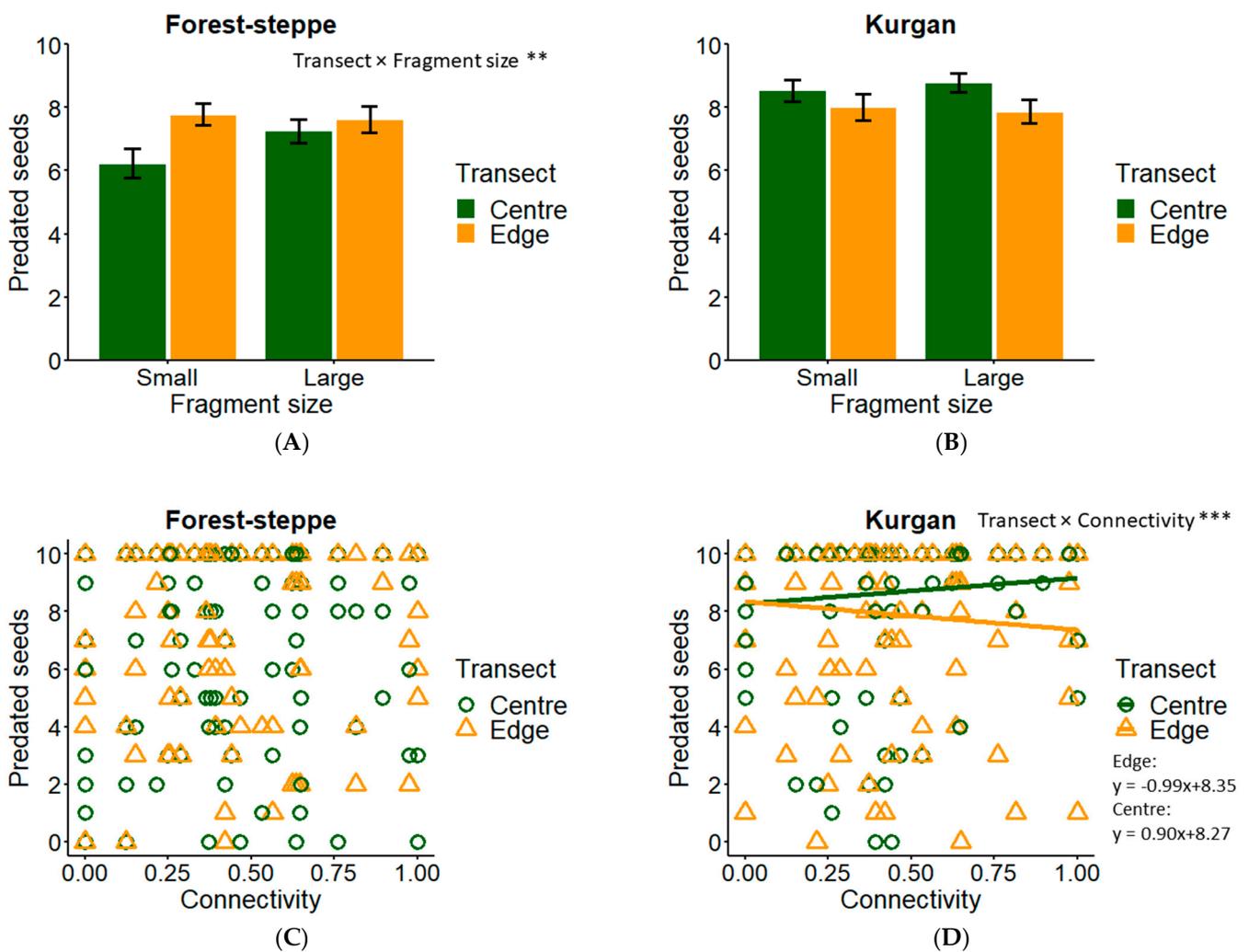

Figure 2. Insect predation. Interacting effect of (**A**) fragment size and edge effect on insect predation in forest-steppes; (**B**) fragment size and edge effect on insect predation in kurgans (mean ± SE); (**C**) connectivity and edge effect on insect predation in forest-steppes; and (**D**) connectivity and edge effect on insect predation in kurgans. Green, centre position; orange, edge position. Significance levels: *: <0.05, **: <0.01.

3.2. Seed Predation

In total, 77.58% (3724/4800) of the seeds had predation marks or been carried away. Similar to the results of insect predation, we found a significant interaction between fragment size and edge effect in case of forest-steppes, but not in kurgans (Table 1, Figure 3A,B). We found higher seed predation rates in edge in centre transects in forest-steppes, and this difference was more pronounced in small than in large fragments (Figure 3A). Connectivity and transect position did not affect seed predation in forest-steppes (Table 1, Figure 3C); however, seed predation in kurgans was affected by connectivity, transect position, and their interaction (Table 1, Figure 3D). In kurgans, we found a negative effect of connectivity on seed predation rates in edge and positive effect in centre transects (Figure 3D).

Figure 3. Seed predation. Interacting effect of (**A**) fragment size and edge effect on seed predation in forest-steppes; (**B**) fragment size and edge effect on seed predation in kurgans (mean ± SE); (**C**) connectivity and edge effect on seed predation in forest-steppes; and (**D**) connectivity and edge effect on seed predation in kurgans. Green, centre position; orange, edge position. Significance levels: **: <0.01, ***: <0.001.

