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Abstract The role of fragment size, isolation and habitat diversity in the conservation of spider assemblages living in fragmented landscape were studied in dry sandy grasslands (East Hungary, Nyírség). Spiders were collected using pitfall traps at eight dry grassland fragments from 2001 to 2009 from March to October fortnightly. We tested the rules of island biogeography, which suggest that the species richness increases with the size and decreases with the isolation of fragments. The habitat diversity is an important factor for species richness, since large areas usually have more habitats; therefore, the number of species may be higher in these areas. During the 9-year study period, altogether 10,544 individuals belonging to 106 species were collected. Contradicting the classical theory, we found a significant negative relationship between the total number of spider species and the grassland size, while the ratio of sandy grassland specialist spider species increased with fragment size. The relationship between the ratio of generalist species and the fragment size was not significant. The overall species richness and the isolation of studied grasslands did not show a significant relationship. The ratio of sandy grassland specialist species decreased, while the ratio of generalist species increased with the increasing of isolation. The habitat diversity did not show any effect on spider species richness. We concluded that to conserve the habitat specialist species it is recommended to preserve the large and least isolated grassland fragments, furthermore to increase the size of small fragments with the restoration of the adjacent croplands.

Keywords (separated by '-') Island biogeography - Fragmentation - Species richness - Sandy grassland specialist species - Generalist species - Habitat heterogeneity

Footnote Information **Electronic supplementary material** The online version of this article (doi:10.1007/s10531-013-0439-y) contains supplementary material, which is available to authorized users.

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Electronic supplementary
material

Below is the link to the electronic supplementary material.

MOESM1: Supplementary material 1 (PDF 21 kb).

MOESM2: Supplementary material 2 (KML 27 kb).

2 **Large and least isolated fragments preserve habitat**
3 **specialist spiders best in dry sandy grasslands in Hungary**4 **Roland Horváth · Tibor Magura · Csaba Szinetár · János Eichardt ·**
5 **Béla Tóthmérész**6 Received: 29 June 2012 / Accepted: 21 January 2013
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27 **Keywords** Island biogeography · Fragmentation · Species richness · Sandy grassland
28 specialist species · Generalist species · Habitat heterogeneity

29 Introduction

30 Reduction and fragmentation of natural and semi-natural habitats became a major threat to
31 biodiversity and these processes cause a significant loss of biodiversity (Harrison and
32 Bruna 1999; Henle et al. 2004). Habitat reduction and alteration negatively influence the
33 distribution, abundance and diversity of characteristic plant and animal species of natural
34 habitats (Quinn and Harrison 1988; Baur and Erhardt 1995; Gilbert et al. 1998) and have
35 been regarded as the main threats to compositional and structural biodiversity (Noss 1991;
36 Didham et al. 1996). Therefore, disturbance sensitive species may disappear from natural
37 and semi-natural habitats.

38 During the last century there was a significant reduction in the size and continuity of
39 diverse natural and semi-natural grasslands in whole Europe (Poschlod and WallisDeVries
40 2002; WallisDeVries et al. 2002). Grasslands are usually sensitive to habitat alteration and
41 fragmentation (Poschlod and WallisDeVries 2002; Novák and Prach 2010). The reasons
42 for alteration and fragmentation are the increase of large-scale farming and abandonment
43 of the traditional management practices (Taboada et al. 2011). The efficiency of conser-
44 vation actions depends on the management activities (livestock grazing, mowing and
45 burning), which are important for the maintenance and preservation of grasslands
46 (Poschlod and WallisDeVries 2002). These natural and semi-natural grasslands often harbor
47 a high number of invertebrate species including several threatened, rare and endemic species
48 (WallisDeVries et al. 2002; Kotze and O'Hara 2003; Woodcock et al. 2005).

