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Agricultural intensification often leads to fragmentation of natural habitats, such as forests, and thereby negatively affects forest specialist species. However, human introduced habitats, such as hedges, may counteract negative effects of forest fragmentation and increase dispersal, particularly of forest specialists. We studied effects of habitat type (forest edge versus hedge) and hedge isolation from forests (connected versus isolated hedge) in agricultural landscapes on abundance, species richness and community composition of mice, voles and shrews in forest edges and hedges. Simultaneously to these effects of forest edge/hedge type we analysed impacts of habitat structure, namely percentage of bare ground and forest edge/hedge width, on abundance, species richness and community composition of small mammals. Total abundance and forest specialist abundance (both driven by the most abundant species *Myodes glareolus*, bank vole) were higher in forest edges than in hedges, while hedge isolation had no effect. In contrast, abundance of habitat generalists was higher in isolated compared to connected hedges, with no effect of habitat type (forest edge versus hedge). Species richness as well as abundance of the most abundant habitat generalist *Sorex araneus* (common shrew), were not affected by habitat type or hedge isolation. Decreasing percentage of bare ground and increasing forest edge/hedge width was associated with increased abundance of forest specialists, while habitat structure was unrelated to species richness or abundance of any other group. Community composition was driven by forest specialists, which exceeded habitat generalist abundance in forest edges and connected hedges, while abundances were similar to each other in isolated hedges. Our results show that small mammal forest specialists prefer forest edges as habitats over hedges, while habitat generalists are able to use unoccupied ecological niches in isolated hedges. Consequently even isolated hedges can be marginal habitats for forest specialists and habitat generalists and thereby may increase regional farmland biodiversity.

Agricultural intensification often leads to the destruction and fragmentation of natural habitats, such as forests. Thereby the resulting isolation of these natural habitats in agricultural landscapes boosts local population extinction of many organisms (Fischer and Lindenmayer 2007, Bennett and Saunders 2010). Increasing landscape heterogeneity by adding areas of natural and semi-natural habitats can counteract this negative trend by increasing habitat connectivity and additionally often contributes to the conservation of farmland biodiversity (Tewksbury et al. 2002, Bennett and Saunders 2010). Hedges are human introduced linear woody elements consisting of shrubs and/or trees in the agricultural landscape that provide various ecological functions, such as

corridors for forest species or refuges for open land species (Baudry et al. 2000). Therefore, hedges function as semi-natural habitat and can increase connectivity between forests in agricultural landscapes, mitigating potential negative effects of habitat fragmentation (Niemelä 2001, Bennett and Saunders 2010). However, the extent to which species use different habitat types and are affected by habitat isolation depends on species specific habitat specialisation, dispersal ability and their ability to cope with landscape modifications (Niemelä 2001, Fischer and Lindenmayer 2007).

Small mammals are of ecological importance as they represent an important link in the food chain and their occurrence may not only influence their food resources, such as seeds and invertebrates (Abt and Bock 1998), but also population densities of their predators (Aschwanden et al. 2005, Koks et al. 2007). On the other hand, small mammals, such as *Microtus arvalis* (common vole), are often considered as agricultural pests in central Europe, causing

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economic damage to crops (Jacob et al. 2014) or preying on invertebrates that perform ecosystem services, such as spiders, carabid beetles or earthworms (Abt and Bock 1998). Small mammals can also be reservoir hosts and vectors of zoonotic diseases, such as hantavirus and therefore source of infection in humans (Voutilainen et al. 2012).

Small mammal communities, and individual species e.g. *Myodes glareolus* (bank vole) and *Apodemus sylvaticus* (long-tailed field mouse, wood mouse), are often positively affected by large size of forest patches, high connectivity of patches of old forest and structural heterogeneity of the forest floor (Fitzgibbon 1997, Vieira et al. 2009, Mortelliti et al. 2011). However, studies analysing the impact of forest patch isolation in agricultural landscapes on small mammals were often conducted in forests or forest patches, but not in smaller woody landscape elements such as hedges (but see Michel et al. 2006, Gelling et al. 2007, Silva and Prince 2008) and did not take species specific habitat specialisation into account (but see Yahner 1983, Bentley et al. 2000, Tattersall et al. 2002). Small mammals show distinct habitat specialisation and can be classified into forest and open land specialists and habitat generalists, each responding differently to changes in landscape complexity (Gentili et al. 2014). Forest specialists such as *Apodemus flavicollis* (yellow-necked mouse) and *M. glareolus* mainly live in forest habitats, avoiding open agricultural areas (Pollard and Relton 1970, Kotzageorgis and Mason 1996, Tattersall et al. 2002, but see Broughton et al. 2014). Therefore, forest specialists may benefit from hedges, which generally can function as habitat, dispersal corridors or stepping stones for different species (Davies and Pullin 2007). In contrast, habitat generalists, such as *Sorex araneus* (common shrew) and *A. sylvaticus*, are able to thrive in a wide range of environmental conditions and frequently occur in open agricultural landscapes (Heroldová et al. 2007, Tattersall et al. 2002, Wang and Grimm 2007). Thus, habitat generalists should benefit less from decreasing isolation of forests through hedges compared to forest specialists (Bentley et al. 2000).

