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# Secondary habitats are important in biodiversity conservation: a case study on orthopterans along ditch banks

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**Abstract**

*Secondary habitats are important in biodiversity conservation: a case study on orthopterans along ditch banks.* It has been shown that native biota can survive in secondary habitats such as road verges, dikes and hedges. We aimed to assess the conservation value of ditch banks for orthopterans in an agricultural landscape in Hungary, based on the analyses of species richness and abundance data using mixed–models. We did not find any differences in the species richness between isolated ditch banks, semi–isolated ditch banks and control meadows. The extent of isolation had a significantly negative effect, however, on the abundance of sedentary species. We found that the density of woody vegetation along ditch banks had a negative effect on the total abundance and the abundance of mobile species. Positive relationships were found between the width of ditch bank vegetation and the abundance of Caelifera, mobile, xerophilous and mesophilous species. Our results suggest that the density of orthopterans may be a more sensitive measure for habitat quality than their species richness. We concluded that ditch banks are a suitable habitat for the majority of orthopterans, including rare and endangered species, emphasizing that ditch banks and similar linear habitats should receive more attention and should be given a more prominent role in invertebrate conservation.

Key words: Invertebrate diversity, Species traits, Linear habitat, Agricultural landscape

**Resumen**

*Los hábitats secundarios son importantes en la conservación de la biodiversidad: un estudio práctico sobre los ortópteros en orillas de acequias*. Se ha demostrado que la biota autóctona puede sobrevivir en hábitats secundarios como cunetas, diques y setos. La finalidad de este estudio es evaluar el valor de las orillas de acequias para la conservación de los ortópteros en un paisaje agrícola en Hungría, a partir del análisis de los datos relativos a la riqueza y la abundancia de especies utilizando modelos mixtos. No encontramos ninguna diferencia en cuanto a la riqueza de especies entre las orillas de acequias aisladas, semiaisladas y en praderas de control. Sin embargo, el grado de aislamiento tuvo un efecto negativo significativo en la abundancia de especies sedentarias. Constatamos que la densidad de vegetación leñosa junto a las orillas de las acequias tenía un efecto negativo en la abundancia total y la abundancia de especies móviles. Se observó la existencia de una relación positiva entre la anchura de las orillas de acequias que estaba cubierta por vegetación y la abundancia de especies del suborden Caelifera y de especies móviles, xerófilas y mesófilas. Nuestros resultados sugieren que la densidad de ortópteros puede ser una medida más sensible de la calidad del hábitat que la riqueza de especies. Concluimos que las orillas de las acequias son un hábitat adecuado para la mayoría de ortópteros, incluidas las especies raras o en peligro de extinción, lo que pone de relieve que debería prestarse más atención a estos y otros hábitats lineales parecidos y que se les debería dar más importancia en la conservación de invertebrados.

Palabras clave: Diversidad de invertebrados, Características de las especies, Hábitat lineal, Paisaje agrícola

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## Introduction

Natural and semi–natural grasslands in Europe still contain a diverse fauna and flora, but recent studies (e.g. Hernández–Manrique et al., 2012; Torma and Bozsó, 2016) conclude that existing conservation strategies based mainly on the protection of areas of high natural value may be insufficient to ensure conservation of the invertebrate species pool at landscape scale. Conservation of the invertebrate diversity thus needs a landscape perspective. In Europe, habitat destruction and deterioration caused by the intensification of agriculture and the change in landscape patterns such as increasing fragmentation and isolation of habitats have been shown to result in a decline of biodiversity (Kruess and Tscharntke, 1994; Stoate et al., 2001; Jongman, 2002). As conservation strategies, agri–environmental schemes aim to reduce the impact of agricultural activities on species that inhabit the agricultural landscape. However, these programs have only a limited effect on European agriculture due to land–owners' reluctance to participate (Espinosa–Goded et al., 2010), and their efficiency in biodiversity conservation is under debate. Tscharntke et al. (2005) suggested that agri–environmental programs may be effective in simple, but not in complex landscapes where a biodiversity is already likely to be higher. In contrast, Duelli and Obrist (2003) highlighted that these programs have a major chance of success in complex landscapes where arthropods can also survive in nearby habitats. To avoid a decrease in the diversity of arthropods and thus, in the ecosystem services and functions provided by them, we urgently need to seek possibilities for proper conservation strategies adapted to the regional landscape features and history (Tscharntke et al., 2005; Batáry et al., 2015).

Many recent studies have highlighted the importance of linear secondary habitats such as road verges (e.g. Saarinen et al., 2005; Söderström and Hedblom, 2007), dikes (e.g. Torma and Császár, 2013; Bátori et al., 2016), and hedges (e.g. Ernoult et al., 2013; Morandin and Kremen, 2013) in biodiversity conservation. It has been shown that native biota can survive in these habitats. Such anthropogenic habitats often have a long history, facilitating development of species–rich habitats (Musters et al., 2009), and they may provide resources for populations of rare and endangered species (Torma and Bozsó, 2016). In contrast, newly established sawn grass strips and abandoned field margins are comparatively species poor and are beneficial particularly for common species (Musters et al., 2009; Ernoult et al., 2013). If they remain intact for the long term, it is possible they will develop to a species rich secondary habitat, similarly to road verges, dikes, etc.

