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# Effects of hedgerows and riparian margins on aerial web-building spiders in cereal fields

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**Abstract.** Spiders (Araneae) are dominant predators in agro-ecosystems. Terrestrial seminatural habitats, such as hedgerows and grassy field margins, can enhance the abundance and diversity of spiders in adjoining fields, whereas the potential of riparian margins has rarely been studied. We compared the effects of hedgerows and riparian margins on aerial web-building spiders in adjacent cereal fields. While species richness and overall abundance did not significantly respond to distance from or type of field margin, each of the four dominant species responded differently. The abundance of *Tetragnatha* cf. *montana* Simon 1874 increased towards both hedgerows and riparian margins. *Tetragnatha extensa* (Linnaeus 1758) differentiated between field margin types and abundances increased only towards riparian margins. By contrast, *Phylloneta impressa* (L. Koch 1881) abundances decreased from field centers towards the field margins irrespective of the type. Type of field margin and distance showed an interactive effect on *Mangora acalypha* (Walckenaer 1802) abundances, which decreased from field centers towards hedgerows but changed only little towards riparian margins. Increasing spider densities towards field margins can be explained by the preference of spiders for adjoining seminatural habitats (overwintering, food availability, microclimate, vegetation structure), whereas increases towards field centers might be caused by interspecific competition and enhanced predation pressure near seminatural habitats and high prey numbers in crop fields. Overall, our study demonstrates that aerial web-building spider species respond differently to hedgerows and riparian margins.

**Keywords:** Agro-ecosystems, Araneae, edge effects, seminatural habitat

Spiders (Araneidae) are among the most abundant and species-rich invertebrate predators in agricultural landscapes. They are important predators of crop pests, and high spider abundance and diversity are important for successful biological control (Marc et al. 1999; Nyffeler & Sunderland 2003). Agro-ecosystems are usually dominated by few spider species (Schmidt & Tscharntke 2005; Prieto-Benitez & Méndez 2011) and, in Europe, less than ten agrobiont species constitute 60–90% of the individuals of spider communities in fields with only little variation among crops and regions (Samu & Szinetár 2002).

Most agricultural landscapes are a mosaic of fields, seminatural habitats (e.g., field margins, hedgerows) and roads (Marshall & Moonen 2002). Spiders use seminatural habitats as refuges during disturbances in the field (ploughing, harvesting, pesticide application), for overwintering and as source habitat for recolonization (Pfiffner & Luka 2000; Prieto-Benítez & Méndez 2011). Additionally, seminatural habitats provide alternative food sources and complex vegetation structures for web attachment (Dix et al. 1995). Thus, seminatural habitats subsidize within-field spider populations and can enhance the predation pressure on crop pests (Clough et al. 2005; Öberg et al. 2008). These positive effects often decline with increasing distance from the field margin (Denys & Tscharntke 2002), usually within a few or tens of meters (Dennis & Fry 1992; Bedford & Usher 1994; Sunderland & Samu 2000). However, opposite patterns with higher spider abundances within crop fields have also been reported (Birkhofer et al. 2014).

Most studies analyzing the effects of seminatural habitats on spiders in fields focussed on terrestrial habitats such as forest edges (Bedford & Usher 1994; Kajak 2007; Oleszczuk et al. 2010) or grassy field boundaries (Dennis & Fry 1992; Baines et al. 1998; Huusela-Veistola 1998; Denys & Tscharntke 2002, Birkhofer et al. 2014). In contrast, studies analyzing the effects of riparian margins on spiders in crop fields are scarce. In addition to their function as refuge habitat, riparian margins can provide supplemental food to spiders in adjoining crop fields. Fluxes of aquatic insects emerging from streams can be as high as 10,000–20,000 insects $m^{-2}$ $year^{-1}$ (mainly adult Diptera, Ephemeroptera, Plecoptera, Trichoptera and Odonata) and can provide an important energy subsidy to adjacent terrestrial habitats (Baxter et al. 2005). Emergence may exceed terrestrial production per unit area in the surrounding landscape, especially in May and June, when emergence is usually highest in temperate zones. This additional prey-availability can lead to high densities of consumers in aquatic-terrestrial ecotones independent of the habitat type (Kato et al. 2003; Ballinger & Lake 2006), though this can be affected by land use (Krell et al. 2015; Stenroth et al. 2015). Aquatic prey can be an important component of spider diets, up to 99% in Tetragnathidae and 64% in Linyphiidae and, hence, might influence the biomass, abundance and species composition of spiders (Iwata 2007). Thus, the abundance of web-building spiders can be enhanced by emergence and be related to the proximity to the body of water (Henschel 2004; Iwata 2007; Marczak & Richardson 2007; Burdon & Harding 2008). In turn, the emergence can indirectly lead to a higher predation on terrestrial herbivores (Henschel et al. 2001; Henschel 2004). However, most of these findings are based on studies of forest–stream boundaries.