49 During the last decades the increase of agricultural management has resulted in a
50 significant decrease and degradation of the sandy grasslands. Therefore, this grassland type
51 is the most threatened ecosystem in Central Europe (Eichberg et al. 2007). Agricultural
52 intensification caused a decrease in biomass production and vegetation coverage, whereas
53 it increased the areas covered by bare sand. Nowadays the development of sustainable
54 agriculture can help the conservation of sandy grassland ecosystem (Xu et al. 2001).

55 Spiders are diverse and abundant predatory animal group of grasslands. They have been
56 studied in various grassland types: sand dunes (Bonte et al. 2002), limestone grasslands
57 (Rushton 1988) and moorlands (Cameron et al. 2004). However, spider assemblages of dry
58 sandy grasslands were investigated rarely (but see Szinetár et al. 2005; Horváth et al. 2009;
59 Buchholz 2010). Spider assemblages are important in natural and agricultural ecosystems
60 by shaping the structure of arthropod communities due to the fact as that they are generalist
61 predators and they provide biological pest control (Marc et al. 1999; Sunderland and Samu
62 2000). In general, they are useful taxa to understand the effects of land use changes,
63 because they have short life cycles, high abundances, their ecology and systematics are
64 well known and they are sensitive to environmental changes and fragmentation (Miyashita
65 et al. 1998; Marc et al. 1999).

66 The classical theory of island biogeography explains patterns of both animal and plant
67 species composition on real islands (MacArthur and Wilson 1967). This theory emphasizes
68 the importance of the size and isolation as the two major factors determining the species
69 richness of islands. This assumption predicts that there are more species on large islands
70 than on small ones, because large islands have larger populations, therefore the extinction
71 rates are lower on these islands. Isolated islands have fewer species than islands with close



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vicinity to other islands or mainland, because they have lower immigration rates; therefore the colonization of these islands is more difficult. Although this theory originally used to explain variation in diversity on real islands, it has later been applied to inland habitat islands. Recently, more authors refined the original hypothesis of the classical island biogeography theory as the surrounding habitats (edge and matrix) could have important effects on the species richness (Lövei et al. 2006; Devictor and Jiguet 2007; Magura and Ködöböcz 2007).

The habitat diversity is also an important factor for species richness especially at local scales (Davidowitz and Rosenzweig 1998). Large areas usually have more habitats; therefore in these areas there may be more species than in the smaller ones, which have less different habitat types (Davidowitz and Rosenzweig 1998; Ricklefs and Lovette 1999). Of the approximately same sized habitats, the more heterogeneous can maintain assemblages with higher species richness and a greater number of individuals than those which are more homogeneous (MacDonald and Johnson 1995). Nevertheless there are such smaller, spatially heterogeneous habitats, which also contain species rich assemblages (Martin et al. 2012).

Species with different habitat affinity (generalist and specialist) respond variously to the habitat size (Zabel and Tschartke 1998; Bonte et al. 2002), isolation (Magura et al. 2001; Jonsson et al. 2009) and habitat diversity (Ricklefs and Lovette 1999; Kruess and Tschartke 2002). Therefore, it is important to investigate the groups of species with different habitat affinity separately. Besides overall species richness we also analyzed the number of generalist and specialist species. In this study those species which occurred in high number in most grassland types were categorized as generalists, and those open habitat species which were associated with sandy soils were regarded as specialists (Buchar and Ruzicka 2002).

In our study, spider assemblages in dry sandy grassland fragments were investigated in Eastern Hungary (Nyírség) to study the relationship between fragment size, isolation and habitat diversity and the species richness of spider assemblages. Our hypotheses were as follows: (i) The fragment size and isolation should affect the opposite way the habitat specialist species richness and the generalist species richness. We expect that the increase of habitat size and decrease of isolation increases the habitat specialist species richness, while the generalist species richness should increase with the decrease of habitat size and increase of isolation. (ii) More isolated grassland fragments should increase the species richness, as the generalist species can enter from the surrounding habitats. (iii) Furthermore, increasing habitat diversity within habitat fragments should be more favorable for generalist species than sandy grassland specialist species, because generalist species can settle down permanently in more habitat types.

