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Insect Conservation and Diversity (2016) doi: 10.1111/icad.12210

Ground beetle (Coleoptera: Carabidae) diversity is higher in narrow hedges composed of a native compared to non-native trees in a Danish agricultural landscape

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Abstract. 1. Non-cultivated areas in agricultural landscapes can substantially contribute to biodiversity. Therefore, to examine the role of tree-line hedges in supporting arthropod diversity in an agricultural landscape, we sampled carabid beetles in three replicates of a native deciduous (hawthorn, *Crataegus monogyna*), non-native deciduous (rowan, *Sorbus intermedia*), and a non-native coniferous (spruce, *Picea* spp.) hedge in Jytland, Denmark.

2. We hypothesised that hedgerows with deciduous trees harbour more diverse carabid assemblages than hedges composed of non-native trees.

3. The number of carabid individuals and species was highest in the hawthorn hedges and significantly lower in rowan and spruce. This was caused by the presence of forest specialist species. Differences in the number of the grassland and the cropland specialist ground beetle individuals and species were not statistically significant among the hedges.

4. Litter depth and the density of herbs and grasses negatively, while hedge width positively influenced carabid diversity.

5. Overall, hedges composed of the native, deciduous hawthorn were superior to ones composed of the non-native rowan, and especially to coniferous ones to conserve and maintain carabid diversity in this cultivated Danish landscape.

Key words. Carabids, character species, diversity, hawthorn, IndVal, rowan, spruce.

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Introduction

Although the species richness found on cultivated land
2 can be high (Mészáros *et al.*, 1984; Kromp, 1999), non-cultivated areas in an agricultural landscape significantly contribute to biodiversity (Maudsley, 2000). With the increasing human pressure, more and more non-cultivated habitats are enclosed in a cultivated habitat matrix, and their significance as biodiversity refuges increases (De la Pena *et al.*, 2013). Click here to enter text.The overall level of biodiversity that cultivated landscapes, however, can support over the long term is neither well characterised nor understood (Daily, 1999). An improved understanding of these factors would help to achieve a more efficient management of biodiversity as well as of the ecosystem services they provide (Daily, 1999; Isbell *et al.*, 2011).

Hedgerows can support regional biodiversity of agricultural landscape in several ways. For species inhabiting cultivated land, they can provide shelter, refuge during and possible source (recolonisation) habitats after agricultural operations (Marchi *et al.*, 2013). Moreover, hedges serve as overwintering (Pywell *et al.*, 2005) or oversummering sites (Varchola & Dunn, 2001; Fischer *et al.*, 2013), and provide alternative food sources (Maudsley, 2000) for species living in cultivated habitats. Hedges can support shrub and tree-living species as well as edge-preferring ones. Hedges also add to the fauna through supporting grassland or forest species (Šustek, 1992; Petit & Usher,

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1998; Toft & Lövei, 2002) and can link fragmented habitats, thus enabling dispersal and survival of metapopulations (Marchi *et al*., 2013).

Non-sprayed field edges and flowering strips have been more extensively studied than hedges (Maudsley, 2000). Most of the studied hedgerows were wide, usually 10–20 m (Fournier & Loreau, 2001; reviews in Kromp, 1999; Niemelä, 2001; Šustek, 1992). The ground beetle fauna of tree-line hedgerows is not much studied (but see Petit & Usher, 1998). These, due to their narrowness, are expected to be heavily influenced by influx from the adjacent cultivated fields, but have, to our knowledge, not specifically been analysed.

The aim of this study was to evaluate differences in ground beetle (Coleoptera: Carabidae) assemblages in different narrow hedgerows in a Danish agricultural landscape. We hypothesised that hedgerows with native deciduous trees will harbour more diverse ground beetle assemblages than hedges composed of non-native deciduous or needle-leaved ones. Moreover, we investigated which vegetation and habitat structure characteristics of the hedges might be the most important to influence the number of individuals and species of the ground beetles.

Material and methods

Sites and sampling procedure

Our study area was near Bjerringbro (56°38′08′′N, 09°05′44′′E), central Jutland, Denmark. Nine, old (30–50 years), well-established hedges of the tree-line type were selected for study, three each of hawthorn (*Crataegus monogyna*), rowan (*Sorbus intermedia*), or spruce (two of white spruce *Picea glauca,* and one of sitka spruce*, Picea sitchensis*). Hawthorn is native to Denmark, rowan is a supposedly Baltic floral element and is widely planted as a hedge, but in Denmark, the species is only native to the island of Bornholm (Lindman, 1965). Species of spruce are frequently planted, non-native trees. Although there was some variation regionally in the composition of hedgerows (Ravn & Sigsgaard, 1999), the selected hedgerows were mainly monospecific, except some presence of elderberry (*Sambucus nigra*) in the hawthorn hedges. The total width of the hedgerows was variable. The means (±SD) at the three locations were as follows: hawthorn, 3.10 m (SD = 0.92 m) m; rowan, 3.58 m (SD = 1.24 m) m; and spruce, 3.13 m (SD = 0.18 m) m. The sitka hedge was planted in a zig-zag pattern, creating a centre with strong shade, where there was little vegetation. The height of the studied hedges was 2.5–3.5 m. The nine sample locations were at a distance of 200 m to 10 km from each other, all enclosed within a 4 × 10 km area.