We examined the influence of streams on aerial web-building spiders in adjacent crop fields and compared the effects of hedgerows and riparian margins. We tested the following hypotheses: (i) the type of field margin (riparian margin, hedgerow) influences the composition, abundance and species richness of spiders in adjoining fields, with (ii) riparian margins exhibiting a stronger influence than hedgerows, and (iii) decreasing influence with increasing distance to the field margins.

Table 1.—ANODEV table of the effect of field margin type and distance from the field margin on spider species richness, overall abundance, and abundance of the four dominant species (quasi-Poisson GLMM). Significant *P*-values are marked with asterisks ('*' $P < 0.05$, '**' $P < 0.01$), '***' $P < 0.001$).

| | Distance (log transformed) | | | Field margin type | | | Distance x margin | | |
|---|---|---|---|---|---|---|---|---|---|
| | df | t | *P* | df | t | *P* | df | t | *P* |
| Species richness | 39 | −1.68 | 0.10 | 3 | −0.93 | 0.42 | – | – | – |
| Overall abundance | 38 | 2.01 | 0.051 | 3 | 3.10 | 0.053 | 38 | −2.86 | 0.007** |
| *Mangora acalypha* | 38 | 2.55 | 0.015* | 3 | 3.14 | 0.052 | 38 | −2.31 | 0.027* |
| *Phylloneta impressa* | 39 | 4.68 | <0.001*** | 3 | −0.91 | 0.43 | – | – | – |
| *Tetragnatha extensa* | 38 | 1.80 | 0.080 | 3 | 3.35 | 0.044* | 38 | −2.66 | 0.012* |
| *Tetragnatha* cf. *montana* | 38 | −3.71 | 0.001** | 3 | 0.56 | 0.62 | 38 | −3.27 | 0.002** |

## METHODS

We investigated four conventionally managed winter cereal fields in an intensely used agricultural landscape near the city of Landau, Germany (49°12N, 8°7E). Prior to sampling, only herbicides, which are typically not directly toxic to arthropods (Bell et al. 2002; Pékar 2002), were applied to the fields. The fields had a size of at least 2 ha and were bordered at one side by a hedgerow and on the opposite side by a riparian margin. At two sampling sites, the two different field margins belonged to different adjacent fields with the same crop type. Three hedgerows and three riparian buffer strips were adjacent to wheat fields (*Triticum aestivum*), while one hedgerow and one riparian buffer strip were adjacent to rye fields (*Secale cereale*). Hedgerows had a width of about four meters and were dominated by shrubs such as *Rubus* sp., *Rosa canina*, *Sambucus nigra*, *Prunus spinosa*, and *Cornus sanguinea*. Riparian margins were three to five meters wide and had a dense and tall herb and grass layer. On the other side of the stream was a three meter broad hedgerow with trees.

Twelve transects were made in each field, i.e., six transects per field margin at distances of 1, 3, 5, 9, 17 and 25 meters into the field ($N_{total} = 48$ transects with an area of ca. 3,840 $m^2$). To account for possible confounding effects, structural parameters of the fields and the field margin were recorded (Appendix 2). Aerial web-building spiders were sampled between 13 and 21 May 2011, when the recolonization of spiders from the field margins should have occurred and the emergence of aquatic insects is expected to be high (Kato et al. 2003; Öberg et al. 2008). Spiders were sampled by sweep netting under dry and warm weather conditions, which is an effective method to catch web-building spiders in the vegetation layer (Amalin et al. 2001). A sweep net with a diameter of 30 cm was moved 200 times per transect corresponding to a length of approximately 40 m and a width of 2 m per transect (area = 80 $m^2$ per transect).