Besides habitat type and effects of isolation, habitat structure described through e.g. hedge width, height and ground cover can also influence small mammal occurrence. A high level of microhabitat complexity through high shrub diversity, high vegetation cover and low percentage of ground covered by bare-soil provide refuges from predators and are known to increase overall small mammal abundance and species richness (Gelling et al. 2007, Silva and Prince 2008). Additionally, increasing hedge width increases the amount and quality of the habitat and thereby may positively affect small mammal abundance of forest specialists as well as habitat generalists (Gelling et al. 2007, but see Bellamy et al. 2000).

In the present study we investigated the effects of habitat type and isolation on small mammal abundance, species richness and community composition, paying particular attention to the abundance of forest specialists and habitat generalists. We therefore compared three different types of structurally similar linear woody landscape elements (hereafter referred to as 'forest edge/hedge type'): shrub dominated forest edges, sharing large parts of their borders with the forest; hedges connected to forest, sharing a small part of their borders with the forest; hedges isolated from forest by at least 300 m, with

no structural connectivity to forests. Along with effects of habitat type (forest edge versus hedge) and hedges' isolation (connected versus isolated hedge), we tested the influence of habitat structure (percentage of ground covered by bare-soil and forest edge/hedge width) on small mammal occurrence.

We hypothesised that

- 1) forest specialists are affected by habitat type and isolation, with highest abundance in forest edges, intermediate abundance in connected hedges and lowest abundance in isolated hedges, and that there is no influence of habitat type or isolation on habitat generalists;
- 2) small mammal community composition changes with decreasing dominance of forest species from forest edges to isolated hedges;
- 3) abundance of both forest specialists and habitat generalists increases with decreasing percentage of ground covered by bare-soil and increasing forest edge/hedge width.

Material and methods

Study sites and sampling design

The study sites were located in the surroundings of Göttingen, Lower Saxony, Germany (51°5'N, 9°9' E; for a map see Batáry et al. 2012). We chose six forest edges, six hedges connected to forest and six hedges isolated from forest (Fig. 1, Supplementary material Appendix 1 Fig. A1). Forest edges with a distinct shrub layer distinguishable from the inner part of the forest were chosen, which were structurally similar to hedges regarding plant composition, stratification, shrub height, or width and can be essentially viewed as hedges bordering forest (Supplementary material Appendix 1 Fig. A1a; for a detailed list of hedge characteristics see Table 1). Vegetation of forest edges and hedges was dominated by *Prunus spinosa* (blackthorn), *Crataegus* spp. (hawthorn), and *Rosa* spp. (rose), and trees and shrubs such as *Acer* spp. (maple) and *Cornus sanguinea* (dogwood) were frequently interspersed. Forest edges and connected hedges adjoined deciduous forests dominated by *Fagus sylvatica* (beech), which was not masting in 2008 in Lower Saxony, the year before our study took place (Nordwestdeutsche Forstliche Versuchsanstalt 2008). Forest edges and hedges were either bordered by winter cereal fields or winter oilseed rape fields (cf. Kovács-Hostyánszki et al. 2013). Landscape composition around all 18 study sites was dominated by

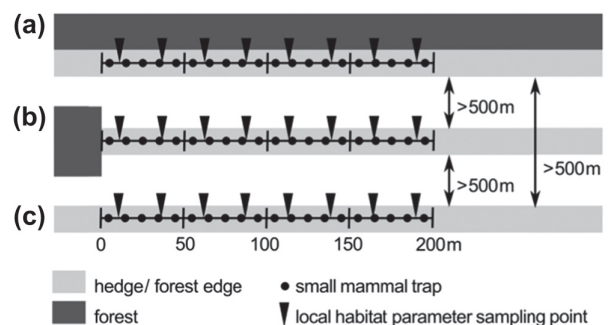


Figure 1. Study design: (a) forest edge, (b) connected hedge, (c) isolated hedge.

Table 1. Parameters describing habitat structure of forest edges, connected hedges and isolated hedges. Overall minimum and maximum values and mean values with standard errors per forest edge/hedge type are given. Differences of habitat structure between forest edges, connected hedges and isolated hedges were assessed by calculating F- and p-values from a one-way ANOVA (DF 2,15) when parameters were normally distributed or by χ^2 -values from a Kruskal–Wallis rank sum test (DF 2) when parameters were not normally distributed.

| Parameter | Definition | Minimum | Maximum | Forest edge | Connected hedge | Isolated hedge | F/ χ^2 -value | p-value |
|------------------|---|---------|---------|-------------|-----------------|----------------|--------------------|---------|
| Bare ground | bare ground % cover estimated from 1 m ² | 6.3 | 43.8 | 17.5 ± 4.5 | 27.4 ± 5.3 | 22.4 ± 3.2 | 1.25 ^a | 0.32 |
| Height | height of shrub layer in m (without trees) | 2.9 | 4.8 | 3.5 ± 0.2 | 3.7 ± 0.2 | 4.0 ± 0.2 | 1.39 ^a | 0.28 |
| Litter cover | litter % cover estimated from 1 m ² | 51.3 | 93.8 | 80.2 ± 4.9 | 66.0 ± 6.1 | 73.5 ± 4.5 | 1.85 ^a | 0.19 |
| Vegetation cover | vegetation % estimated from 1 m ² | 2.5 | 78.1 | 24.0 ± 11.5 | 22.5 ± 4.3 | 22.5 ± 1.8 | 0.83 ^b | 0.66 |
| Width | width of shrub layer (in m, measured at the ground) | 1.9 | 9.3 | 5.0 ± 0.9 | 4.5 ± 0.8 | 5.7 ± 1.1 | 0.82 ^b | 0.66 |

^aF-value.