Individual hedgerows were sampled twice yearly, for 1 week each during the early (June 1999) and late (early September 1999) ground beetle activity peak, using 20 pitfall traps per habitat patch. Ten of the traps were set at the edge, and ten in the centre of the hedgerow, at a distance of 10 m between individual traps. Neighbouring traps alternated with respect to position to have a minimum distance of 20 m between two traps in identical position. Spatial autocorrelation analyses of our data revealed that there was no positive spatial autocorrelation between neighbouring traps, therefore our pitfall trap distance could be regarded as statistically independent (Appendix S1). Digweed *et al*. (1995) and Niemelä *et al*. (2000) also claimed that pitfall traps installed at least 10 m apart ensure independent sampling. The same sampling procedure yielded 85% of the ground-active spider species that were found with whole-year sampling in Jutland (S. Toft, University Århus, Denmark, pers. comm. 2003).

Individual pitfall traps were 500 ml plastic cups of 10 cm diameter, filled with about 200 ml of 70% ethylene glycol solution and a drop of odourless detergent. Traps were sunk into the ground so that their rim was level with the soil surface. Every trap was covered with a square (20 × 20 cm) galvanised metal cover to protect the trap contents from rain and disturbance by frogs, birds, or small mammals (Lövei & Sunderland, 1996). Trap catches were sieved in the field, and transferred into glass vials containing 70% ethyl alcohol; the killing/preservative solution was changed if soiled. Trap catches with small mammals or frogs as well as displaced or raised traps (33 of a total of 360 samples) were not included in the evaluation. In the laboratory, the samples were sorted under a microscope, ground beetles were put into separate vials, and stored in 70% ethyl alcohol until identification. All beetles were identified to species using the keys by Lindroth (1985, 1986) and Freude *et al*. (1976). Habitat preference (forest, grassland, and cropland specialist) of the collected species was designated from the literature (Lindroth, 1985, 1986).

Vegetation structure

The structure of ground vegetation was described using a pin frame (Greig-Smith, 1983). The frame holds 10 pins at a distance of 10 cm from each other along a horizontal support rail. Individual pins were 1-m-long steel pins (2 mm diam.) marked every 1 cm between 0 and 5 cm from the ground, and every 5 cm between 5 and 50 cm. The number of plants touching a pin at any of these intervals was counted, giving a 'vertical density profile' of the habitat close to the ground. Plants touching pins >50 cm were summarised into one category.

Four frames (total of 40 pins) were taken from each shelterbelt during late August 1999. Pin frames were randomly positioned, but always between two traps, within the shelterbelt, avoiding the last 15 m of the hedges at either end. The pin frame was positioned at a ca. 30° angle with respect to the edge to span the vegetation between the edge and the tree line. Any plant touching the pins at every 1 cm interval between 0 and 5 cm height, and every 5 cm interval above that was counted.

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Ground cover at the base of each pin was also noted (bare ground or litter), and litter depth was measured. Plants were not identified to species but categorised as herbs, forbs, or dead plant material/litter.

Data processing

For evaluation, the catches of the individual traps were summarised, giving 180 samples (3 locations × 3 hedge types × 20 traps). Catches of edge and centre traps were not significantly different within any of the locations, therefore during further evaluations we did not distinguish between the traps on the basis of their position. The number of individuals and the species richness of the trapped ground beetles were examined by generalised linear mixed-effects model (GLMM). In the model hedge type was regarded as fixed factor, whereas spatial replicate (location) as random factor. The response variables (ground beetle abundance and species richness) were defined as a quasi-Poisson distribution with log-link function (Zuur *et al*., 2009). When GLMM revealed a significant difference between the means, a Tukey's HSD test was performed for multiple comparisons among means.

Habitat affinity

The characteristic species of the hedgerows was explored by the IndVal (Indicator Value) procedure (Dufrêne & Legendre, 1997). It is a useful method to find indicator species and/or species assemblages characterising groups of samples. This approach combines a species' abundance with its frequency of occurrence in the various groups of samples. The indicator value is maximum (100) when all individuals of a species are found in a single group of sites (high specificity) and the species occurs at all sites of that group (high fidelity). The statistical significance of the species indicator values is evaluated by a Monte Carlo reallocation procedure. The IndVal method is robust to differences in the numbers of sites between site groups, to differences in abundance between sites within a particular group, and to differences in the absolute abundances of different species or taxa (McGeoch & Chown, 1998). The IndVal method is a quantitative characterisation of the idea of indicator species of the classical plant sociology, based on a computerised randomisation procedure. Therefore, we used the term 'quantitative character species' as proposed by Elek *et al*. (2001). In the IndVal analysis, we involved only species with ≥10 individuals captured.