Web-building spiders were identified alive in the field or, if necessary, in the laboratory. Identification and nomenclature followed Roberts (1996) and World Spider Catalog (2015). A few spiders were only identified to genus level and, within the genus *Tetragnatha* Latreille 1804, we only distinguished between *Tetragnatha extensa* (Linnaeus 1758) and *Tetragnatha* cf. *montana* Simon 1874 (comprising all individuals with uniformly dark sternum). Spider density per square meter was calculated by dividing the number of individuals by the area sampled. Note that these results are lower-bound abundance estimates, because of limited sampling efficiency.

The explanatory power of environmental variables (Appendix 2) for community composition was assessed using permutational analysis of variance (PERMANOVA) (Anderson 2001) with Bray Curtis dissimilarity as distance measure (function 'adonis' in R package "vegan", Oksanen et al. 2010). We used strata to account for our nested design (strata = field). The number of species and individuals were related to the field margin type and the distance to the field margin with generalized linear mixed models (GLMM) using the function glmmPQL (packages "MASS", Venables & Ripley 2002, and "nlme", Pinheiro et al. 2009). The function glmmPQL fits GLMM via penalized Quasi-Likelihood. We used a Poisson GLMM for count data and corrected the standard errors based on a quasi-Poisson model because overdispersion was detected. We used field margin type and the distance to the field margin as fixed effects and transects nested in field as a random effect. Distances from the field margin were log(x+1)-transformed to account for the expected exponential change of spider abundance from the margin towards the field centers, owing to the likely exponential decrease of the aquatic prey within a short distance to the field margin (Sunderland & Samu 2000). Interaction terms between distance and type of field margin were only retained in the models if significant. Model performance was checked graphically using diagnostic plots and potential outliers were identified using Cook's distance (Zuur et al. 2009). Statistical analyses were done in R 3.1.2 (R Development Core Team, 2014).

## RESULTS

Overall, 767 individuals of aerial web-building spiders from the families Araneidae, Linyphiidae, Tetragnathidae and Theridiidae were caught (spider density = 0.2 ind/$m^2$) (Appendix 1). Eighteen juveniles of Araneidae and Linyphiidae were excluded from further analysis because they were too small for identification. The remaining individuals comprised 14 genera and 16 species. Most abundant were *Mangora acalypha* (Walckenaer 1802) (49%), *Tetragnatha extensa* (19%), *Phylloneta impressa* (L. Koch 1881) (16%), and *Tetragnatha* cf. *montana* (6%). All other species accounted for less than 1% of all individuals. The composition of spider assemblages was significantly affected by the distance from field margins, but not by any of the remaining habitat parameters (Appendix 2). Species richness and overall abundance of web-building spiders was not significantly related to the field margin type (hedgerow or riparian margin) or the distance to the margin (Table 1). By contrast, the field margin type and the distance to the margin significantly