The goal of our study was to assess the ecological value of ditch banks as secondary habitats for invertebrate conservation in an agricultural landscape. While the remaining natural and semi–natural habitats within arable fields are generally regarded as crucial for wildlife, the value of ditch banks for providing habitats and refugia remains an open question (Herzon and Helenius, 2008; Musters et al., 2009). We studied species richness and abundance of orthopterans at ditch banks in the Tisza–Maros angle in the southern part of the Great Hungarian Plain. We chose to study orthopterans because they are among the most important consumers and abundant prey sources for many vertebrates (Rodríguez and Bustamante, 2008; Kiss et al., 2014), and their diversity is currently declining in many temperate regions (Berg and Zuna–Kratky, 1997; Maas et al., 2002; Reinhardt et al., 2005; Krištin et al., 2007; Holuša et al., 2012). The sensitivity of species to environmental conditions is a function of their ecological and life history traits. In the present study, we considered dispersal ability, habitat affinity and reproduction strategy traits because they are hypothesized to be key determinants of species persistence (Kotiaho et al., 2005). The dispersal ability and habitat affinity of species highly influences their responses to landscape features (Joern and Laws, 2013). Sedentary species are generally more affected by fragmentation and isolation of habitats than mobile species that can (re)colonize relatively distant habitat patches (e.g. Marini et al., 2010, 2012). Similarly, generalist species are more likely to find suitable habitat patches in a fragmented landscape than specialist species (e.g. Collinge, 2000). Besides the number of offspring, reproduction strategy can influence species persistence in various manners. For instance, Ensifera species usually produce larger eggs then Caelifera, and lay those individually in plants or under tree bark, and this can increase, for example, the chance of hydrochory (Dziock et al., 2011). We also focused on immature orthopterans as they are usually sedentary and a large number of immature specimens indicates reproductive sites.

We addressed the following questions: (1) are there significant differences between isolated ditch banks, semi–isolated ditch banks and control meadows in species richness and abundance of orthopterans? (2) are there significant relationships between the width of ditch bank vegetation and Orthopteran species richness and abundance? and (3) do the presence and density of woody vegetation along ditch banks influence species richness and abundance of orthopterans?

## Material and methods

### Study region

The study was carried out in an approximately 150 km$^2$ area close to the confluence of the Maros and Tisza rivers in Csongrád County, Hungary (fig. 1). As a part of the Great Hungarian Plane, the area is characterized by dry continental climatic conditions. The annual mean temperature is 10.5–10.6 °C and the average annual rainfall is 570 mm. Before the rivers were regulated, the area was frequently flooded and characterized by wet grasslands (Bátori et al., 2016). After river regulation and drainage works, which were typical in the 19th and 20th centuries, the lowered water levels and desiccation of habitats induced secondary salt accumulation in higher soil layers, especially in former wet, non–alkali meadows (Molnár and Borhidi, 2003). Although most grasslands

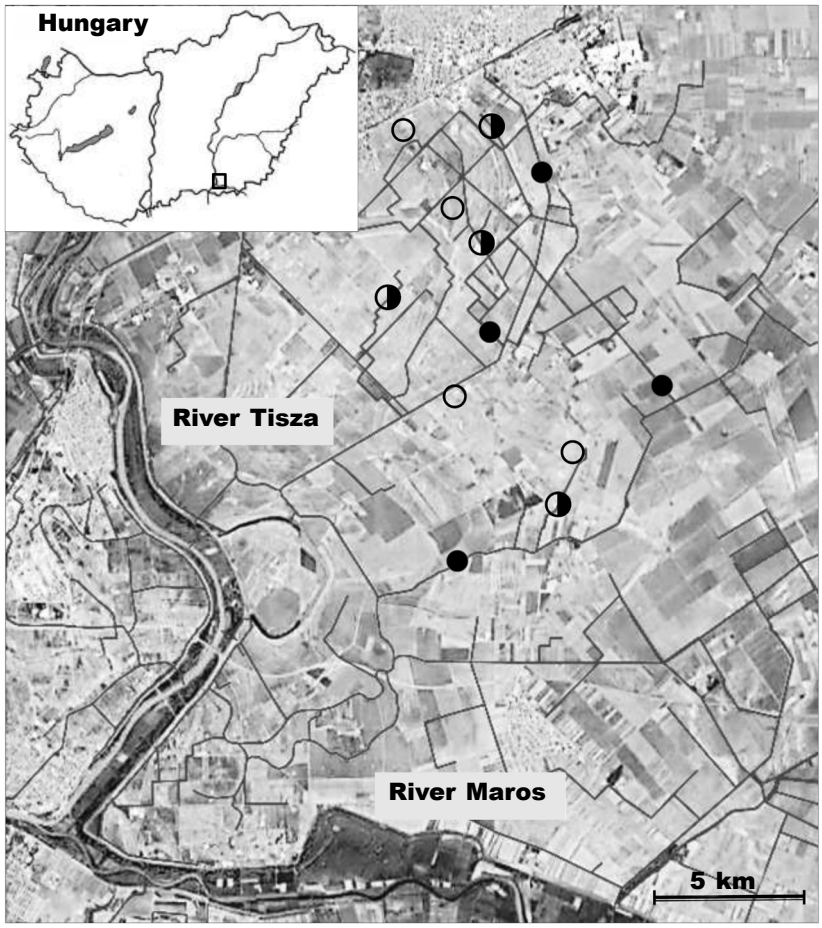


Fig. 1. On the schematic map of Hungary (upper left corner), the empty square represents the locality of the study area. The satellite imagines show the study area with the drainage system and the localities of sampling sites. Black circles and half–black circles represent isolated ditch bank sections and connected ditch bank sections, respectively. Empty circles represent control meadows.