Effect of vegetation characteristics on ground beetle assemblages

The relationship between the number of ground beetle individuals and species captured and the selected vegetation and habitat structure characteristics was examined by generalised linear model (GLM) using the multiple regression design. We first fitted the full model containing all vegetation and habitat structure characteristics. We evaluated models based on Akaike's Information Criterion (Akaike, 1973) and accepted the model with the lowest AIC as the final model. Differences between the AIC value of the candidate models and those of the best models were expressed by the ΔAIC values. In the final model the dependent variables (ground beetle abundance and species richness) were defined as a quasi-Poisson distribution with log-link function (Zuur *et al*., 2009). The following vegetation and habitat structure characteristics were involved in the analysis: the total number of touches by herbs, grasses, and all plants; touches of same below 5 cm, and above 50 cm, average vegetation height for the same categories, thickness of litter layer, and the width of shelterbelt. All vegetation characteristics were calculated as per-pin averages.

Results

Assemblage composition

A total of 2865 individuals were captured, belonging to 71 ground beetle species: 52 species (1450 individuals) were found in hawthorn hedges, 56 species (919 individuals) in rowan, and 42 species (496 individuals) in spruce. Overall, the most common species were *Platynus dorsalis*, *Pterostichus melanarius, Calathus fuscipes, Calathus melanocephalus,* and *Carabus nemoralis* (Table 1). These species were common in all three hedgerow types studied but there were variations in rank (Table 1). In rowan, *Bembidion tetracolum, Trechus quadristriatus,* and *Pterostichus versicolor* were third, fourth, and fifth in the capture rank. In spruce, *Bembidion lampros* was the fifth most common species. In hawthorn, *Nebria brevicollis* (third most common species) and *Calathus rotundicollis* (fifth most common) were in the first five common species (Table 1).

Effect of hedgerow type on carabid diversity

The number of ground beetle individuals and species was significantly the highest in the hawthorn hedges and decreased from the hedges with rowan towards the spruce hedges (Estimate = −0.52; SE = 0.02; $z = -21.35$; $P < 0.001$ and Estimate = −0.25; SE = 0.04; $z = -6.72$; $P < 0.001$, respectively; Fig. 1).

The number of forest specialist ground beetle individuals and species was significantly higher in the hawthorn hedges compared to the hedges with rowan and spruce (Estimate = −1.03; SE = 0.07; $z = -15.65$; $P < 0.001$ and Estimate = −0.55; SE = 0.09; $z = -6.35$; $P < 0.001$, respectively; Fig. 2).

Differences in the number of the grassland specialist ground beetle individuals and species were not statistically

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Table 1. The list and habitat preference of the ground beetle species commonly captured in pitfall traps in different hedgerows in the Bjerringbro area, central Jutland, Denmark, in 1999.

Species	Habitat preference	Spruce	Rowan	Hawthorn	Total
Platynus dorsalis		70	169	351	590
Pterostichus melanarius		57	101	301	459
Calathus fuscipes		51	57	102	210
Calathus melanocephalus		61	72	71	204
Carabus nemoralis	forest	33	58	90	181
Trechus quadristriatus		25	82	34	141
Nebria brevicollis	forest	13	3	118	134
Pterostichus versicolor	grassland	18	76	29	123
Bembidion lampros	cropland	38	50	27	115
Calathus rotundicollis	forest	2	4	99	105
Bembidion tetracolum		2	93	4	99
Harpalus quadripunctatus	forest	0	0	32	32
Harpalus rufipes	cropland	6	10	16	32
Amara familiaris		19	4	5	28
Leistus ferrugineus		6	4	15	25
Harpalus tardus		15	8	1	24
Pterostichus cupreus	cropland	12	9	3	24
Pterostichus oblongopunctatus	forest	1	16	7	24
Syntomus truncatellus		12	12	0	24
Carabus coriaceus	forest	3	10	8	21
Calathus erratus		1	4	12	17
Notiophilus palustris	grassland	4	3	9	16
Bembidion obtusum	cropland	1	2	12	15
Harpalus rufibarbis		0	3	12	15
Syntomus foveatus		4	11	0	15
Notiophilus biguttatus	forest	0	1	11	12
Calathus micropterus	forest	4	2	5	11
Carabus violaceus		7	3	1	11
Pterostichus niger	forest	2	1	8	11
Total number of individuals		496	919	1450	2865
Total number of species		42	56	52	71

Only species with ≥10 individuals captured are included. Sequence is by rank, considering the total numbers captured.

significant among the hedges (Estimate = −0.17; SE = 0.10; $z = -1.63$; $P = 0.103$ and Estimate = −0.19; SE = 0.16; $z = -1.24$; $P = 0.215$, respectively, Fig. 3). Similarly, the number of the cropland specialist ground beetle individuals and species did not differ significantly among the hedges (Estimate = −0.04; SE = 0.09; $z = -0.44$; $P = 0.658$ and Estimate = −0.08; SE = 0.11; $z = -0.67$; $P = 0.501$, respectively, Fig. 4).