4. Discussion

We addressed the effect of connectivity, fragment size, edge effect, and their interactions on insect and seed predation of arthropods. The predation rates of forest-steppes and kurgans responded differently to the effects of fragmentation depending on the fragmented grassland ecosystem. Predation pressure was higher in the edges of small fragments of

forest-steppes and in the edges of more isolated landscapes of kurgans. Thereby, our results emphasize the differences of the two fragmented grassland ecosystems.

4.1. Predation in Forest-Steppe

Connectivity did not affect predation (Hypothesis 1); however, our second and third hypotheses about edge effect and fragment size, respectively, were partly supported, as the difference between edges and centres was more pronounced in small than in large fragments. In the case of insect predation, we found higher predation rates in the edges in the centres of small fragments, but we found the opposite pattern in the case of large fragments. Seed predation was higher in the edges of both small and large fragments, but the difference was more pronounced in small fragments.

Edge effects were stronger in small than in large fragments, which was in line with the findings of Laurance and Yensen [58]. This was explained partly by the higher edge/area ratio, i.e., smaller fragments had longer edges related to their area [59]. The edge effect on arthropod predation, and on other interspecific interactions and functional trait composition of arthropods, is relatively well-known [60–62]. Some of them measured with the very same sentinel prey method [40]. It is expected that resource consumption in terrestrial arthropod communities is higher at fragment edges [63]. The abundance of generalist predators increases near edges, which may alter food webs [64]. However, the response of insect predation by arthropods to edges is highly variable. Although there is a general positive correlation between the abundance of predators and predation rates [65,66], predation rates were found to be even higher in the habitat interior than in the edges in some cases [40]. There are contradictory results for seed removal ratios at edges vs. centres, with negative [67], or neutral [53] responses to edges. Fragmentation may shape many attributes of edges [10,11]; landscape and fragment-scale factors may interact with edge effects [63,67]. Our results emphasize that several effects may modify seed predation at edges, as we found higher rates at edges than in centres, but this effect was modified by fragment size. The interaction of these factors may explain the variability of predation responses to edges.

The main difference between forest-steppe and kurgan systems is the size of the fragments. Forest-steppe fragments (0.16–6.88 ha) were an order of magnitude larger kurgan fragments (0.01–0.44 ha), presumably maintained by abundant predator and seed predator assemblages. This might have had an effect on predation rates, which caused fragment size to override the effect of connectivity that we expected in the hypothesis (1).

4.2. Predation in Kurgan

Our first hypothesis that predation pressure increases with decreasing connectivity was supported for insect and seed predation in edges of kurgans. We found that increasing connectivity had a negative effect on predation rates in the edges but had a minor effect in the centres of kurgans. In addition, predation rates of edges mainly stayed under the rates of centres, in contrast to our presumptions during the hypothesis (2). Presumably, spillover from arable lands to grasslands increased predation rates in the edges.

We assumed that predators of arable fields dominated the predator assemblages in the edges of kurgans, therefore the decreasing amount of agricultural fields associated with increasing connectivity in the matrix had a negative effect on predation in the edges. Spillover between agricultural fields and natural habitats is recognised as an important mechanism shaping biodiversity, biotic interactions in communities, and ecosystem functions [19,68,69]. In order to gain insight into these mechanisms, not only should the number of species and individuals that move between adjacent habitats be observed, but also the functional responses should be addressed directly [70]. Native herbivores in natural habitats may experience increased predation pressure in landscapes with increasing habitat loss, due to spillover of generalist predators from surrounding cropland habitats [71]. Agricultural landscapes appear to augment generalist predators resulting in dramatically higher predator–prey ratios and reduced herbivore abundance [72].

Seed predation also decreased in the edges of kurgans when connectivity increased. Granivorous arthropods from the agricultural matrix may contribute greatly to seed predation rates in the edges of grasslands. When the proportion of arable fields decreased in the surrounding matrix; i.e., connectivity of habitat fragments increased, it led to a decrease in seed predation by arthropods. Our presumption about the tendency of movement from arable field to the adjacent habitat is recognised for some seed consumer carabids [73]. Furthermore, our results align with those of the study of Craig et al. [67], who found that seed predator arthropods cause higher predation rates with decreasing connectivity in the landscape. Taken together, connectivity had similar effects on insect and seed predation, presumably due to the same phenomenon: spillover.

Connectivity moderated the edge effect on predation; however, we did not find an effect of fragment size (Hypothesis 3), in contrast to in the forest-steppes. All kurgan fragments were relatively small. Presumably, the effect of connectivity overrode the effect of fragment size. These results are in line with those of Rösch et al. [23], emphasising that connectivity is more important for small, isolated fragments, whereas fragment size is more relevant for large fragments.

5. Conclusions

Landscape and fragment-scale factors interact in shaping predation pressure by arthropods in natural grassland fragments. Thus, the edge effect was stronger in small forest-steppes and isolated kurgan fragments. Although our data were obtained only during a single year, our study assessing predation in seminatural grasslands improved our understanding of responses of predators to different local and landscape factors. Our study emphasizes that a multispatial scale approach is needed for the effective assessment of ecosystem functions, which may contribute to the conservation and maintenance of high-value seminatural grasslands.

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