*Fig. 1. En el mapa esquemático de Hungría (esquina superior izquierda), el cuadrado vacío representa la localidad de la zona de estudio. La imagen por satélite muestra la zona de estudio con el sistema de drenaje y la ubicación de los sitios de muestreo. Los círculos negros y los que tienen una mitad de color negro representan las secciones de orillas de acequias aisladas y conectadas, respectivamente. Los círculos vacíos representan las praderas de control.*

were transformed into arable fields, alkaline grassland patches were not cultivated because their poor soil quality was unsuitable for intensive agriculture and forestry (Bátori et al., 2016). Currently, the area is dominated by arable fields with a considerable drainage system that encloses the grassland remnants.

Sampling design

We applied a nested balanced design. Five sites were sampled within each c.a. 500 m long selected section of ditches and within each control meadow. Sections of ditches were selected according to isolation treatment i.e., isolated or semi–isolated. Sections of ditches were considered isolated when running through arable fields with no meadows in their surroundings, such as in a buffer of 1,000 m radius. Sections connected with meadows were considered as semi–isolated sections. For controls, we chose meadows because they are presumably the preferred habitats for orthopterans in the landscape. Arable fields were not targeted in the present study because they generally provide a poor habitat for most orthopterans (e.g. Marshall et al., 2006). Four replicates were selected for each treatment and control, and they were located at least two kilometers apart from each other. Minimal distance between sites within each section and within control meadows was 100 m. Orthopterans were sampled by

sweep netting. In each site 50 sweeps were performed four times (25 VI, 28 VII, 29 VIII and 27 IX) in 2012. Since our focus was not on the seasonal dynamics of the orthopterans, species–abundance data matrix were pooled according to sampling periods. At each site, the width of the strip–like vegetation was measured, and the density of woody vegetation was assessed by visual observation. We used three categories: absent (no woody vegetation), present (a single tree or one–two single bushes), dense (more than one tree and/or more than three bushes).

Species traits

Based on the mobility index as a measure of dispersal ability (Reinhardt et al., 2005), two mobility classes (sedentary and mobile species) were analyzed (Marini et al., 2012).

The specific preferences for humidity were used to group them in relation to their habitat specialization, and they were sorted into xerophilous, mesophilous and hygrophilous species groups (cf. Fartmann et al., 2012).

We distinguished Ensifera and Caelifera groups to represent the differences between them e.g. in reproductive potential and egg deposition of females (Torma and Bozsó, 2016). Based on the mean number of ovarioles (Reinhardt et al., 2005), Ensifera species are usually considered to have a high reproductive potential compared to Caelifera.

Statistical analyses

According to the nested design, generalized linear mixed models (GLMM, Poisson and negative binomial errors, maximum likelihood fit) were applied and the effect of sites nested within sections was used as random effect. First, we analyzed the species richness and abundance of orthopterans in relation to the treatment, that is, isolated, connected and control. Pairwise comparisons were carried out with the help of 'relevel' function and Bonferroni corrections were applied. In a second set of models, we analyzed the species richness and abundance data in relation to the width of ditch bank vegetation and the density of woody vegetation along ditch banks.

Since hygrophilous species were represented by very restricted numbers of species and individuals, we analyzed their presence / absence using a binomial model.

All statistical analyses were carried out in an R Statistical Environment (R Core Team, 2013), using lme4 package (Bates et al., 2013).

## Results

Altogether, we collected 4,212 and 940 adult individuals of 17 Caelifera and 13 Ensifera species, respectively (table 1). Immature specimens of Acrididae were also collected in a high number (table 1). Therefore, their abundance was only considered in the analyses. According to the mobility of species, 18 mobile and nine sedentary species were distinguished; 19 and nine species were sorted into the categories of xerophilous and mesophilous species, respectively; however only two hygrophilous species were collected. The most abundant species were *Euchorthippus declivus* (Brisout de Barneville, 1849) (with a frequency of 29.3 %), *Omocestus haemorrhoidalis* (Charpentier, 1825) (16.5 %), *Chorthippus brunneus* (Thunberg, 1815) (10.6 %) and *Oecanthus pellucens* (Scopoli, 1763) (10.2 %). Species with a high natural value were also collected. However, *Gampsocleis glabra* (Herbst, 1786) and *Modicogryllus frontalis* (Fieber 1844), for example, were represented by only one specimen. *Epacromius coerulipes* (Ivanov, 1887) was collected in only one ditch bank section beside control meadows, whereas e.g. *Ruspolia nitidula* (Scopoli, 1786) was collected only along ditch banks. *Acrida ungarica* Herbst 1786 and *Tessellana veyseli* (Koçak, 1984) were collected in almost all sites.

Species richness and abundance pattern of Orthoptera assemblages

The results of GLMM did not show any significant differences in the species richness of orthopterans between isolated ditch banks, semi–isolated ditch banks and control meadows; nearly significant differences were found in the species richness of mobile and mesophilous species between control meadows and isolated ditch banks (table 2). The extent of isolation had a significant effect on the abundance of sedentary species (table 2). The highest and lowest abundances of sedentary species were found in control meadows and isolated ditch banks, respectively (fig. 2). No other significant differences in the abundance of orthopterans were found between isolated ditch banks, semi–isolated ditch banks and control meadows. We analyzed the presence / absence of hygrophilous species using a binomial model and we did not find any significant effects (control vs. connected: $z = 1.135$, $p = 0.257$; control vs. isolated: $z = 0.624$, $p = 0.532$; isolated vs. connected: $z = 0.550$, $p = 0.582$).