Effect of vegetation and habitat structure on carabid diversity

Only a few of the measured vegetation and habitat structure characteristics indicated a significant relationship between the number of ground beetle individuals and species and the tested vegetation and habitat structure variables (Table 2). Candidate models had higher AIC value (ΔAIC > 2) compared to the best model. Litter depth and number of herbs and grasses negatively, whereas hedge width positively influenced both the number of ground beetle individuals and the number of species. This was, however, not hedge species specific, as there were no significant differences between litter depth or hedge width among the three species, analysed by generalised linear models (litter depth: estimate = 0.276: SE = 0.301; $t = 0.917$; $P = 0.390$; hedge width: estimate = 0.018; SE = 0.11; $t = 0.16$; $P = 0.878$).

Habitat affinity of individual species

According to the IndVal analysis (Fig. 5), 13 species did not show affinity to any of the three hedge types studied. These species can be considered generalists, at least in the studied landscape. *P. oblongopunctatus* was the only species avoiding spruce hedges but not discriminating between the two different deciduous hedges. Eleven more species were identified as preferring hawthorn or rowan (Fig. 5). This preference, however, was not always accompanied by an avoidance of spruce. For example, *Leistus ferrugineus,* while identified as linked to hawthorn hedges, was captured more in spruce than rowan hedges. Four species preferred spruce – all of these occurred also in

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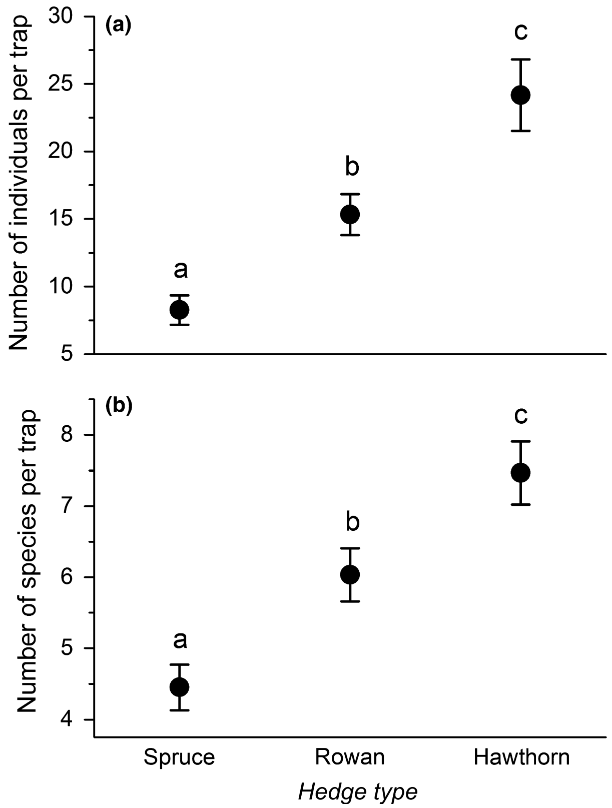

Fig. 1. The average number of ground beetle individuals (A) and species (B) captured in pitfall traps in hawthorn, rowan, and spruce hedgerows in Bjerringbro area, central Jutland, Denmark. The error bars indicate ± one standard error of the mean. $n = 60$ in each hedge type. Different letters indicate statistically significant ($P < 0.05$) differences by Tukey test.