^b χ^2 -value.

arable land and forest in a 500 m radius around study sites, but differed between forest edges and hedges due to their different configuration (cf. Batáry et al. 2012).

To reduce spatial autocorrelation the minimum distance between study sites was 500 m. The distance between isolated hedges and the nearest forest was at least 300 m, exceeding mean distances of small mammal movements (Kozakiewicz et al. 1993, Kotzageorgis and Mason 1996, Shchipanov et al. 2011), even though in some cases *Myodes glareolus* are able to move larger distances, depending on sex and season (Kozakiewicz et al. 2007). Forest edge or hedge length was at least 200 m and connected hedges adjoined perpendicular to the forest.

Parameters characterising habitat structure of forest edges (by its distinct shrub layer) and hedges (Table 1, Supplementary material Appendix 1 Table A1) were measured in August 2009 at eight sampling points spacing 25 m (Fig. 1). Percentage of hedges' ground covered by bare-soil, litter and vegetation (grasses and herbs) were estimated with 10% precision at each sampling point from both sides of the forest edge or hedge within 1 × 1 m. Height and width of the shrub layer were measured with 0.5 m precision, excluding the forest tree layer in case of forest edges. Mean values of variables describing habitat structure were calculated per study site.

Small mammal sampling

Small mammal sampling was conducted twice, in May and in July 2009 during the growing season, before the crop harvest. 20 multiple-capture live-traps (Ugglan-traps, 240 × 60 × 90 mm; Grahnab, Sweden) were placed with 10 m spacing in the middle of each forest edge or hedge (Fig. 1) (cf. Silva and Prince 2008). In case of connected hedges starting point of trap lines was 5 m away from forest edges. Trapping took place for three consecutive trapping nights. Before the first trapping night traps were pre-baited for one night to increase trapping efficiency. Traps were baited with rolled oats in the evening before sunset and checked in the early morning after sunrise. To sample the small mammal community representatively without any bias to species with certain food preference, no high-energy bait for shrews was used, since a pilot study in the area showed that capture probability but also mortality of shrews increased by additionally using mealworms as bait. Trapped small mammals were identified to species and marked with permanent micro tattoos (FST

Laboratory Animal Microtattoo System, green tattoo paste, sterile hypodermic needles 27 G × ½") on the tail base to enable identification when recaptured.

Abundance of small mammals per forest edge or hedge was calculated by excluding recaptures (cf. Fischer et al. 2011, Michel et al. 2006), as there was no difference in trappability (percentage of recaptures) among forest edges, connected and isolated hedges (one-way analysis of variance: $F_{2,15} = 0.44$, $p = 0.65$). Further, in case of the connected hedges, there was no difference in the number of trapped individuals among traps with different distance from the forest edge (analysis of variance: $F_{19,215} = 1.34$, $p = 0.16$), therefore we pooled these data. Small mammal species were classified after Niethammer and Krapp (1978, 1982, 1990) and IUCN (2013) according to their habitat specialisation. *M. glareolus* and *Apodemus flavicollis* were categorised as 'forest specialists' (depend on forests, forest edges and forest patches), *Apodemus agrarius* (striped field mouse), *A. sylvaticus*, *S. araneus* and *Sorex minutus* (pygmy shrew) as 'habitat generalists' (no distinct habitat preference) and *Crocidura leucodon* (bicoloured white-toothed shrew) and *M. arvalis* as 'open land specialists' (depend on open agricultural landscapes).

Statistics

Correlation analyses (Pearson's product-moment correlation when both variables were normally distributed and Spearman's rank correlation when at least one variable was non-normally distributed) were performed to test for multicollinearity between all measured variables that describe habitat structure. Correlated variables (threshold level: $|r| > 0.7$; Table 2; Dormann et al. 2013) and variables that were highly skewed (vegetation cover; Table 1) were excluded from further analysis. The independent variables selected that describe habitat structure were percentage of ground covered by bare-soil and forest edge/hedge width (hereafter referred to as bare ground and width).

Linear mixed-effects models (lme function; Pinheiro and Bates 2000) with a maximized log-likelihood implemented in the R package nlme (ver. 3.1-111; Pinheiro et al. 2013) were used to test the effects of forest edge/hedge type (forest edge versus connected hedge versus isolated hedge), habitat structure (bare ground and width) and all two-way interactions using R 3.0.2 software (<www.r-project.org>).

