

Shelter benefits less mobile moth species: The field-scale effect of hedgerow trees

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ABSTRACT

Agri-environment schemes are the main policy instruments for reversing declines in farmland biodiversity, but there is scope for improvement. Within an intensive agricultural landscape, a mark-release-recapture experiment was used to investigate the relative effects on the number of adults of 23 moth species of two landscape features (wide field margins and hedgerow trees) that may feature within agri-environment schemes. Species belonged to either the grass/herb- or shrub/tree-feeders' guild. Margin width did not affect the number of individuals, in either guild. Numbers of shrub/tree-feeding individuals were higher at sites with hedgerow trees, but not so for this guild's two most mobile species, nor for the grass/herb-feeders, which were 30% more mobile. The results show that hedgerow trees increase adult moth numbers because they are shelter-providing resources in typically exposed agricultural landscapes, rather than due to being larval food resources. Hedgerow tree retention and establishment options should be part of efficient general agri-environment schemes, while grassy wide field margins may not always deliver gains, at least not when implemented at the field-scale.

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1. Introduction

Agri-environment schemes (AES) are considered to be the only realistic policy instruments for reversing widespread biodiversity declines in agricultural landscapes (Donald and Evans, 2006). This paper concerns the relative impacts on two moth guilds of two prominent landscape features (wide grassy field margins and hedgerow trees) with potential to feature within national AES. Wide field margins are an important conservation tool (Macdonald et al., 2000). Their management is financially rewarded in a number of EU countries. By early 2008 more than half of agricultural land in England was under AES, and grass/buffer strips on arable land were one of the most popular scheme options (DEFRA/NE, 2008). Hedgerow trees are characteristic of many European agricultural landscapes. In England, their abundance has dramatically declined since the late 18th century to an estimated 1.6 million, of which the annual recruitment is currently only half the level required to maintain a healthy population (Stokes and Hand, 2002; DEFRA, 2010).

Although proactive conservation management of hedgerow trees was until recently not financially rewarded in any of the EU countries, it is now a recent addition to the set of general AES options within England (DEFRA/NE, 2009) (see also the new Scottish Rural Development Priorities).

Larger moths (macro-moths) are a species-rich group, playing important ecological roles within many terrestrial ecosystems, and occurring often abundantly in farmed landscapes. Rapid and significant declines have been recorded for the majority of common and widespread macro-moth species that inhabit farmland in the UK (Conrad et al., 2006), and it seems likely that a similar trend is occurring in other temperate-zone industrialized regions (Groenendijk and Ellis, in press). Partly because of their ecological diversity and species richness, they are considered a sensitive indicator group for biodiversity in terrestrial ecosystems (New, 2004; Thomas, 2005), suggesting that findings for this group may have relevance for the conservation of other winged insects on farmland.

Hedgerow trees have a larger impact on macro-moth abundance and diversity than the 6 m wide grassy field margins (data on 243 species: Merckx et al., 2009a). However, what remains unclear is the mechanism behind the observed effect of hedgerow trees. It is difficult indeed to disentangle the relative effect of shelter vs. larval foodplant, since the sampled hedgerow trees in the study were predominantly pedunculate oak *Quercus robur*. Although overall species not dependent on *Q. robur* as a larval foodplant benefited (+43%) from their presence, which points to an effect of shelter,

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there was a much stronger response (+300%) to the presence of these trees for those moth species that use *Q. robur* as a larval food-plant, which would point to a combined effect of foodplant and shelter.

Here, a mark-release-recapture (MRR) experiment was conducted at a field-scale that allows addressing this remaining question: do hedgerow trees increase moth numbers mainly because they are shelter-providing resources, or because they are larval food resources? This question is of particular relevance for designing effective AES. In case of the latter outcome, (i) hedgerow tree options will favour significantly less species, and (ii) spatial abundance of not only hedgerow trees in general, but also of specific tree species need to be taken into account in order to optimise the biodiversity gain from AES. Instead of using predominantly *Q. robur* as hedgerow trees, a whole variety of tree species (see Section 2) was now used so as to avoid a strong biased response towards one specific tree species. Moreover, eight out of the 13 selected moth species of the shrub/tree-feeding guild did not use this particular set of tree species as hostplants, as they feed on other plant species associated with hedgerows (such as traveller's-joy *Clematis vitalba*, blackthorn *Prunus spinosa*, hawthorn *Crataegus monogyna*, spindle *Euonymus europaeus*, brambles *Rubus* sp., and other berries; Waring and Townsend, 2009). The hypothesis is that if the positive effect of hedgerow trees on adult moth numbers can mainly be ascribed to the shelter they provide, one would under this particular experimental set-up still see numbers of moths to be higher at sites with hedgerow trees than at sites without them. Also, one would expect this effect to be stronger for less mobile species as poorer fliers would generally be more prone to convective cooling, and would hence rely more strongly on shelter in typically exposed agricultural landscapes (Dover and Sparks, 2000; Pywell et al., 2004).