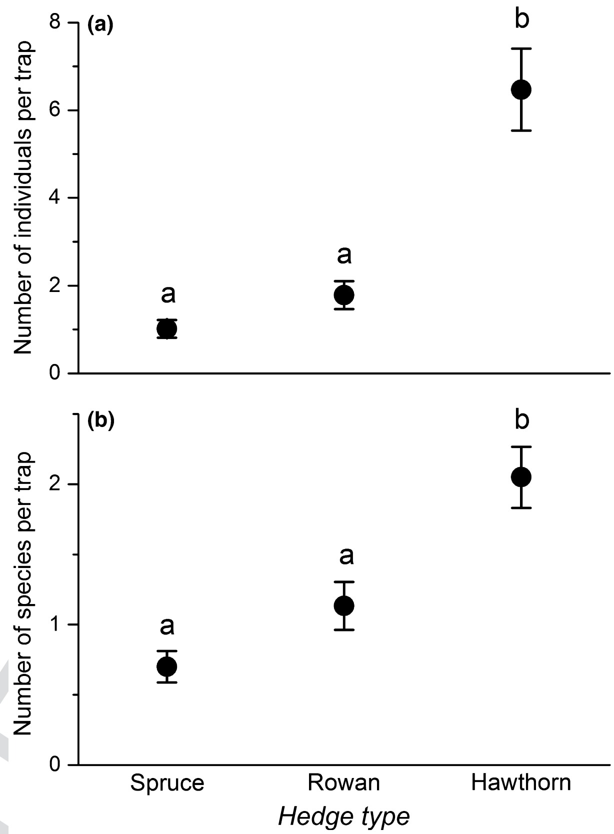

Fig. 2. The average number of forest specialist ground beetle individuals (A) and species (B) captured in pitfall traps in hawthorn, rowan, and spruce hedgerows in Bjerringbro area, central Jutland, Denmark. The vertical lines indicate ± one standard error of the mean. $n = 60$ in each hedge type. Different letters indicate statistically significant ($P < 0.05$) differences by Tukey test.

rowan hedges, and only one of them was not captured at all in hawthorn hedges (Fig. 5).

Discussion

The detected level of diversity (species richness) in our studied hedges, compared to other European studies indicated the presence of a rather diverse carabid fauna. Only 22 carabid species were found in hawthorn hedgerows in the UK (Pollard, 1968). In Scotland, narrow hedgerows supported 41 species (Petit & Usher, 1998), and in France, 30–33 species were reported (Fournier & Loreau, 1999, 2001). Extensive studies in Western France (Burel, 1989, 1992) have indicated the presence of 42–59 species. Other factors such as pesticide use, the intensity and frequency of agricultural operations, and general landscape structure may play a role, but given the generally decreasing species richness gradient from southern towards northern Europe, the 71 species found in this study indicate that other studies may have underestimated the true ground beetle diversity supported by hedgerows.

Our sampling regime was restricted to certain parts of the season. This decision was supported not only by the high number of species found with respect to other European studies but also by spider data from the surrounding area where the spiders in our pitfall traps were a representative sample of the cursorial spider fauna of the surrounding area (Toft & Lövei, 2002). Such a sampling could be questionable when biology or reproduction is the focus of the studies. In biodiversity studies, we would argue that if a smaller trapping effort gives acceptable results, there is no need to kill a large number of arthropods. Click here to enter text.This should be carefully assessed because expanding along the spatial versus temporal dimension could yield different results, however (Gruttke & Kornacker, 1995; Lövei & Magura, 2011).

Carabid assemblages in our narrow hedgerows did not differ with respect to trap position (edge vs. centre). The narrow hedges supported several forest species. Spreier (1982) found that in a land consolidation area in Germany, the minimum width should be 4 m before the hedge becomes suitable for forest species (Spreier, 1982).

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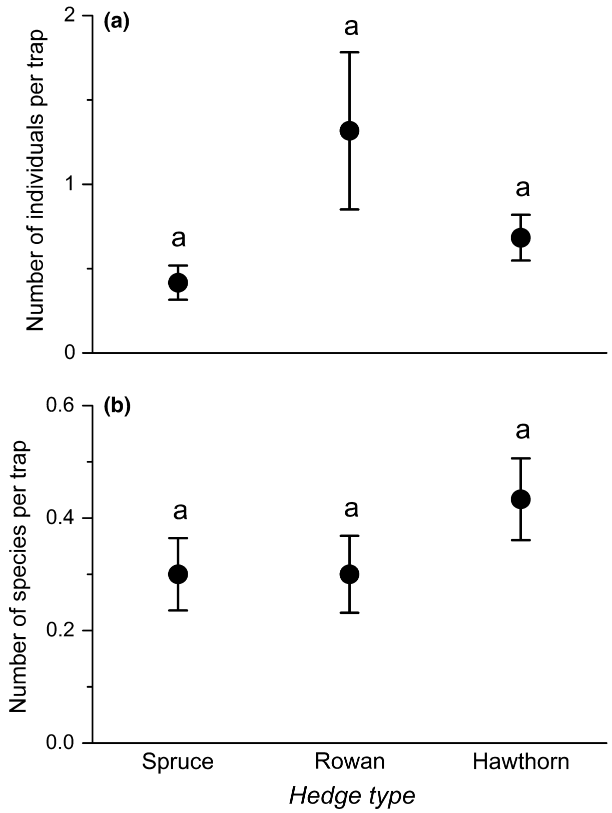

Fig. 3. The average number of grassland specialist ground beetle individuals (A) and species (B) captured in pitfall traps in hawthorn, rowan, and spruce hedgerows in Bjerringbro area, central Jutland, Denmark. The vertical lines indicate ± one standard error of the mean. $n = 60$ in each hedge type. Different letters indicate statistically significant ($P < 0.05$) differences by Tukey test.