Table 2. Correlation coefficients of parameters describing habitat structure of hedges and forest edges. Variables highlighted in grey exceeded threshold level of $|r| > 0.7$. Bare ground and width were used for further analysis.

| | Bare ground | Height | Litter cover | Vegetation cover | Width |
|-------------------------------|-------------|--------|--------------|------------------|-------|
| Bare ground ^a | – | | | | |
| Height ^a | 0.77 | – | | | |
| Litter cover ^a | –0.91 | –0.70 | – | | |
| Vegetation cover ^b | –0.16 | –0.29 | –0.07 | – | |
| Width ^b | 0.45 | 0.65 | –0.47 | –0.26 | – |

^aPearson correlation.

^bSpearman correlation.

Total small mammal abundance, species richness, abundance of each of the different habitat specialisation groups, and abundance of each of the two most abundant species (*M. glareolus*, *S. araneus*) were used as response variables. Study sites were included as random effect to model the independence of errors with respect to temporal autocorrelation (two trapping sessions within the same study site; Pinheiro and Bates 2000). To account for normal error distribution and homoscedasticity, response variables were square root transformed when necessary. Model selection and averaging was done by an information criteria approach using multi-model inference from the R package *MuMIn* (ver. 1.10.5; Barton 2014). From the global model, all candidate models (18 different models) were generated and ranked based on their AICc values (Akaike information criterion for small sample size corrections). Further, Δ AICc values in relation to the model with the minimum AICc, and Akaike weights, which provide a relative weight of evidence for each model and likelihood-ratio based R^2 -values were calculated. Models with Δ AICc ≤ 2 , which provide substantial empirical evidence for the model (Burnham and Anderson 2002), were averaged and the relative variable importance, weighted averages of parameter estimates, standard errors and confidence intervals were calculated. Confidence intervals of parameter estimates, which did not include zero, were considered to influence response variables significantly (Grueber et al. 2011). Contrasts between forest edges, connected and isolated hedges were investigated by re-ordering factor levels.

Small mammal community composition was assessed in relation to forest edge/hedge type (forest edge versus connected versus isolated hedge) and habitat structure (bare ground and width) by using a constrained ordination model. To decide on the ordination method, we first ran a DCA (detrended correspondence analysis, an indirect gradient analysis) to estimate the gradient length which measures the beta diversity in small mammal community composition (Leps and Smilauer 2003), for species data summed up over both trapping sessions. If the gradient length is shorter than 3.0 a linear constrained ordination method (RDA, redundancy analysis) is appropriate and if the longest gradient is larger than 4.0 the data are heterogeneous and a unimodal method (CCA, canonical correspondence analysis) should be applied (Leps and Smilauer 2003). Since the gradient length was shorter than 3.0, indicating species with a linear response, we decided to perform partial RDA (Leps and Smilauer 2003) using the R package *vegan* (ver. 1.17; Oksanen et al. 2011). Prior to analysis the species matrix was square root transformed. The species matrix was constrained by either forest edge/hedge type, bare ground or width, with the other two variables used as conditioning variables. The significance of constrained variables for each partial model was assessed by calculation of permutation tests based on 999 permutations. Pseudo-F-values with the corresponding p-values and ordination plots are given. To test for possible shifts of community composition among habitat specialisation groups, abundances of forest specialists and generalists were compared for forest edges, connected and isolated hedges, respectively using two-tailed Student's t-tests.

Results

We recorded 805 individuals (representing the first capture) of 11 species from 2160 trapping nights (1335 captures including recaptures; for total abundance, species richness and abundance of the different species within the forest edges/hedges: Table 3, Supplementary material Appendix 1 Table A1). Trap mortality, calculated as the number of animals that unintentionally died in traps, divided by the total number of captures, was 10% for all

Table 3. Total small mammal abundance, species richness and abundances of captured species per trapping session per forest edge, connected and isolated hedge (2 trapping sessions, 6 study sites: n = 12 respectively). Total values and mean values with standard errors are given.

| | Total | Forest edge | Connected hedge | Isolated hedge |
|------------------------------------|-------|-------------|-----------------|----------------|
| Total abundance | 801 | 30.5 ± 3.1 | 17.9 ± 2.2 | 18.3 ± 2.6 |
| Species richness | 8 | 3.8 ± 0.5 | 3.4 ± 0.6 | 3.3 ± 0.7 |
| Abundance of forest specialists | 527 | 23.4 ± 3.6 | 12.6 ± 2.1 | 7.9 ± 1.8 |
| <i>Myodes glareolus</i> | 465 | 21.5 ± 3.6 | 11.0 ± 2.1 | 6.3 ± 1.5 |
| <i>Apodemus flavicollis</i> | 62 | 1.9 ± 0.4 | 1.6 ± 0.7 | 1.7 ± 0.5 |
| Abundance of habitat generalists | 242 | 7.0 ± 1.0 | 4.9 ± 0.8 | 8.3 ± 1.1 |
| <i>Sorex araneus</i> | 173 | 4.9 ± 1.1 | 3.9 ± 0.8 | 5.6 ± 1.2 |
| <i>Apodemus sylvaticus</i> | 36 | 0.7 ± 0.3 | 0.8 ± 0.2 | 1.6 ± 0.6 |
| <i>Apodemus agrarius</i> | 22 | 0.8 ± 0.3 | 0.3 ± 0.2 | 0.8 ± 0.4 |
| <i>Sorex minutus</i> | 11 | 0.7 ± 0.3 | 0.0 ± 0.0 | 0.3 ± 0.1 |
| Abundance of open land specialists | 32 | 0.1 ± 0.1 | 0.4 ± 0.2 | 2.2 ± 1.4 |
| <i>Microtus arvalis</i> | 31 | 0.1 ± 0.1 | 0.3 ± 0.2 | 2.2 ± 1.4 |
| <i>Crocidura leucodon</i> | 1 | 0.0 ± 0.0 | 0.1 ± 0.1 | 0.0 ± 0.0 |