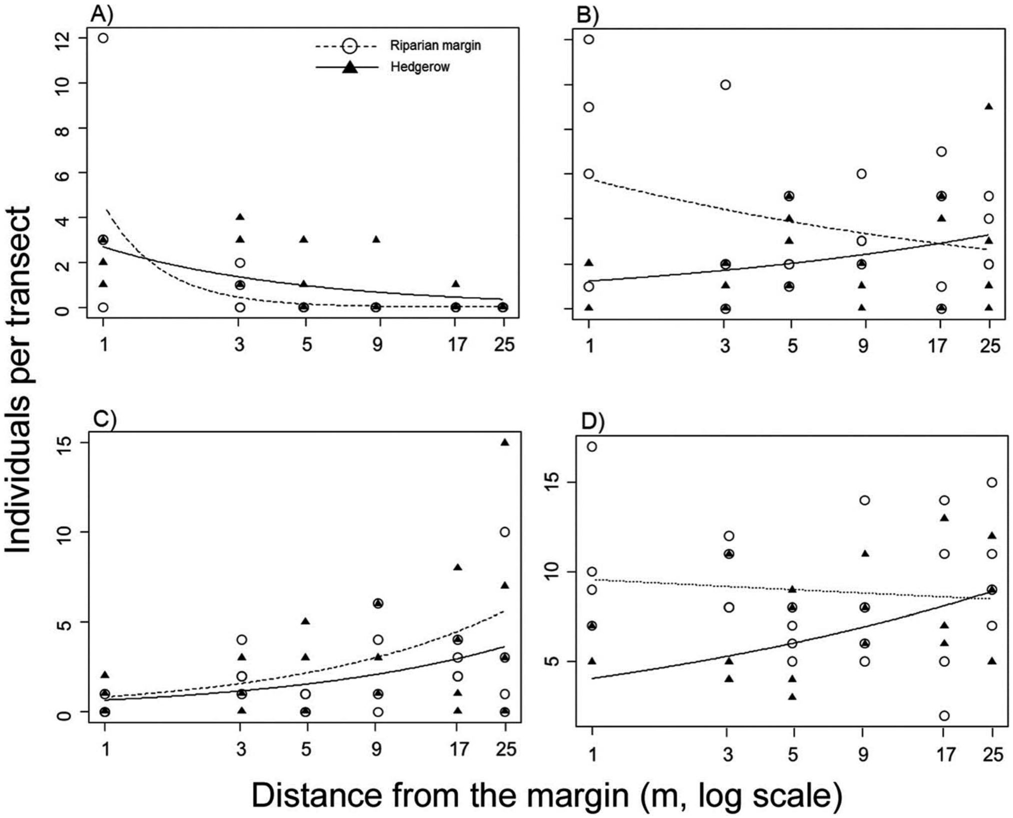

Figure 1.—Effects of field margin type and distance from field margin on the abundance of A) *Tetragnatha* cf. *montana* (hedgerow: $P < 0.001$, riparian margin: $P = 0.007$); B) *Tetragnatha extensa* (hedgerow: $P = 0.085$, riparian margin: $P = 0.125$); C) *Phylloneta impressa* (hedgerow: $P = 0.011$, riparian margin: $P = 0.026$); D) *Mangora acalypha* (hedgerow: $P = 0.013$, riparian margin: $P = 0.630$).

affected the four most abundant species (Table 1). Abundances of *T.* cf. *montana* increased from the field centers towards both margin types (Fig. 1A). Abundances of *T. extensa* responded significantly to the interaction of margin type and distance. Abundances increased towards riparian margins from the field centers, but decreased towards hedgerows (Fig. 1B). The abundance of *P. impressa* decreased towards both field margin types (Fig. 1C). Type of field margin and distance to the margin showed an interactive effect on *M. acalypha* abundances, which decreased from field centers towards hedgerows but changed little towards riparian margins (Fig. 1D).

## DISCUSSION

Our results showed that the type of field margin and the distance to the margin affected spider species abundances differently, leading to a change in species composition rather than to a change in overall abundance or species richness. Such patterns are known for ground-dwelling spiders (Clough et al. 2005; Schmidt-Entling & Döbeli 2009) and for other macro-invertebrates (Holland et al. 1999; Anjum-Zubair et al. 2010; Hof & Wright 2010), but, to our knowledge, not for spiders that build their webs high in the vegetation. In the following, we describe the patterns of the four dominant species and discuss potential mechanisms.