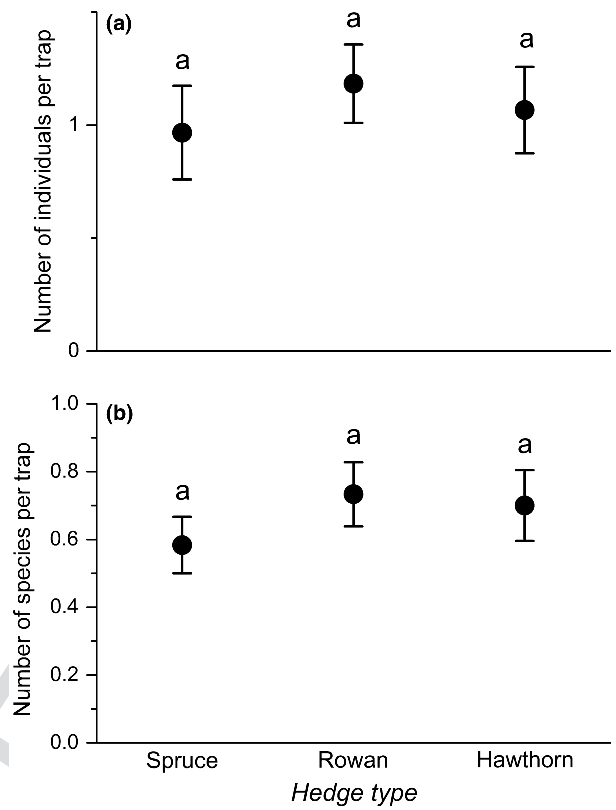

Fig. 4. The average number of cropland specialist ground beetle individuals (A) and species (B) captured in pitfall traps in hawthorn, rowan, and spruce hedgerows in Bjerringbro area, central Jutland, Denmark. The vertical lines indicate ± one standard error of the mean. $n = 60$ in each hedge type. Different letters indicate statistically significant ($P < 0.05$) differences by Tukey test.

Table 2. Negative (–) and positive (+) relationship between the species richness and number of individuals captured in different hedgerows in central Jutland, Denmark, and the selected vegetation and habitat structure characteristics by generalised linear model (GLM) using the multiple regression design.

Characteristic	Number of individuals	Number of species	Number of forest specialist individuals	Number of forest specialist species
Hedge width, cm	+***	+*	+***	not entered
Litter depth, cm	–***	–*	–***	–*
Grass density <5 cm	not entered	not entered	not entered	not entered
Grass density >5 cm	not entered	not entered	not entered	not entered
Grass density, total	not entered	not entered	not entered	not entered
Herbs <5 cm	not entered	not entered	not entered	not entered
Herbs >5 cm	not entered	not entered	not entered	not entered
Herbs Total	not entered	not entered	not entered	not entered
Grass + Herbs <5 cm	not entered	not entered	not entered	not entered
Grass + Herbs >5 cm	not entered	not entered	not entered	not entered
Grass + Herbs Total	–**	not entered	–***	not entered

Significant relationships are indicated by asterisks: *$P < 0.05$, **$P < 0.01$, and ***$P < 0.001$, whereas ns, not significant. Not entered denotes that the given characteristic was not entered into the final model based on Akaike's Information Criterion (AIC).