Materials and methods

Study area

Eight dry sandy grassland fragments were selected for the investigation of ground-dwelling spider assemblages, located in the Nyírség region of the Great Hungarian Plain (Eastern Hungary) (Table 1; Electronic Supplementary Material (ESM) Map 1). The sampling sites were selected in the way that every sampling site has the same vegetation type, the same intensity of management (moderate grazing) and these are embedded in the same matrix. These criteria were assured for eight fragments. In the 19th century the natural habitat



Table 1 Habitat characteristics of the eight studied dry sandy grassland fragments in Nyírség

Site name	Size (ha)	Inverse isolation index (ha)	Habitat diversity (Shannon index)
1. Bagamér	99.0	121.5	0.40589
2. Bátorliget	249.7	122.1	0.22711
3. Hajdúbagos	250.6	58.3	0.40917
4. Martinka	353.5	137.6	0.48714
5. Nyíregyháza	188.7	130.5	0.07685
6. Nyírtura	29.1	1.6	0.24182
7. Rohod	51.8	7.3	0.28886
8. Újtanya	2.3	137.3	0.16139

117 types in this region were dry habitats (sandy grasslands and sandy oak woods) and wet-
118 lands (marshes, fen meadows and mires). Due to increasing agricultural intensification
119 since the mid 20th century these habitats have disappeared or have become highly frag-
120 mented. In present days, these fragmented dry sandy grassland fragments are encompassed
121 by arable lands and non-native tree plantations. In all dry sandy grassland fragments, the
122 typical grassland vegetation was *Cynodonti-Festucetum pseudovinae* (Török et al. 2008).
123 These fragments have been lightly or moderately grazed by cattle and sheep. All of the
124 studied fragments were surrounded by both arable lands (maize and corn) and non-native
125 tree plantations (black locust and ennobled poplar species). Thus, the matrix habitats were
126 similar to all the investigated fragments. The shortest distance between the studied
127 grassland fragments was 2 km, while the distance of the two furthest fragments was 75 km.

128 Sampling design

129 Spiders were collected using pitfall traps during the 9-year investigating period
130 (2001–2009). There were 10 randomly placed traps in all studied fragments. Each trap was
131 at least 50 m from the grassland edges, in order to avoid edge effects (Horváth et al. 2002).
132 Traps consisted of 100 mm diameter plastic cups and contained about 200 ml 70 % eth-
133 ylene glycol as a killing-preserving solution. Pitfall traps were protected by fiberboard
134 from litter and rain. Spider species were collected every 2nd week from the end of March
135 to the end of October. Spiders were identified to species level using standard keys (Heimer
136 and Nentwig 1991; Roberts 1995). Nomenclature follows Platnick (2012).

137 Data analyses

138 The size of the investigated dry sandy grasslands was measured using the ArcGIS program
139 on a digitized 1:25000 map. Isolation of a habitat island (grassland fragment in our case) is
140 often measured as the distance to the nearest fragment, although isolation also depends on
141 the size of the nearest fragment. Isolation of the grassland fragments was measured by the
142 inverse isolation index, defined as the total dry sandy grassland size within a radius of
143 1,000 m around the investigated grassland fragment. Its value decreases as the isolation of
144 the grassland increases (Magura et al. 2001). The radius was selected 1,000 m, because
145 spiders can cover this distance easily with their silk (Foelix 2011). Identification of dif-
146 ferent vegetation patches was based on aerial photographs (see Map 1 in ESM). Based on
147 this map we expressed the habitat diversity with Shannon index of diversity.



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148 The relationships between the habitat characteristics (size, isolation and habitat diver-
149 sity) and the species richness of spider assemblages were examined by multiple linear
150 regression analyses (Kutner et al. 2005). We analyzed the 9 years average value of each
151 trap, weighted with the standard error (SE), depending on fragment size, isolation and
152 habitat diversity. The total number of species, the ratio of generalist species and the ratio of
153 sandy grassland specialist species were analyzed. Before the statistical analyses the given
154 traps catches were pooled from the nine trapping years. The distribution of data used in the
155 multiple linear regression analyses was normal (tested by the Kolmogorov–Smirnov test,
156 Sokal and Rohlf 1995). Residuals are examined visually for normality; the distribution of
157 residuals was normal (Kéry and Hatfield 2003).