Abundances of *T.* cf. *montana* increased from the field centers towards both margin types, whereas *T. extensa* abundances increased only towards riparian margins. The increase of both *Tetragnatha* species towards field margins can be explained by the general preference of spiders for field margins, which offer suitable overwintering sites, alternative food, microclimate, and vegetation structure. First, most spiders overwinter outside arable fields, and recolonize from the margin (Dix et al. 1995; Pfiffner & Luka 2000; Öberg et al. 2008). Spiders heavier than 15 mg cannot disperse via ballooning, and cursorial movement is less effective for moving far into the fields (Samu et al. 1999; Bell et al. 2001; Entling et al. 2011). As a result, the interior of arable fields is likely to be colonized mostly by small spiders, for most families by younger instars, which are able to balloon (Samu & Szinetár 2002). Individuals that are too large for ballooning or species that never balloon should be restricted to areas near the field margin. All abundant spider species in this study are able to balloon (Bell et al. 2005). However, *Tetragnatha* sp. balloon mostly as immatures and may be too heavy for aerial dispersal during spring (Nyffeler & Benz 1989; Blandenier 2009), which may explain the increased *Tetragnatha* densities towards field margins. Second, food availability can be higher in field margins than in field centers (Huusela-Veistola 1998). Hence, the concentration of spiders near the field margin can be caused by their preference for web sites with high prey resources (Harwood et al. 2003). Moreover, *Tetragnatha* sp. are positively related to aquatic insect flux and react strongly to the availability of aquatic prey (Kato et al. 2003; Baxter et al. 2005; Iwata 2007; Marczak & Richardson 2007). This can explain the differentiation of *T. extensa* between hedgerows and riparian margins in this study. Third, fields and margins differ in microclimate and moisture, which are important factors for the distribution and web site selection of spiders (Samu et al. 1999; Bell et al. 2001). The sensitivity of *Tetragnatha* sp. to desiccation might be a further explanation for their preference for moist conditions near streams (Power et al. 2004). Finally, web-building spiders often prefer microhabitats with complex vegetation structure (Bell et al. 2001) and vegetation in cereal fields is generally more homogeneous than in field margins (Cole et al. 2005).

Both *M. acalypha* and *P. impressa* showed increased abundances towards the field center. For *M. acalypha*, the increase towards the field center was especially high at hedgerows while *P. impressa* preferred field centers regardless of the field margin type. In contrast to *Tetragnatha* sp., these species are able to balloon in spring, which enables an effective dispersal far into the fields (Blandenier 2009), and are less responsive to aquatic prey (Iwata 2007). Among farmland spiders, *P. impressa* is one of the species with the strongest preference for fields over perennial habitats during the vegetation period (Schmidt & Tscharntke 2005), which may be explained by the availability of high prey numbers during certain parts of the season (Pekár 2000; Jurczyk et al 2012). However, *P. impressa* does not appear to overwinter in arable fields (Pfiffner & Luka 2000), suggesting that it actively moves into cereal fields. A reason for its preference for field interiors might be avoidance of competition and predation (Sunderland & Samu 2000). Intraguild interference in structurally simple agro-ecosystems is often high, and at low prey density, many spiders feed on other spiders (Nyffeler 1999). *Phylloneta impressa* is a powerful colonizer that can easily reach central parts of crop fields in contrast to many of their intraguild competitors (Blandenier 2009). In the presence of chemical cues of ants, *P. impressa* increase their propensity for silk-based dispersal (Mestre et al. 2014). Thus *P. impressa* may prefer field centers to avoid interference with species that are limited to the vicinity of the margins. Furthermore, a higher predation pressure along seminatural habitats can be assumed. For example *P. impressa* and *M. acalypha* are the main prey of *Trypoxylon figulus* (Linnaeus 1758), a wasp that is particularly abundant along woody habitats such as hedgerows (Coudrain et al. 2013). Thus, field centers may represent areas of both low competition and low predation pressure for both spider species.

To conclude, aerial web-building spiders showed species-specific responses to the distance and type of field margin. The lack of an overall positive influence of riparian margins on spiders in arable fields contrasts with findings from more natural systems. Future studies should explore whether environmental stress on streams (e.g., in the form of agricultural inputs) can explain the lack of a more positive influence on terrestrial predators. The potential role of predators and competitors in reducing spiders near field margins could be resolved with field experiments.