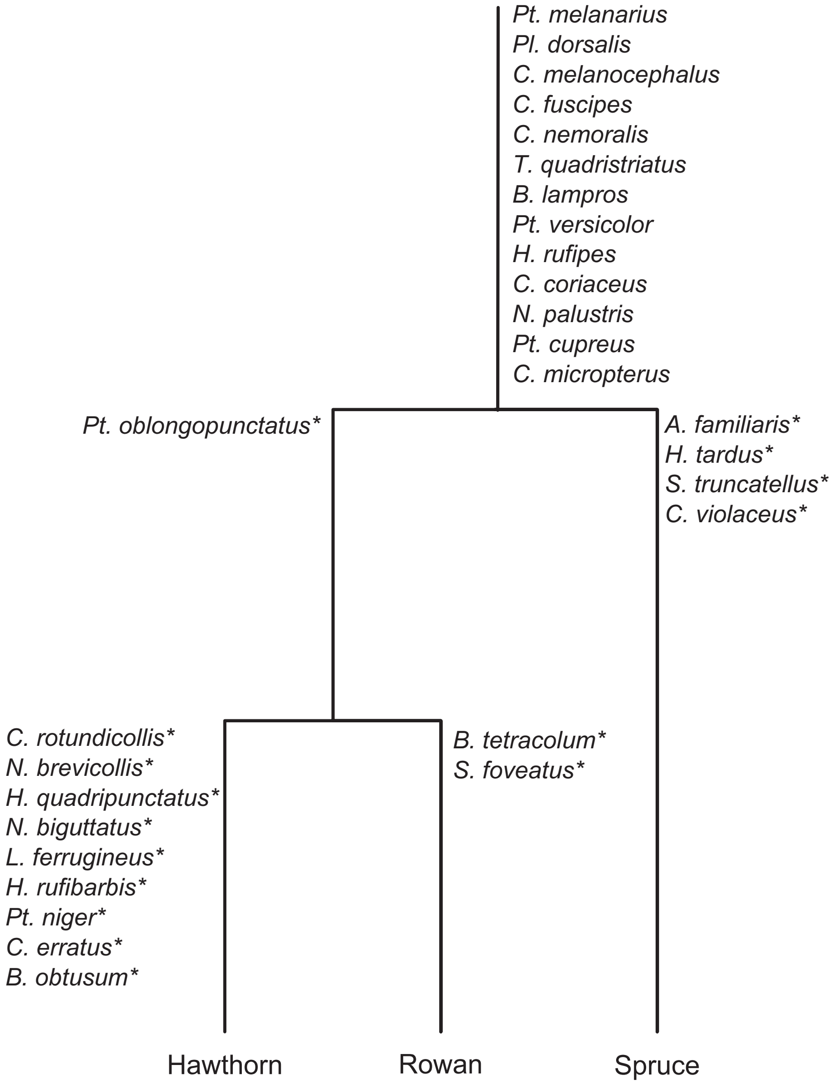

Fig. 5. Dendrogram showing quantitative character species for three different hedge types based on pitfall trap catches in central Jutland, Denmark. Only species represented by ≥10 individuals are shown. Significant character species are marked with an asterisk. Full names are listed in Table 1.

The reason for this difference could be in the landscape structure. A wider hedge with trees can generate more favourable humidity and temperature conditions for forest species, more variable microsites, more prey, or better protection from predators (or several of these together), and can attract forest species to an otherwise non-supportive landscape. Nonetheless, it is likely that a major determinant of the forest species-supporting effect is linked to the presence of trees, even if those are few. It is plausible to assume that trees, through their root system, together with their fungal and other symbionts, influence the soil properties and chemistry, which may be crucial for ground beetles, especially for their soil-bound larvae (Lövei & Sunderland, 1996). In addition, the landscape in our study area had numerous narrow hedges and sporadic forest patches. Petit and Usher (1998) have also found forest species present in narrow hedges in Scotland.

Comparing the carabid assemblages detected in the hedgerows with carabid assemblages collected in large natural forests in the Jutland Peninsula (Jensen & Toft, 2014) showed that the highest share of the assumed 'original' forest fauna was retained by the hawthorn edge (41% average similarity), followed by the two non-indigenous hedge species (25% for rowan, 28% for spruce). The presence of field-living species, such as *P. dorsalis*, *P. melanarius*, and *T. quadristriatus* (Kromp, 1999), indicated the influence of the surrounding matrix as also found in south-eastern Europe (Lövei *et al.*, 2006). Field-living ground beetle species use hedges and field edges as overwintering sites (review in Kromp, 1999). Overall, it seems

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that narrow hedges provide habitat for both field-living and forest-living species. The surrounding matrix influenced hedgerow ground beetles more than hedgerow spiders (Toft & Lövei, 2002).

Hedges in agricultural landscapes have several functions: they can be buffer zones, refuges, and sources for field colonisation (Varchola & Dunn, 2001; Pywell *et al*., 2005; Fischer *et al*., 2013). Hedges can support wildlife, plant, and invertebrate biodiversity and can serve as corridors linking suitable habitat patches in a hostile landscape matrix (Marchi *et al*., 2013). The importance of hedges in intensively cultivated country sides, such as on the British Isles, is significant (Maudsley, 2000). Our results underline that the composition of the hedge could also be important. Hedges are not merely physical structures and their plant composition significantly influences the assemblages that live in hedges.

Hedge species composition also had a profound influence on ground beetle assemblages, and native plants harboured more species than non-native ones. This was also found in Moravia, central Europe (Šustek, 1992). Overall, hawthorn can be considered the best habitat type in this study for beetle diversity. This can be explained because this species is native, and for ground beetles, this hedge could provide the best combinations of conditions (vegetation structure, microclimate, soil, available food, protection from predators, etc.) within their tolerance limits. Rowan also had high number of individuals and species, although ground beetle diversity was significantly lower in the rowan hedges, compared to the hawthorn ones. Rowan is not a native species to the study area, although it is widely present in Denmark, and native in southern Sweden, areas of the Baltic, and on the island of Bornholm (Frederiksen *et al*., 2006). As this species is thought to have developed after the last Ice Age (Lindman, 1965), rowan cannot be considered fully 'native' habitat for extant Scandinavian ground beetle species. The thick deciduous litter produced by rowan trees seemed to be advantageous for some species. Deciduous litter can provide favourable microclimate, and creates a complex spatial structure through generating stratification that can allow the coexistence of some ground beetle species (Loreau, 1987). Click here to enter text.From the patchiness of occurrences at regional scale, however, rowan seems to provide a more coarse-grained habitat, i.e. there are more areas where conditions are not favourable for ground beetles than in hawthorn.