Neither the width of ditch bank vegetation nor the density of woody vegetation had any significant effects on the species richness of orthopterans, but both had effects on their abundance pattern according to the results of the GLMM (table 3). Presence of dense woody vegetation had a significant negative effect on the total number of individuals and the number of mobile individuals (fig. 3), and had a marginally significant negative effect on the abundance of Caelifera and xerophilous species. Significant positive relationships were found between the width of ditch bank vegetation and the abundance of Caelifera, mobile, xerophilous and mesophilous species (fig. 4). We also found a marginally significant effect of the width of ditch bank vegetation on the total individual number of orthopterans. We did not find any significant effects of ditch bank vegetation on the presence /absence of hygrophilous species (width of vegetation: $z = –0.423$, $p = 0.679$; woody vegetation: $z = –0.064$, $p = 0.949$; dense woody vegetation: $z = 0.045$, $p = 0.964$).

Table 1. Collected species of Orthoptera: Trait 1, mobility (Mob, mobile; Int, intermediate; Sed, sedentary); Trait 2, humidity preference (Xero, xerophilous; Mezo, mesophilous; Hygro, hygrophilous); Crl, control meadows; Con, connected ditch banks; Iso, isolated ditch banks.

*Tabla 1. Especies de ortópteros recogidas: Trait 1, movilidad (Mob, móvil; Int, intermedia; Sed, sedentaria); Trait 2, preferencia por la humedad (Xero, xerófilas; Mezo, mesófilas; Higro, higrófilas); Crl, praderas de control; Con, orillas de acequias conectadas; Iso, orillas de acequias aisladas.*

| Taxa | Trait 1 | Trait 2 | Crl | Con | Iso | Total |
|---|---|---|---|---|---|---|
| Ensifera | | | | | | |
| *Conocephalus discolor* Thunberg, 1815 | Mob | Hygro | 22 | 32 | 52 | 106 |
| *Gampsocleis glabra* (Herbst, 1786) | Sed | Xero | 1 | 0 | 0 | 1 |
| *Leptophyes albovittata* (Kollar, 1833) | Sed | Xero | 31 | 21 | 59 | 111 |
| *Leptophyes discoidalis* (Frivaldszky, 1868) | Sed | Mezo | 2 | 1 | 3 | 6 |
| *Metrioptera bicolor* (Philippi, 1830) | Mob | Xero | 18 | 3 | 10 | 31 |
| *Metrioptera roeselii* (Hagenbach, 1822) | Int | Mezo | 6 | 6 | 14 | 26 |
| *Oecanthus pellucens* (Scopoli, 1763) | Mob | Xero | 66 | 104 | 354 | 524 |
| *Phaneroptera nana* Fieber, 1853 | Mob | Xero | 0 | 2 | 9 | 11 |
| *Platycleis affinis* Fieber, 1853 | Int | Xero | 2 | 2 | 0 | 4 |
| *Platycleis grisea* (Fabricius, 1781) | Int | Xero | 1 | 0 | 0 | 1 |
| *Tessellana veyseli* (Koçak, 1984) | Sed | Xero | 61 | 22 | 29 | 112 |
| *Modicogryllus frontalis* (Fieber 1844) | Sed | Mezo | 0 | 1 | 0 | 1 |
| *Ruspolia nitidula* (Scopoli, 1786) | Mob | Hygro | 0 | 5 | 1 | 6 |
| Caelifera | | | | | | 0 |
| *Acrida ungarica* Herbst, 1786 | Mob | Xero | 44 | 18 | 2 | 64 |
| *Calliptamus barbarus* (Costa, 1836) | Mob | Xero | 0 | 0 | 2 | 2 |
| *Calliptamus italicus* (Linnaeus, 1758) | Mob | Xero | 0 | 2 | 4 | 6 |
| *Chorthippus oschei* Helversen, 1986 | Mob | Mezo | 64 | 10 | 5 | 79 |
| *Chorthippus dichrous* (Eversmann, 1859) | Mob | Mezo | 9 | 72 | 62 | 143 |
| *Chorthippus dorsatus* (Zetterstedt, 1821) | Mob | Mezo | 20 | 65 | 169 | 254 |
| *Chorthippus parallelus* (Zetterstedt, 1821) | Mob | Mezo | 35 | 20 | 56 | 111 |
| *Chorthippus brunneus* (Thunberg, 1815) | Mob | Xero | 197 | 137 | 216 | 550 |
| *Chorthippus mollis* (Charpentier, 1825) | Mob | Xero | 30 | 26 | 78 | 134 |
| *Chorthippus vagans* (Eversmann, 1848) | Sed | Xero | 1 | 1 | 1 | 3 |
| *Chorthippus biguttulus* (Linnaeus, 1758) | Mob | Xero | 1 | 1 | 0 | 2 |
| *Epacromius coerulipes* (Ivanov, 1887) | Mob | Xero | 4 | 0 | 4 | 8 |
| *Euchorthippus declivus* (Brisout de Barneville, 1849) | Mob | Xero | 621 | 646 | 247 | 1,514 |
| *Omocestus haemorrhoidalis* (Charpentier, 1825) | Sed | Mezo | 476 | 277 | 98 | 851 |
| *Omocestus petraeus* (Brisout de Barneville, 1855) | Sed | Xero | 5 | 1 | 0 | 6 |
| *Omocestus rufipes* (Zetterstedt, 1821) | Sed | Xero | 18 | 14 | 8 | 40 |
| *Pezotettix giornae* (Rossi, 1794) | Mob | Xero | 77 | 140 | 235 | 452 |
| Acrididae nymph | | | 694 | 485 | 504 | 1,683 |
| Catantopidae nymph | | | 5 | 21 | 13 | 39 |
| Conocephalidae nymph | | | 2 | 11 | 7 | 20 |
| Tettigonidae nymphs | | | 23 | 19 | 31 | 63 |

Table 2. The effects of the extent of isolation of ditch banks on species richness (left side) and abundance (right side) of orthopterans delineated by mixed models (GLMM). Poisson and negative binomial error terms were used to analyse species richness and abundance data, respectively. Pairwise comparisons were carried out with the help of the 'relevel' function in R, and Bonferroni corrections were applied: Crl, control meadows; Iso, isolated ditch banks; Con, connected ditch banks.