Table 4. Effects of forest edge/hedge type (forest edge versus connected hedge versus isolated hedge) and habitat structure (bare ground and width) on small mammal abundance, species richness and abundance of forest specialists and habitat generalists (for composition of forest specialists and habitat generalists see Table 3). Results of multi-model averaging from linear mixed effects models with $\Delta AICc \leq 2$ are given (parameter estimates with standard error, confidence intervals and levels of significance denoted with * = $p < 0.05$ and ** = $p < 0.01$). Variables indicated by ‘-’ were not part of the averaged model. LWLE: linear woody landscape element (F: forest edge, C: connected hedge, I: isolated hedge); %BG: bare ground, W: edge/hedge width, “:” indicates two-way interaction.

| | LWLE | | | %BG | W | LWLE:%BG | LWLE:W | W:%BG |
|---|--------------------------------|-----------------------------------|--------------------------------|---------------------------------|------------------------------|----------|--------|-------------------------------|
| | F-C | F-I | C-I | | | | | |
| Total abundance | -9.51 ± 5.57 (-21.21, 2.18) | -11.72 ± 4.41* (-21.17, -2.26) | -2.20 ± 5.35 (-13.46, 9.05) | -0.36 ± 0.36 (-1.13, 0.41) | 3.06 ± 2.19 (-1.50, 7.61) | - | - | -0.11 ± 0.08 (-0.29, 0.06) |
| Species richness ^a | - | - | - | 0.02 ± 0.01 (-0.01, 0.05) | 0.11 ± 0.10 (-0.10, 0.32) | - | - | -0.01 ± 0.00 (-0.01, 0.00) |
| Abundance forest specialists ^a | -0.69 ± 0.79 (-2.34, 0.96) | -2.05 ± 0.59** (-3.31, -0.79) | -1.36 ± 0.74 (-2.93, 0.21) | -0.07 ± 0.03* (-0.14, -0.00) | 0.28 ± 0.14* (0.05, 0.70) | - | - | - |
| <i>M. glareolus</i> ^a | -1.06 ± 0.70 (-2.55, 0.43) | -2.18 ± 0.62** (-3.50, -0.86) | -1.12 ± 0.69 (-2.57, 0.34) | -0.06 ± 0.03 (-0.13, 0.02) | 0.21 ± 0.17 (-0.15, 0.57) | - | - | - |
| Abundance habitat generalists | -2.08 ± 1.44 (-5.15, 0.98) | 1.25 ± 1.44 (-1.81, 4.31) | 3.33 ± 1.44* (0.27, 6.40) | - | - | - | - | - |
| <i>S. araneus</i> | - | - | - | - | - | - | - | - |

^aSquare root transformed.

species, with 1% mortality rate among rodents and 59% among shrews. Individuals from *Neomys fodiens* (Eurasian water shrew), *Arvicola amphibius* (European water vole), and *Glis glis* (edible dormouse) were excluded from analyses as these captures (four individuals in sum) were not representative due to unsuitable trapping method for this species or specialisation on aquatic habitat structures. We were not able to apply linear mixed effects models for open land specialists, as their abundance was highly right skewed, with only one or two individuals occurring in five forest edges and connected hedges and 26 individuals occurring in one isolated hedge.

Total abundance, abundance of forest specialists, as well as abundance of *Myodes glareolus* were higher in forest edges than in hedges, while isolation of hedges had no effect (forest edge > connected hedge = isolated hedge; Table 4, Fig. 2a, c, e). In contrast, abundance of habitat generalists was higher in isolated hedges than in connected hedges, while habitat type (forest edge versus hedge) had no effect (Table 4, Fig. 2d). For total species richness and abundance of *Sorex araneus* we did not find an influence of forest edge/hedge type (Table 4, Fig. 2b, f). Abundance of forest specialists was positively associated with decreasing percentage of bare ground and increasing forest edge/hedge width (Table 4). Species richness or abundance of any other group or species were not influenced by habitat structure (bare ground and width; Table 4; for the model selection table containing all models with $\Delta AICc \leq 2$ see Supplementary material Appendix 1 Table A2).

Small mammal community composition was affected by forest edge/hedge type (variation explained = 28.6 %, pseudo- $F_{2,13} = 3.14$, $p < 0.01$; Fig. 3a) and width (variation explained = 12.5%, pseudo- $F_{2,13} = 2.76$, $p < 0.05$; Fig. 3b), but not by bare ground (variation explained = 10.4%, pseudo- $F_{1,13} = 2.29$, $p = 0.09$). *Myodes glareolus* dominated the small mammal community in forest edges. The other species contributed similarly to the small mammal communities of forest edges and hedges. *Myodes glareolus* and

Apodemus flavicollis were predominantly present in small mammal communities in wide forest edges or hedges.