158 Results

159 During the 9-year study period, 10,544 spider specimens belonging to 106 species were
160 collected from the eight dry sandy grassland fragments (Electronic supplementary material
161 (ESM) Table 1). Twenty-one species (about 20 % of the collected species) were identified
162 as sandy grassland specialist species.

163 Multiple linear regression analysis pointed out that only the size of the grassland
164 fragments had an influence on the overall species richness. The total number of spider
165 species and the size of the dry sandy grassland showed a significant negative relationship
166 (Fig. 1a; Table 2). There was no statistically significant relationship between the overall
167 species richness and the inverse isolation index of grassland fragments (Fig. 1b; Table 2).
168 The ratio of generalist species decreased with the increasing of fragment size, but this
169 relationship was not significant (Fig. 1c, Table 2), while their ratio significantly increased
170 with the decreasing of inverse isolation index (Fig. 1d; Table 2). A significant positive
171 relationship was found between the ratio of open-habitat species associated with sandy
172 soils to the total number of species and the size of grasslands (Fig. 1e; Table 2), showing
173 the importance of habitat specialist spiders with increasing fragment size. The ratio of
174 habitat specialist species and the inverse isolation index of the fragments also showed a
175 significant positive relationship (Fig. 1f; Table 2). There was no significant importance of
176 the habitat diversity on any of the dependent variables (Table 2).

177 Discussion

178 Effect of fragment size

179 The results of several authors corroborated the theory of island biogeography as they
180 pointed out a significant positive correlation between the overall species richness and the
181 size of habitat islands (Toft and Schoener 1983; Webb and Hopkins 1984; Ricklefs and
182 Lovette 1999; Tscharnke et al. 2002; Watson et al. 2005). In other studies the number of
183 all animal species did not depend on the size of the habitat (Dauber et al. 2006; Kapoor
184 2008; Kappes et al. 2009; Muriel and Kattan 2009). Our results contrary to the classical
185 theory of island biogeography showed that there was significant negative relationship
186 between the size of the grassland fragments and the total number of spider species.
187 Similarly to our results other investigations in which ground beetles (Webb and Hopkins
188 1984; Bauer 1989; Halme and Niemelä 1993; Magura et al. 2001; Jonsson et al. 2009) and
189 spiders (Jonsson et al. 2009; Bailey et al. 2010) were studied showed that contrary to the