*Tabla 2. Los efectos del grado de aislamiento de las orillas de las acequias en la riqueza (izquierda) y la abundancia (derecha) de especies de ortópteros definidos por los modelos mixtos (GLMM). Se utilizaron los términos de error que siguen una distribución de Poisson y binomial negativa para analizar los datos relativos a la riqueza y la abundancia de especies, respectivamente. Se realizaron comparaciones por pares con la ayuda de la función de reordenación de niveles (relevel) en R y se aplicaron las correcciones de Bonferroni: Crl, praderas de control; Iso, orillas de acequias aisladas; Con, orillas de acequias conectadas.*

| | Treatment | Parameter estimation (± SE) | *z* | *p* | Parameter estimation (± SE) | *t* | *p* |
|---|---|---|---|---|---|---|---|
| Orthoptera | Crl vs. Con | 0.041 (0.095) | 0.430 | 0.669 | –0.128 (0.248) | –0.517 | 0.605 |
| | Crl vs. Iso | 0.125 (0.093) | 1.350 | 0.178 | –0.041 (0.247) | –0.166 | 0.868 |
| | Iso vs. Con | –0.085 (0.092) | –0.920 | 0.357 | –0.087 (0.248) | –0.351 | 0.726 |
| Caelifera | Crl vs. Con | 0.056 (0.118) | 0.475 | 0.635 | –0.189 (0.323) | –0.586 | 0.558 |
| | Crl vs. Iso | 0.142 (0.116) | 1.218 | 0.223 | –0.234 (0.323) | –0.725 | 0.468 |
| | Iso vs. Con | –0.085 (0.114) | –0.744 | 0.457 | 0.045 (0.323) | 0.139 | 0.889 |
| Ensifera | Crl vs. Con | –0.150 (0.213) | –0.703 | 0.482 | –0.155 (0.517) | –0.300 | 0.764 |
| | Crl vs. Iso | 0.148 (0.202) | 0.731 | 0.465 | 0.540 (0.515) | 1.050 | 0.294 |
| | Iso vs. Con | –0.298 (0.208) | –1.430 | 0.153 | –0.695 (0.516) | –1.348 | 0.178 |
| Mobile species | Crl vs. Con | 0.076 (0.117) | 0.647 | 0.517 | 0.056 (0.386) | 0.146 | 0.884 |
| | Crl vs. Iso | 0.253 (0.113) | 2.237 | 0.075 | 0.358 (0.385) | 0.930 | 0.352 |
| | Crl vs. Con | –0.177 (0.111) | –1.597 | 0.165 | –0.302 (0.385) | –0.785 | 0.433 |
| Sedentary species | Crl vs. Iso | –0.197 (0.182) | –1.085 | 0.278 | –0.544 (0.230) | –2.362 | 0.027 |
| | Crl vs. Con | –0.127 (0.178) | –0.712 | 0.476 | –0.991 (0.233) | –4.239 | < 0.001 |
| | Crl vs. Iso | –0.070 (0.187) | –0.375 | 0.708 | 0.447 (0.236) | –2.029 | 0.049 |
| Xerophilous species | Crl vs. Con | –0.119 (0.118) | –1.006 | 0.314 | –0.198 (0.277) | –0.717 | 0.473 |
| | Crl vs. Iso | 0.013 (0.114) | 0.115 | 0.909 | –0.169 (0.277) | –0.610 | 0.542 |
| | Iso vs. Con | –0.132 (0.118) | –1.121 | 0.262 | –0.029 (0.277) | –0.107 | 0.915 |
| Mesophilous species | Crl vs. Con | 0.175 (0.203) | 0.860 | 0.390 | 0.101 (0.440) | 0.229 | 0.818 |
| | Crl vs. Iso | 0.426 (0.193) | 2.201 | 0.067 | 0.889 (0.404) | 2.199 | 0.083 |
| | Iso vs. Con | –0.180 (0.160) | –1.119 | 0.263 | –0.758 (0.434) | –1.743 | 0.122 |
| Acrididae nymphs | Crl vs. Con | | | | –0.779 (0.688) | –1.133 | 0.257 |
| | Crl vs. Iso | | | | –0.950 (0.686) | –1.383 | 0.167 |
| | Iso vs. Con | | | | 0.170 (0.690) | 0.247 | 0.805 |

## Discussion

To assess the ecological value of ditch banks, we compared species richness and abundance of orthopterans between isolated ditch banks, semi–isolated ditch banks and control meadows. Species richness did not differ between ditch banks and control meadows, but significant differences were found in the abundance pattern of orthopterans. Braschler et al. (2009) suggested that fragmentation and isolation may have a stronger effect on the abundance of orthopterans than on their species richness. Similarly, farming practices are also known to particularly influence the density of orthopterans (Badenhausser and Cordeau, 2012). It seems that the density of orthopterans is a more sensitive measure of the quality of grassy habitats than their species richness, as was previously concluded by Báldi and Kisbenedek (1997).

Table 3. The effects of vegetation in ditch banks on species richness (left side) and abundance (right side) of orthopterans delineated by mixed models (GLMM). Poisson and negative binomial error terms were used to analyze species richness and abundance data, respectively: Width, width of ditch bank vegetation; Present, presence of woody vegetation; Dense, presence of dense woody vegetation.