Similar factors can explain why spruce hedges had a relatively poor ground beetle assemblage. The soil underneath is acidic, due to the breakdown of needle leaves. This could decrease the density of other arthropods and thus the food supply for ground beetles (Magura *et al*., 2003). Pitfall trapping is a passive catching method; therefore, catches are a function of the species' true population size and its activity (activity–density; Lövei & Sunderland, 1996). Habitat features (such as cover and density of litter and herbs) may influence the walking speed of species, so also the number of individuals caught by traps (Lövei & Sunderland, 1996). Our study indicated that deeper litter and denser habitat at ground level negatively influenced pitfall trap catches. Click here to enter text.None of the habitats were consistently without litter or grass, however. The overall impact of this would be to even out differences between ground beetle assemblages in various hedges, which was not found. Thus, our results seem to be robust against this potential distortion. The high number of carabid species detected (with respect to similar studies in Europe, see above) testify that the existing assemblage was effectively sampled, and the differences among the hedgerow types are not artefacts.

The causes of individual species habitat preferences are not always known. *P. oblongopunctatus* has a preference for habitats covered with dense deciduous litter (Koivula *et al*., 1999; Magura *et al*., 2005). This species is active inside the litter layer rather than on the surface (Loreau, 1987) and thus in a microhabitat that is not used by other, larger species. Among the species classified as hedge-preferring ones in this study, only *L. ferrugineus* has previously been classified as such (in Scotland, Petit & Usher, 1998). Petit and Usher (1998), however, found that *N. biguttatus* is a field-preferring species in Scotland, whereas in our study, it was linked to hawthorn hedges. *T. quadristriatus* preferred hedgerows in Scotland (Petit & Usher, 1998), but was a generalist in Denmark. *N. brevicollis* was reported not to distinguish between hawthorn hedges with or without ground vegetation (Pollard, 1968). These differences are further proof that ground beetle species do not have the same habitat preference throughout their whole distribution range, as also found by Tyler (2008).

Litter depth and the number of herbs and grasses negatively, while hedge width positively influenced both the number of individuals and species in the ground beetle assemblages. This can be influenced by beetles entering the hedges from the neighbouring agricultural habitats – they are not adapted to thick deciduous litter. There is probably an added factor of physical complexity that slows down the movement speed by walking beetles, and influences their trappability.

Our results, although obtained on a limited set of hedge-forming species, indicate that to conserve and maintain arthropod (ground beetle) biodiversity, hedges composed of native deciduous species may be more favourable than non-native, and especially needle-leaved species. While the 'native deciduous – non-native deciduous – non-native, needle-leaved' sequence seems logical, more types of hedges have to be compared before firm generalisation can be drawn on their biodiversity-supporting role. **Click here to enter text.**Species presence, however, does not automatically mean that the given species is thriving in the habitat. Additional support for our conclusion could be sought by analysing reproductive conditions (Kádár *et al*., 2015), fitness-related characters such as fluctuating asymmetry (*Elek et al.,* 2014), or temporal occurrence patterns (Howe & Enggaard, 2006) that could indicate impacts that may otherwise remain hidden.

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Acknowledgements

We thank L. Sigsgård and H.-P. Ravn for selecting study sites, U. Althoff, J. Lilholt, L. M. Hansen, U. Sandberg, and L. Christensen for practical help, and our handling editor and anonymous reviewers for comments and suggestions. This work was done under the framework of 'Boundaries in the landscape' programme, supported by the Danish Research Agency. TM was supported by the SROP4.2.2.B15/1/KONV20150001 project supported by the European Union, co-financed by the European Social Fund.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: doi: 10.1111/icad.12210:

Appendix S1. Autocorrelation coefficient (Moran's I) for carabid beetle numbers caught in nine, old, well-established single-row hedges near Bjerringbro, central Jutland, Denmark, in relation to the distance of the pitfall traps. The spatial autocorrelation analyses revealed that there were no positive spatial autocorrelation between traps located closer to each other, as traps 30 or less metres apart have not higher positive Morans I values than traps at distances of 30 metres or greater.

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Accepted 9 November 2016

Editor: Alan Stewart
Associate editor: Thomas Bolger

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