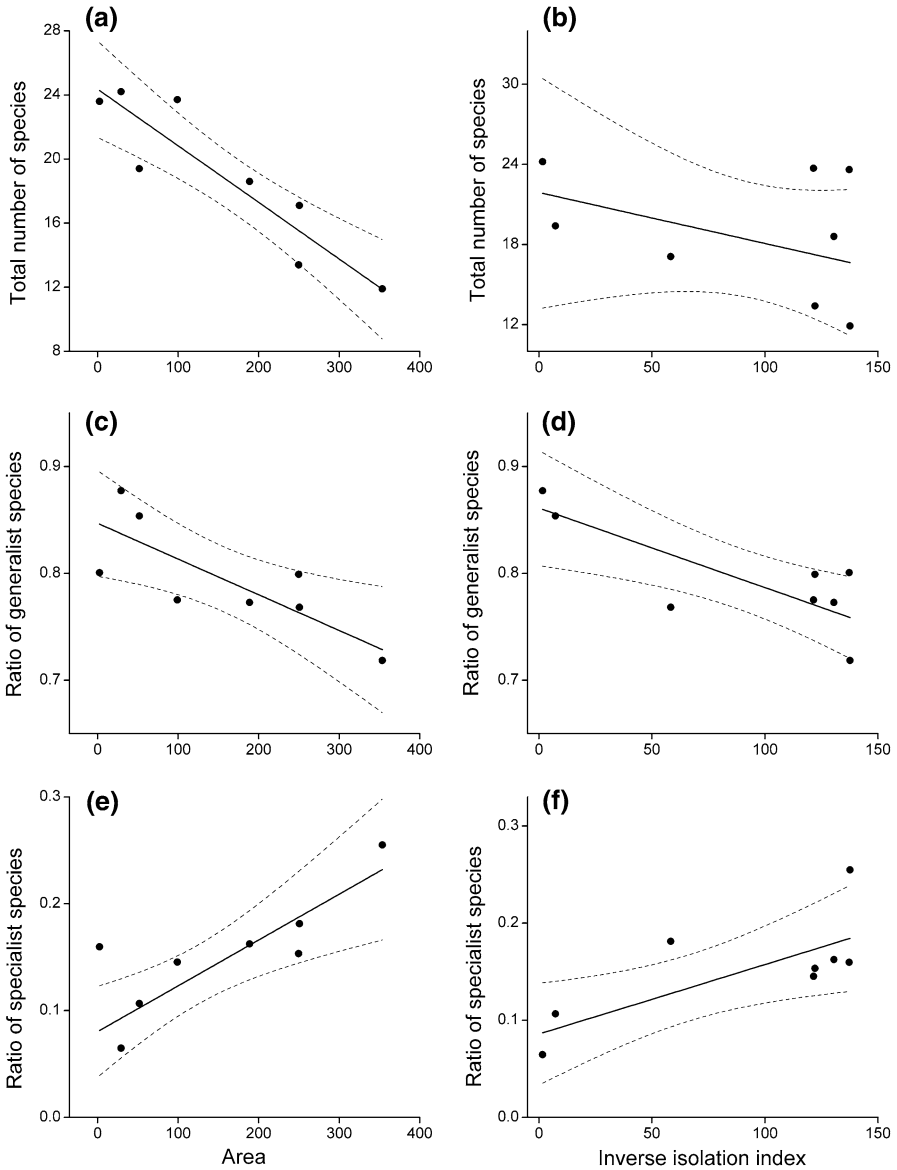


Fig. 1 Relationship between the size of dry sandy grassland fragments and the total number of spider species (a), the ratio of generalist species (c), the ratio of sandy grassland specialist species (e) and relationship between inverse isolation index and the total number of spider species (b), ratio of generalist species (d), ratio of sandy grassland specialist species (f). Dashed lines represent the confidence bands (95 %)

190 classical theory of island biogeography there was significant negative relationship between
191 the size of the fragments and the total number of species. In all of the papers that investi-
192 gated only the habitat specialist species they found that this relationship was significantly
193 positive with the size of the habitat similarly to our results (Zabel and Tschardtke 1998;



Table 2 Relationship between the spider species and the studied habitat characteristics, determined by multiple linear regression

	Overall species richness	Ratio of generalist species	Ratio of sandy grassland specialist species
	$F_{(3,7)} = 10.332$ $p = 0.024$ $r = 0.941$	$F_{(3,7)} = 18.329$ $p = 0.008$ $r = 0.966$	$F_{(3,7)} = 11.818$ $p = 0.019$ $r = 0.948$
Size of the grassland fragments	–*	ns	+*
Inverse isolation index	ns	–*	+*
Habitat diversity calculated by Shannon index	ns	ns	ns