*Tabla 3. Los efectos de la vegetación de las orillas de las acequias en la riqueza (izquierda) y la abundancia (derecha) de especies de ortópteros definidos por los modelos mixtos. Se utilizaron los términos de error que siguen una distribución de Poisson y binomial negativa para analizar los datos relativos a la riqueza y la abundancia de especies, respectivamente: Width, anchura de la orilla de la acequia cubierta por vegetación; Present, presencia de vegetación leñosa; Dense, presencia de vegetación leñosa densa.*

| | Variable | Parameter estimation (± SE) | *z* | *p* | Parameter estimation (± SE) | *t* | *p* |
|---|---|---|---|---|---|---|---|
| Orthoptera | Width | –0.003 (0.035) | –0.071 | 0.943 | 0.105 (0.062) | 1.680 | 0.093 |
| | Present | 0.047 (0.109) | 0.437 | 0.662 | –0.025 (0.128) | –0.195 | 0.845 |
| | Dense | –0.110 (0.155) | –0.711 | 0.477 | –0.559 (0.191) | –2.921 | 0.003 |
| Caelifera | Width | 0.036 (0.043) | 0.839 | 0.402 | 0.246 (0.078) | 3.127 | 0.002 |
| | Present | 0.037 (0.136) | 0.270 | 0.788 | –0.087 (0.109) | –0.791 | 0.428 |
| | Dense | –0.184 (201) | –0.917 | 0.359 | –0.289 (0.174) | –1.661 | 0.096 |
| Ensifera | Width | 0.005 (0.087) | 0.065 | 0.947 | 0.065 (0.139) | 0.467 | 0.640 |
| | Present | –0.048 (0.207) | –0.234 | 0.814 | 0.273 (0.233) | 1.172 | 0.241 |
| | Dense | 0.017 (0.311) | 0.054 | 0.956 | –0.353 (0.361) | –0.978 | 0.328 |
| Mobile species | Width | 0.017 (0.041) | 0.410 | 0.682 | 0.177 (0.066) | 2.670 | 0.007 |
| | Present | 0.088 (0.129) | 0.681 | 0.496 | 0.060 (0.103) | 0.580 | 0.561 |
| | Dense | –0.171 (0.192) | –0.889 | 0.374 | –0.416 (0.164) | –2.535 | 0.011 |
| Sedentary species | Width | 0.051(0.071) | 0.726 | 0.468 | 0.003 (0.098) | 0.037 | 0.970 |
| | Present | –0.161(0.235) | –0.687 | 0.492 | –0.013 (0.196) | –0.070 | 0.944 |
| | Dense | –0.091 (0.314) | –0.290 | 0.771 | 0.063 (0.314) | 0.203 | 0.839 |
| Xerophilous species | Width | 0.002 (0.045) | 0.053 | 0.958 | 0.168 (0.007) | 2.389 | 0.016 |
| | Present | 0.085(0.139) | 0.612 | 0.541 | –0.011 (0.116) | 0.098 | 0.922 |
| | Dense | –0.067 (0.197) | –0.341 | 0.733 | –0.342 (0.181) | –1.885 | 0.059 |
| Mesophilous species | Width | 0.095 (0.065) | 1.456 | 0.145 | 0.251 (0.009) | 2.575 | 0.010 |
| | Present | –0.086 (0.215) | –0.403 | 0.686 | 0.013 (166) | 0.080 | 0.936 |
| | Dense | –0.335 (0.332) | –1.009 | 0.312 | –0.185 (0.276) | –0.670 | 0.503 |
| Acrididae nymphs | Width | | | | 0.029 (0.073) | 0.396 | 0.692 |
| | Present | | | | –0.135 (0.196) | –0.690 | 0.490 |
| | Dense | | | | –0.046 (0.322) | –0.144 | 0.885 |

Based on the analyses of the trait groups separately, we showed that the mobility of species has a prominent role in shaping the abundance pattern of orthopterans, and sedentary species are presumably not able to build viable populations along ditch banks. This is in accordance with numerous studies highlighting the importance of dispersal ability of orthopterans in agricultural landscapes (Dziock et al., 2011; Marini et al., 2010, 2012; Torma and Bozsó, 2016; Poniatowski and Fartmann, 2010). In general, low mobility of insects is linked to their increased vulnerability to extinctions in a fragmented landscape since sedentary species, for instance, are less able to (re)colonize remaining suitable habitats in the unsuitable matrix (Braschler et al., 2009; Bommarco et al., 2010; Habel et al., 2016). Linear habitats in the agricultural matrix, however, have shown to be preferred for insect dispersal (Berggren et al., 2002;

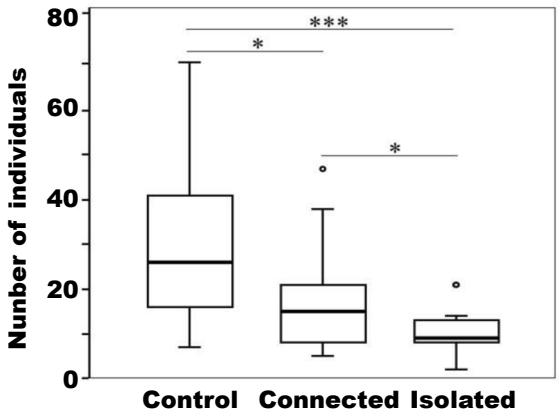


Fig. 2. Box plots represent the differences in the abundance of sedentary species of Orthoptera between isolated ditch banks, connected ditch banks and control meadows, delineated by the GLMM: * P < 0.05; ** P < 0.01; *** P < 0.001. Circles mark outlier data. (Further details are given in table 2).