These results were also underlined by tests for possible shifts of community composition among habitat specialisation groups. We found a higher abundance of forest specialists compared to habitat generalists in forest edges ($t = 3.58$, $p < 0.05$) and connected hedges ($t = 2.68$, $p < 0.05$). Isolated hedges harboured similar numbers of forest specialist and habitat generalist individuals ($t = -0.12$, $p = 0.91$).

Discussion

Habitat specialisation is a key factor influencing species occurrence in different habitat types, shown for e.g. birds (Batáry et al. 2012) or arthropods (Petit and Usher 1998, Fischer et al. 2013). Studies have shown that small mammal forest specialists avoid the open agricultural matrix and are consistently found in forests and, in accordance to our results, in other woody landscape elements such as forest edges and hedges (Pollard and Relton 1970, Kotzageorgis and Mason 1996, Bentley et al. 2000). Even though our results show effects of habitat type (forest edge versus hedge) on abundance of forest specialists, we could not show an effect of isolation (connected versus isolated hedges). Studies on small mammals in forests have shown negative effects of increasing isolation when focusing on single species, such as *Myodes glareolus* and *Apodemus sylvaticus* (Kozakiewicz 1985, Paillat and Butet 1996, Fitzgibbon 1997, but see Szacki 1987). This is in accordance to our data, as forest edges in our study were linear woody landscape elements sharing half of their borders with the forest while connected and isolated hedges were less or not connected to forests. As habitat connectivity can influence immigration and population growth of forest specialists, with higher immigration, as well as growth rates in well-connected habitats than in isolated habitats, (Fahrig and Merriam 1985, Kozakiewicz 1985, Guivier