* Significant positive or negative relationships are indicated: $p < 0.05$

194 Bonte et al. 2002; Sanchez and Parmenter 2002; Scott et al. 2006; Mohd-Azlan and Lawes
 195 2011).

196 Real islands differ significantly from habitat islands. The surrounding habitats around
 197 real islands are usually rigorous to both plant and animal species; therefore species can
 198 penetrate with a low chance on real islands. Contrarily terrestrial habitat islands are sur-
 199 rounded by a wide range of matrix habitats which are less unfavorable for species. Since
 200 both the habitat specialist and generalist species are alike revealing for the inland habitat
 201 islands, the observed species-area relationship may be positive, negative or neutral
 202 depending on the ratio of habitat specialist and non-habitat specialist species. These results
 203 reveal the refinement necessity of the original hypothesis. When we would like to apply
 204 this prediction to mainland habitat islands, we have to separate specialist and non-habitat
 205 specialist species. The specialist species perceive the habitat fragments as islands (they can
 206 survive and reproduce only in these fragments), while the non-habitat specialist species
 207 occur in large numbers both in the habitat fragments and the adjacent habitats (Magura
 208 et al. 2001; Bonte et al. 2002; Cook et al. 2002; Mohd-Azlan and Lawes 2011).

209 Effect of habitat isolation

210 The isolation of the habitat island may also be very important in the occurrence of the
 211 habitat specialist and the non-habitat specialist species (Magura et al. 2001; Jonsson et al.
 212 2009). However, there were investigations when the species number did not depend on the
 213 habitat isolation (Webb and Hopkins 1984; Jonsson et al. 2009) or the relationship was
 214 negative (Toft and Schoener 1983; Usher et al. 1993; Miyashita et al. 1998; Bailey et al.
 215 2010). We found positive correlation between the total number of species, the ratio of
 216 generalist species and the isolation of the habitat fragments, but it was not significant in
 217 case of total species pool. The reason for this is that the adjacent habitats around grassland
 218 fragments may be the source of the generalist species; therefore, these spiders can spread
 219 from the agricultural areas to the dry sandy grassland fragments (spill-over effect, see
 220 Tscharrntke et al. 2012).

221 The sandy grassland specialist species richness showed a negative significant relation-
 222 ship with isolation in most studies (Magura et al. 2001; Watson et al. 2005; van
 223 Noordwijk et al. 2012), but neutral relationship was also reported (Sanchez and Parmenter
 224 2002; Cardoso et al. 2010). In our study there was a significant positive relationship
 225 between the number of sandy grassland specialist species and the inverse isolation index.
 226 This result showed that due to habitat fragmentation, the increased isolation between the



227 grassland fragments significantly decreased the number of these species. Therefore, the
228 isolation of grassland fragments had more important effect on sandy grassland specialist
229 species, than on generalist species, especially as the ratio of generalist species increased,
230 while the ratio of sandy grassland specialist species decreased with the increase of isolation.
231 Although spiders have a good spreading ability, it is likely that habitat specialist
232 species could not persist in the neighboring arable lands and non-native tree plantations
233 permanently, because these habitats were hostile for them. These unfavorable habitat types
234 acted as barriers for sandy grassland specialist species, thus their proportion decreased in
235 the more isolated fragments. Furthermore, if a sandy grassland specialist species disappears
236 from a given grassland fragment, this species can not recolonize the grassland fragment
237 because it is isolated.

238 The impact of habitat diversity

239 Usually larger habitat diversity increases the number of species in a given area (Ricklefs
240 and Lovette 1999; Weibull et al. 2000; Kruess and Tschardtke 2002), but in some cases,
241 the relationship between habitat diversity and the species richness is not significant
242 (Ricklefs and Lovette 1999; Kruess and Tschardtke 2002). In contrast to our hypothesis the
243 habitat diversity of the grassland fragments did not have any significant effect on the ratio
244 of generalist species, either overall species richness, or the ratio of sandy grassland specialist
245 species. Since there were various adjacent habitats around dry sandy grassland
246 fragments (wetlands, wet grasslands, arable lands, tree plantations and other dry sandy
247 grasslands), the generalist species found suitable circumstances and they could also settle
248 down permanently in these habitats in large numbers. Therefore, the increasing habitat
249 diversity within grassland patches did not influence the generalist species number. Our
250 result suggest, that the size and the isolation of the dry sandy grassland fragments were
251 more important for sandy grassland specialist spiders than the habitat diversity, because the
252 species number was significantly influenced only the size and isolation of fragments, while
253 the habitat heterogeneity did not affect the number of species of these spiders. Furthermore,
254 the distribution of the habitat specialist species also depends strongly on the vegetation
255 type, the structural heterogeneity of the vegetation and the special microclimate
256 conditions in a given habitat (Foelix 2011).