*Fig. 2. El diagrama de caja representa las diferencias en la abundancia de especies sedentarias de ortópteros entre orillas de acequias aisladas, orillas de acequias conectadas y praderas de control, definidas por el modelo lineal generalizado mixto (GLMM): * P < 0,05; ** P < 0,01; *** P < 0,001. Los círculos indican los datos atípicos. (En la tabla 2 pueden consultarse más detalles).*

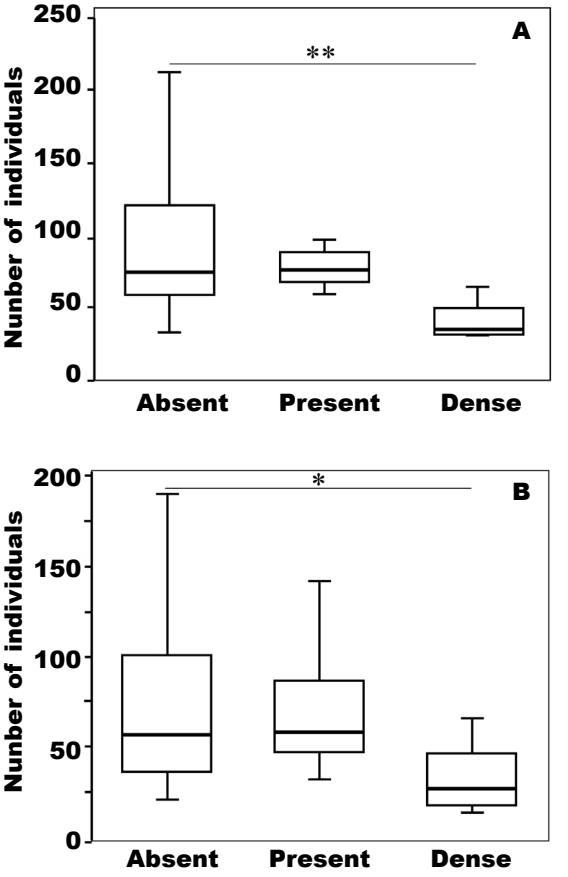


Fig. 3. Box plots show the differences in the total number of individuals (A) and in the number of mobile individuals (B) in relation to the density of woody vegetation: Absent, no woody vegetation; Present, a single tree or one–two single bushes; Dense, more than one tree and/or more than three bushes; * P < 0.05; ** P < 0.01; *** P < 0.001. (Further details are given in table 2).

*Fig. 3. Los diagramas de caja muestran las diferencias en el número total de individuos (A) y en el número de individuos móviles (B) en relación con la densidad de vegetación leñosa. Abreviaciones: Absent, sin vegetación leñosa; Present, un único árbol o uno o dos arbustos individuales; Dense, más de un árbol o más de tres arbustos: * P < 0,05; ** P < 0,01; *** P < 0,001. (En la tabla 2 pueden consultarse más detalles).*

Saarinen et al., 2005; Söderström and Hedblom, 2007), even for flightless and sedentary species (Poniatowski and Fartmann, 2010), suggesting the importance of such habitats in connecting populations. Besides their corridor function, linear habitats in the agricultural matrix can also have an important role in foraging and reproduction of animals (Huusela–Veistola and Vasarainen, 2000; Downs and Racey, 2006; Marshall et al., 2006). As immature orthopterans were present along ditch banks in a similar number to that in control meadows, ditch banks presumably provide suitable conditions for reproduction, particularly for grasshoppers. This is an important issue considering that different ecological conditions are often required for larval development and for spreading and foraging of adults (e.g. Hodek, 2003). In strips of mowed grass, for instance, high grasshopper (Gomphocerinae) densities consisted of a high density of adults but not of immature grasshoppers (Badenhausser and Cordeau, 2012).

The width of the vegetation and the presence of dense woody vegetation along ditch banks affected the orthopterans more than the extent of isolation of ditch banks. Woody vegetation is known to influence arthropod communities via alternating nearby environmental conditions such as soil water content, microclimate, vegetation, light regime, etc. (Sparks and Greatorex–Davis, 1992; Entling et al., 2007; Gossner, 2009; Torma and Gallé, 2011). The negative effect of woody vegetation on orthopterans has been shown in previous studies (Samways and Moore, 1991; Bieringer and Zulka, 2003). However, grasshoppers