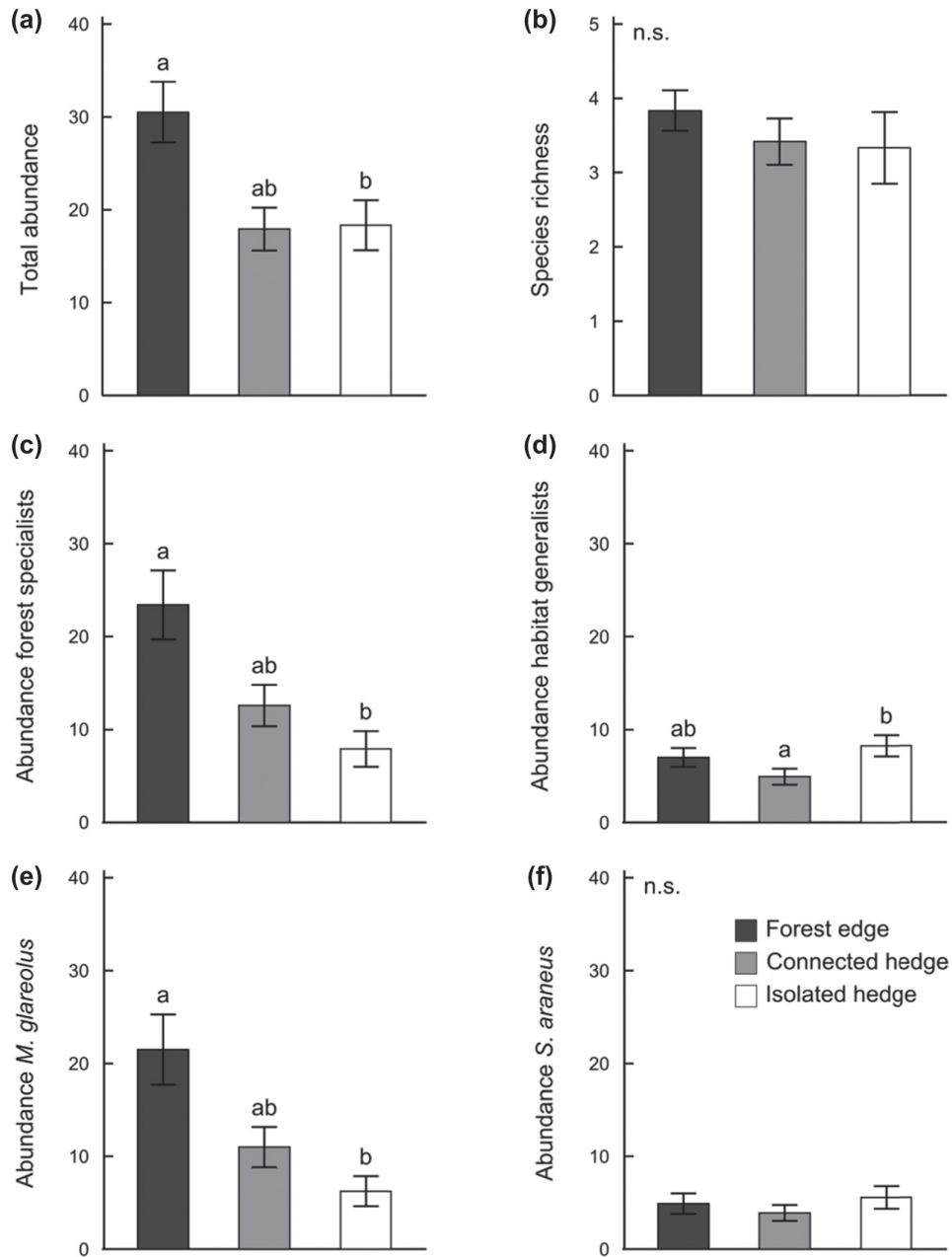


Figure 2. Effects of forest edge/hedge type on small mammals. (a) total abundance, (b) species richness, (c) abundance of forest specialists, (d) abundance of habitat generalists, (e) abundance of *M. glareolus* and (f) abundance of *S. araneus*. Means \pm SE per trapping session per forest edge, connected and isolated hedge (2 trapping sessions, 6 study sites: $n = 12$, respectively) are given. Factor levels containing different letters indicate significant differences at $p < 0.05$, which were determined by re-ordering factor levels between forest edges, connected hedges and isolated hedges. Non-significant results from averaged linear mixed-effects models are indicated by n.s.

et al. 2011), one would expect lower abundances of forest specialists in isolated than in connected hedges. In contrast, emigration from isolated habitats may be lower due to high matrix-patch contrast, influencing annual population densities positively (Fitzgibbon 1997). Here, distances of at least 300 m to the nearest forest seem to be still sufficient for forest specialists to reach hedges without structural connectivity to their main habitat. This is also supported by the population density ratio of forest specialists and habitat generalists: forest specialists showed overall higher population densities than habitat generalists in forest edges and connected hedges

while they were similar in isolated hedges. Further, not only woody structures but also marginal habitats, such as road verges (Bellamy et al. 2000, Broughton et al. 2014), as well as other factors such as habitat configuration in terms of habitat linearity (Tattersall et al. 2002) seem to be important for the occurrence of habitat specialists possibly leading to non-significant effects of isolation in our study.

The higher abundance of forest specialists in forest edges than in hedges, was mainly driven by *M. glareolus*, which was the most abundant, predominant forest specialist and in all but one study site (in one of the isolated hedges). This can

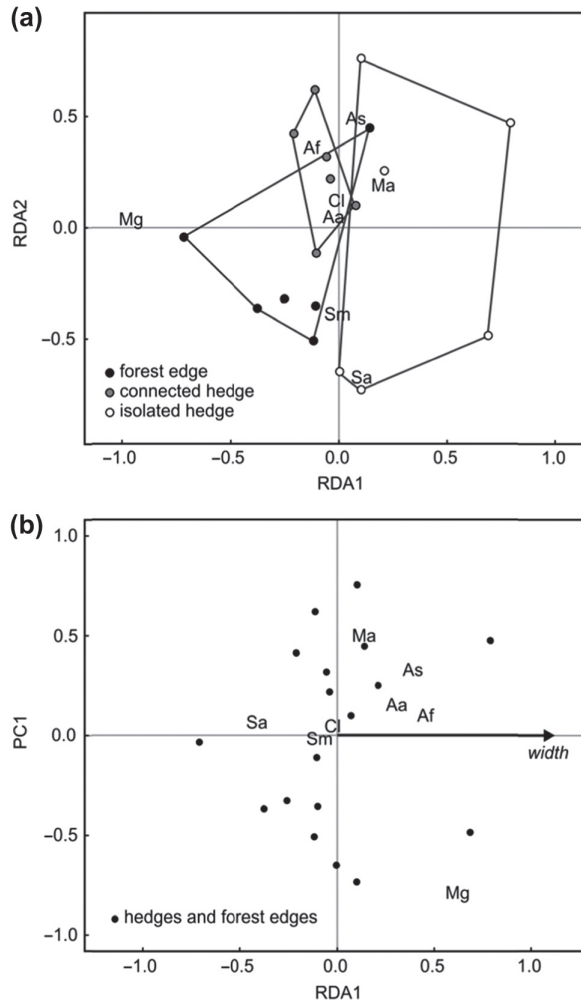


Figure 3. Effects of forest edge/hedge type on small mammal community composition. (a) RDA ordination diagram of small mammal communities in forest edges, connected hedges and isolated hedges shown with minimum convex polygons. (b) RDA ordination diagram for small mammal communities in forest edges and hedges with different widths (arrow). Small mammal species: Mg = *M. glareolus*, Af = *A. flavicollis*, As = *A. sylvaticus*, Aa = *A. agrarius*, Sa = *S. araneus*, Sm = *S. minutus*, Ma = *M. arvalis*, Cl = *C. leucodon*.

also affect the ecological functions provided through small mammals. For example, raptor abundances such as the common buzzard *Buteo buteo* decrease with decreasing prey availability and fragmentation (Butet et al. 2010). Further, the risk of disease emergence is potentially higher in forest edges compared to isolated hedges through higher abundances of *M. glareolus* and therefore higher number of reservoir hosts for e.g. Puumala hantavirus (cf. Voutilainen et al. 2012). In general, our results indicate the importance of hedges as landscape elements enhancing habitat availability for forest specialists and their population survival in fragmented landscapes. However, more clarity and robustness would be obtained with higher sample size over full population cycles and more years (also including masting years, potentially leading to population outbreaks of *M. glareolus*; Imholt et al. 2015), as well as by choosing isolated hedges along a gradient of isolation from forest, and studying small mammals' dispersal among hedges with different degrees of isolation.