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Appendix 1.—Abundance of the web-building spiders per transect at 1, 3, 5, 9, 17, and 25 m distance from the field margin, shown separately for riparian margins (r) and hedgerows (h).

| | | Distance from the field margin [m] | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 1 | | 3 | | 5 | | 9 | | 17 | | 25 | | | Individuals |
| Family | Species | r | h | r | h | r | h | r | h | r | h | r | h | Total | per 100 m$^2$ |
| Araneidae | *Araniella cucurbitina* (Clerck 1757) | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 3 | 0.08 |
| | *Argiope bruennichi* (Scopoli 1772) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0.03 |
| | *Hypsosinga sanguinea* (C. L. Koch 1844) | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0.03 |
| | *Mangora acalypha* (Walckenaer 1802) | 43 | 13 | 39 | 24 | 26 | 24 | 33 | 33 | 32 | 33 | 42 | 31 | 373 | 9.71 |
| | Unidentified juvenile | 2 | 2 | 0 | 4 | 1 | 1 | 1 | 0 | 0 | 4 | 0 | 1 | 16 | 0.42 |
| Linyphiidae | *Erigoninae* sp. | 4 | 4 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 12 | 0.31 |
| | *Tenuiphantes tenuis* (Blackwall 1852) | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 6 | 0.16 |
| | Unidentified juvenile | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0.05 |
| Tetragnathidae | *Metellina mengei* (Blackwall 1869) | 3 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6 | 0.16 |
| | *Tetragnatha extensa* (Linnaeus 1758) | 18 | 6 | 14 | 3 | 10 | 13 | 14 | 5 | 13 | 14 | 13 | 13 | 146 | 3.8 |
| | *Tetragnatha* cf. *montana* Simon 1874 | 18 | 7 | 3 | 11 | 0 | 4 | 0 | 3 | 0 | 1 | 0 | 0 | 47 | 1.22 |
| Theridiidae | *Achaearanea sp.* (Strand 1929) | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0.03 |
| | *Enoplognatha ovata* (Clerck 1757) | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0.05 |
| | *Neottiura bimaculata* (Linnaeus 1767) | 12 | 1 | 3 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 2 | 0 | 29 | 0.76 |
| | *Phylloneta impressa* (L. Koch 1881) | 1 | 3 | 9 | 4 | 2 | 13 | 11 | 13 | 11 | 13 | 14 | 25 | 119 | 3.1 |
| | *Steatoda* sp. Sundevall 1833 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0.03 |
| | *Theridion pinastri* L. Koch 1872 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0.03 |
| | *Theridion* sp. (Walckenaer, 1805) | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0.03 |
| Total | | 112 | 39 | 69 | 49 | 44 | 63 | 61 | 55 | 58 | 69 | 73 | 75 | 767 | 19.97 |

Appendix 2.—Effect of field margin type, distance from the field margin and vegetation parameters on spider species composition. The explanatory power of environmental variables was assessed using permutational analysis of variance with pseudo-F ratios and partial R$^2$ values. The Bray Curtis dissimilarity was used as distance measure and strata to account for the nested design (strata = field). Within the fields, vegetation cover (%) was estimated at four 1-m$^2$ plots every 10 m per transect. In each plot the vegetation height was measured five times with a round disk (diameter: 19 cm, weight: 50 g), which was dropped from a standardised height of 1 m. The height of the grass and the shrub layer of the field margins were quantified eight times every 5 m. The height of the grass layer was measured using a round disk as in cereal fields. The height of the shrub layer was calculated with a declinometer. Significant *P*-values are marked with asterisks ('***' $P < 0.001$).

| | Interval (min – max) | F | R$^2$ | *P* |
|---|---|---|---|---|
| Field margin type | riparian, hedgerow | 1.0 | 0.02 | 0.43 |
| Distance from field margin (log transformed) | 1– 25 m | 7.3 | 0.13 | 0.001*** |
| Vegetation cover in field | 20 – 55% | 1.2 | 0.02 | 0.45 |
| Vegetation cover in field margin | 59 – 100% | 2.0 | 0.04 | 0.072 |
| Vegetation height in field (mean) | 0.31– 0.59 m | 1.6 | 0.03 | 0.28 |
| Herbal height in field margin | 0 – 0.65 m | 2.6 | 0.05 | 0.19 |
| Shrub height (mean) | 2.7 – 21 m | 0.3 | 0.01 | 0.94 |