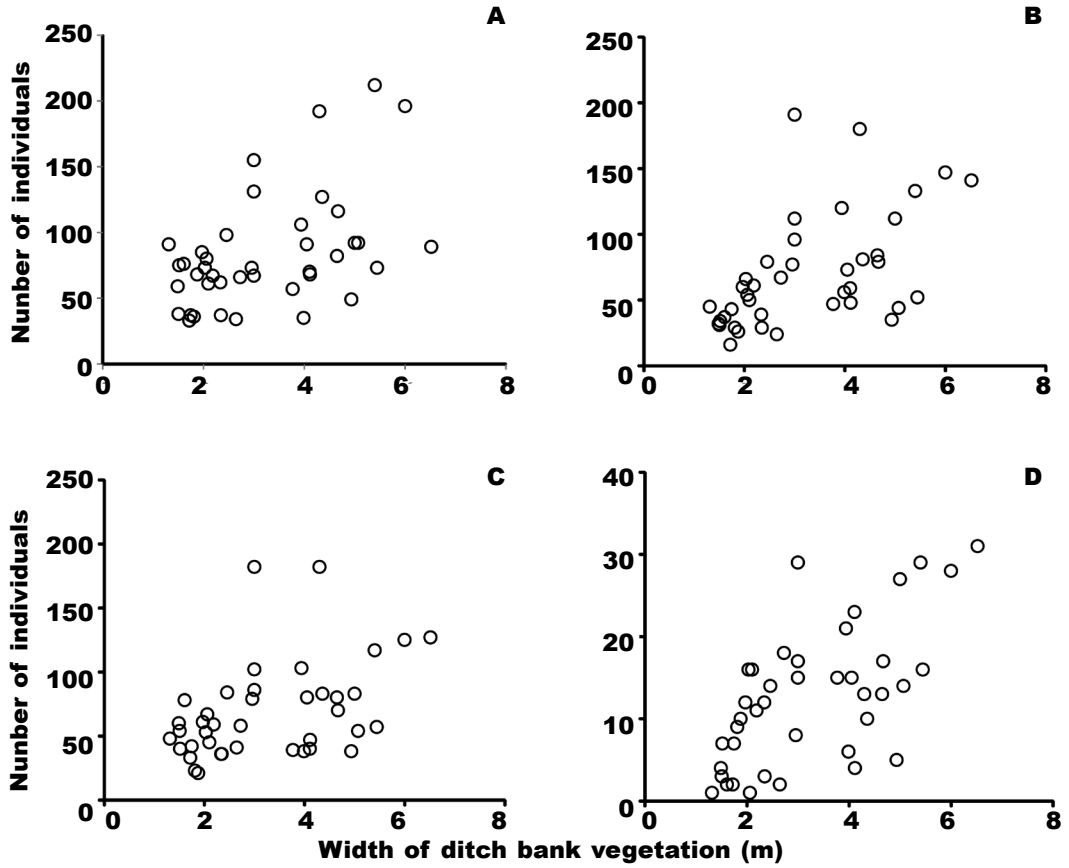


Fig. 4. The relationship between the width of ditch bank vegetation and the abundance of: A, Caelifera; B, mobile species; C, xerophilous species; D, mesophilous species. (Further details are given in table 2).

*Fig. 4. La relación entre la anchura de la orilla de la acequia cubierta por vegetación y la abundancia de: A, Caelifera; B, especies móviles; C, especies xerófilas; D, especies mesófilas. (En la tabla 2 pueden consultarse más detalles).*

seem to be more affected by the presence of dense woody vegetation and the width of grassy vegetation than Ensifera species. Most grasshoppers prefer open habitats whereas Ensifera species often require habitats consisting of both grassy and shrubby vegetation patches (Schirmel et al., 2010).

As artificial strip–like habitats generally have a quasi–constant width, the variation in their width is generally too low to detect effects on the distribution of species (Badenhausser and Cordeau, 2012). In the present study, the width of vegetation along ditches was more variable, resulting in significant effects on orthopterans. This variation in the width of vegetation was presumably due to the differences in the ditches (e.g. the steepness of bank slope, water regime, etc.) and in the surrounding land use. In some cases, arable fields or dirt roads were situated as close to ditches as is physically possible, reducing the width of ditch bank vegetation. Reduced width of vegetation can reduce humidity in ditch banks, whose condition is preferred by certain species (Herzon and Helenius, 2008). Soil moisture also influences the larval development of orthopterans (Hodek, 2003). However, we did not find differences in the distribution of hygrophilous species and immature orthopterans in relation to the width of vegetation. Presumably, a narrower vegetation–strip along ditches gained fewer resources for foraging and fewer resting and hiding places, causing a lower abundance in general.

In a linear habitat it is crucial whether it is functioning as a suitable habitat (provides resources needed for survivorship, reproduction, and movement), a corridor (provides some resources, especially for movement, but not necessarily for reproduction) or an ecological trap or sink for animals (Chetkiewicz et al., 2006). The role of linear grassy habitats as corridors for orthopterans was highlighted by previous studies in the region (Gausz, 1969; Krausz et al., 1995; Kisbenedek et al., 2010). Our findings suggest that ditch banks, like dikes (Torma and Bozsó, 2016),

can be a suitable habitat, providing resources for survivorship, reproduction and movement for most orthopterans including rare and endangered species. Numerous collected species e.g., *T. veyseli, G. glabra*, *E. coerulipes, M. frontalis, R. nitidula, C. italicus and A. ungarica* are included in National Red Lists as endangered or critically endangered species in surrounding countries (e.g., Berg et al., 2005; Maas et al., 2002; Liana, 2007; Holuša et al., 2013). *T. veyseli* is suggested to be close to extinction at the edge of Pannon region (Holuša et al., 2012), while *R. nitidula* is currently spreading (Krištin et al., 2007; Holuša et al., 2013). Some species such as *M. frontalis* and *C. italicus* are locally common in Hungary as well as in eastern and southern countries in Europe respectively, but they are endangered and declining in Central Europe (Liana, 2007). The decline of these species is often considered a consequence of the loss and destruction of their habitats (Liana, 2007; Rada and Trnka, 2016; Holuša, 2012; Holuša et al., 2012).

Considering that the above species generally occur along linear secondary habitats in the region (Gausz, 1969; Krausz et al., 1995; Torma and Bozsó, 2016), and further endangered species such as the endemic *Isophya costata* Brunner von Wattenwyl, 1878 and *Isophya stisy* Cejchan, 1957 were also detected (Kisbenedek et al., 2010), we highlight the importance of linear secondary habitats for orthopterans and presumably for other arthropod groups even in countries where a considerable area of natural, semi–natural grasslands still harbor rich invertebrate fauna.

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