Habitat generalists were affected by isolation (higher abundances in isolated versus connected hedges) but not by habitat type (forest edge versus hedge), probably because they frequently use various landscape elements such as forests, grasslands or agricultural fields as habitat or as food source (Pollard and Relton 1970, Bentley et al. 2000, Ouin et al. 2000, Wang and Grimm 2007). This pattern may be more pronounced after the crop harvest when fields provide little food and cover and generalist species such as *A. sylvaticus* individuals have to retreat into hedges (Fitzgibbon 1997, Tattersall et al. 2001). However, the most abundant generalist species *Sorex araneus* did not show any response to habitat type or to isolation. As shrews are insectivorous species (Wang and Grimm 2007) and therefore exploit different food sources compared to the omnivorous *M. glareolus* which just feeds on $8 \pm 2\%$ high energetic invertebrates (Butet and Delettre 2011), there seems to be a higher niche differentiation resulting in a complete overlap of both species in our study sites. Even if our observed shrew mortality rate of 59% is in line with the literature (Eccard and Klemme 2013, Shonfield et al. 2013) it may have influenced overall shrew abundances blurring our results. Therefore, from a methodological and welfare point of view other methods need to be used such as shorter trapping intervals to reduce shrew mortality (Stromgren and Sullivan 2014).

Species richness did not respond to habitat type or isolation of hedges. However previous studies showed negative effects of increasing forest isolation, due to a decrease of forest specialist species and constant numbers of generalist species (Pardini et al. 2005, Michel et al. 2006). In our study the lack of response of species richness to forest edge/hedge type can be explained by generally very low numbers of species (cf. Gentili et al. 2014), as well as by differences in small mammal community composition among forest edges and hedges. Forest specialists (*M. glareolus* and *A. flavicollis*) occur in all forest edges, but in just 80% of the hedges (connected and isolated hedges), while open land species (*M. arvalis* and *C. leucodon*) occasionally retreat into hedges and could be found in 20% of the hedges compared to 8% of forest edges, resulting in similar species richness. Further, small mammal communities of connected hedges were more similar to small mammal communities of forest edges than to those of isolated hedges, emphasizing an effect of isolation of hedges on small mammal communities (Bentley et al. 2000).

In our study decreasing percentage of bare ground was positively associated with the abundance of forest specialists, but had no influence on any other group. This is in line with other studies showing small mammals' preferences for habitats with low amount of bare ground and dense cover of herbaceous vegetation (Mazurkiewicz 1994, Ouin et al. 2000, Silva and Prince 2008), mostly interpreted as antipredatory behaviour by small mammals. Thereby, not only dense cover of herbaceous vegetation and litter, but also dense shrub layers of hedges and forest edges may protect small mammals from predators (Jedrzejewska and Jedrzejewski 1990, Longland and Price 1991, Weber 2008). Further, increasing forest edge/hedge width was positively associated with the abundance of forest specialists and changed the community composition (cf. Gelling et al. 2007, Michel et al. 2007). Increasing hedge width also increases the available habitat for forest species (Gelling et al. 2007), while habitat generalists

such as *S. araneus*, *A. agrarius* and *A. sylvaticus* also use a variety of habitats within agricultural landscapes (Pollard and Relton 1970, Ouin et al. 2000, Wang and Grimm 2007), being less sensitive to decreasing availability of forest edge or hedge habitats. Since we merely used the naturally occurring variability of percentage of bare ground and forest edge/hedge width as explanatory variables for small mammal occurrence, the variance within sites seems to be rather low to affect abundance of habitat generalists (but see Butet et al. 2006, Silva and Prince 2008).

Conclusions

We found that small mammal forest specialists were more abundant in forest edges than in hedges, while abundance of habitat generalists was higher in isolated compared to connected hedges. However, not only forest edges, but also hedges, harboured a relatively high abundance of forest specialists compared to habitat generalists, probably due to their higher dependency on woody landscape elements in agricultural areas. Isolation of hedges had no significant effect on abundance of forest specialists showing that habitat suitability of hedges without structural connection to the forest was equivalent to connected ones. Thus small mammal forest specialists may profit from even isolated hedges by providing habitat area and refuges in fragmented agricultural areas. However, to make general predictions on the impact of isolation of hedges on generalist small mammal species in agricultural landscapes, also potential positive effects of hedges as refuges after the crop harvest have to be studied. In sum, well connected as well as isolated hedges in agricultural landscapes are marginal habitats for small mammals, independently whether they are forest specialists, habitat generalists or even open land specialists. Thereby the maintenance and creation of hedges in agricultural landscapes may be an effective tool to increase small mammal diversity and thus overall farmland biodiversity.

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Supplementary material (available online as Appendix wlb-00176 at <www.wildlifebiology.org/appendix/wlb-00176>). Appendix 1.