257 Habitat specialist and non-habitat specialist species

258 We pointed out that overall species richness and ratio of generalist species increased with
259 the decreasing size of grassland fragments and the increasing of grassland isolation. Sandy
260 grassland specialist species played a more important role in the assemblage when the size
261 of the habitat fragments increased. We can explain this fact with the following two reasons:
262 (i) generalist species can enter in higher numbers to the more isolated grassland fragments,
263 because the proportion of their source habitats (especially arable lands) is higher around
264 these fragments; (ii) sandy grassland specialist species need a minimum size of their
265 habitat, therefore they occur in higher numbers only in bigger grassland fragments; furthermore
266 they can not immigrate to more isolated fragments, because the environmental
267 factors of the adjacent habitats are hostile for them.

268 Hermann et al. (2010) pointed out that habitat fragmentation and immigration of
269 generalist species from adjacent habitats caused a significant loss of habitat specialist
270 species richness, at the same time these spiders increased the total species richness.
271 Furthermore, strongly isolated fragments were more favorable for the majority of



272 generalist species because they occurred in greater number in these fragments than in the
273 less isolated fragments. There are several publications in which spiders in different
274 grassland types were studied and stressed that landscape features (habitat connectivity,
275 structural heterogeneity, landscape structure) also played a very important role in species
276 composition and abundance (Bonte et al. 2002; Finch et al. 2008). The habitat specialist
277 species demand larger structural heterogeneity and special environmental conditions;
278 therefore they need to have a minimum area size, where the necessary factors are at their
279 disposal (Bonte et al. 2002; Scott et al. 2006) to have a viable population size (Bonte
280 et al. 2002). Moreover, Bailey et al. (2010) showed that source-sink dynamic and trophic
281 interactions may decrease the spider species richness, which correlates with increased
282 area size. Sink populations are preserved by immigrant species, but the number of these
283 species decrease with fragment size. Besides, the important spider predators (birds and
284 wasps) may be present in smaller numbers in small fragments than their preys, therefore
285 spiders could benefit from lower predation risk in smaller fragments (Bailey et al. 2010).
286 The habitat size and the isolation also influences the extinction rate of spider species,
287 because this rate is positively related to isolation and negatively to habitat size (Toft and
288 Schoener 1983).

289 Conclusions

290 The once continuous grasslands became the most threatened habitat types in Europe by the
291 increase of intensity of agricultural practices. Some of the grasslands disappeared, while
292 the other parts of grasslands have become fragmented and reduced their size dramatically.
293 These processes jeopardize the survival of most habitat specialist and rare animal and plant
294 species. Therefore, nowadays there is a growing demand for the conservation of the
295 different grassland types. The main goal is to preserve the larger continuous natural
296 grasslands and to restore the remnant areas of natural and semi natural grasslands, because
297 these remaining fragments can also maintain a diverse fauna. Our results showed that only
298 small and highly isolated fragments can preserve a species rich spider assemblage in the
299 Nyírség region due to the large number of generalist species. In contrast, the habitat
300 specialist species characteristic to dry sandy grasslands occurred in higher number only in
301 the large and less isolated fragments as they can not survive in the adjacent arable lands
302 and they need to have a minimum size of the fragment. Based on our results for the
303 conservation of spider species, we recommend the following measures during a nature
304 conservation program. First as habitat specialist spider species are also present in the small
305 grassland fragments, thus these fragments should be retained to serve as source habitats.
306 Second, since the fragmentation and isolation decrease the number of habitat specialist
307 species in the dry sandy grassland patches, therefore the further fragmentation has to be
308 stopped. Third, there is a need to increase the size of these fragments with the restoration of
309 grassland on the adjacent croplands that may contribute to the conservation of the sandy
310 grassland specialist species.

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