This study also looks at the effect of wide field margins on the adult abundance of the 23 selected moth species belonging to either the grass/herb or shrub/tree larval feeding guilds (see Section 2.1). Wide field margins provide the grass/herb-feeding guild with (i) adult food resources (i.e. nectar), (ii) relatively undisturbed larval habitat, and (iii) buffer zones against the impact of agricultural chemicals – mainly insecticides and herbicides – on larvae and hostplants (Longley and Sotherton, 1997; Pywell et al., 2004). It was relevant to consider this buffer effect as agrochemicals were regularly applied to all five intensively farmed study fields before and during the experiment. Based upon the three points above it was hypothesized that wide field margins would have higher numbers of grass/herb-feeders compared to standard (1–2 m wide, cross-compliance) margins. Additionally, shrub/tree-feeders could also benefit from wide field margins when they act as buffers protecting their larvae and their foodplants within the hedge from the effects of agrochemical drift.

2. Materials and methods

We conducted a MRR experiment across five adjacent, and intensively farmed arable fields (Stonesfield, Oxfordshire, UK, SP3917). Average-sized hedgerows (2–3 m high; 1.5–2.5 m wide) with hedgerow trees scattered throughout bordered the fields. Two fields had surrounding wide (6 m) perennial grass margins (AES option; DEFRA, 2005). The other three fields had standard grass margins (ca. 1–2 m; cross-compliance). Within each of the five fields, one site was sampled at each of four field margins (20 sites in total). In each field, two of these four sites were positioned near one or a small group of hedgerow trees. These hedgerow tree sampling sites were positioned at a distance of ca. 5 m from the hedgerow tree's trunk (minimum height: 8 m; species: *Q. robur*, European ash *Fraxinus excelsior*, field maple

Acer campestre, sycamore *A. pseudoplatanus*, common hazel *Corylus avellana*, lime *Tilia* sp., horse-chestnut *Aesculus hippocastanum*, European holly *Ilex aquifolium*, larch *Larix* sp., pine *Pinus* sp.). Thus, there were four different experimental groups: (i) tree + wide margin, (ii) no tree + wide margin, (iii) tree + standard margin, (iv) no tree + standard margin. Sampling sites were carefully selected so that the variation in hedgerow tree and margin characteristics (e.g. botanical composition and management) other than the subject variables was minimal throughout. All sites were fixed, were located in margins and 1 m from hedgerows, and were more than 100 m apart in order to exclude interference between light traps. Sampling at hedgerow intersections was avoided to reduce bias due to local aggregation of individuals that use hedgerows as flight corridors (e.g. Maudsley, 2000).

2.1. Sampling

We used Heath pattern actinic light traps (6W) (Heath, 1965) to capture moths. These operate on the 'lobster-pot principle', whereby moths are drawn to an actinic tube secured vertically between baffles, fall unharmed down a funnel, and rest on the inside of the trap or on pieces of egg-tray provided. Traps were operated from dusk to dawn, when the live sample of selected species was marked (at first capture) by writing a unique number on the left forewing with a fine (0.4 mm), non-toxic, permanent waterproof marker (Staedtler Lumocolor 313) and released in situ into nearby tall vegetation.

Sampling followed a strict protocol to control for confounding factors between sites and between sampling events. The protocol was designed to ensure that sampling was conducted in similar, sufficiently favourable conditions to minimise bias, as activity levels of nocturnal flying insects are affected by a number of variables. Sampling occurred under pre-defined weather forecast criteria of minimum night temperature (10 °C), maximum wind speed (20 km/h) and maximum precipitation risk (50%), derived from variables as predicted for the nearest town (Chipping Norton, Oxfordshire) between sunset and sunrise on <http://uk.weather.com> (in practice the minimum night temperatures were almost always considerably higher and maximum wind speeds considerably lower).

The experiment ran from 9th June until 19th July 2008 on 33 nights (i.e. all nights with suitable weather conditions). The biggest gap in trapping effort was of two consecutive nights. Trapping was alternated between fields (i.e. individual trap sites were not run on consecutive nights). This method avoids a bias towards recaptures at the same site, as individuals released in situ would otherwise be very likely to end up in the trap nearby when they get active at dusk. Each night 10 sites were sampled: four sites each from a field with wide margins and a field with standard margins, as well as two sites of the central field, one with and one without a hedgerow tree.

Based upon data from a concurrent light trap experiment, 23 species of larger moths were selected: (i) they belonged to one of two contrasting feeding guilds (10 grass/herbaceous plant feeders and 13 shrub/tree-feeders) (Waring and Townsend, 2009), (ii) they were present at the study site the previous year during the same period, and (iii) the period June until mid-July makes up a significant part of their flight period (Waring and Townsend, 2009) (Table 1). All are common species in the wider countryside, and were selected before the start of the experiment so that the marking effort focused only on those species that would enable us to test the hypotheses (see Section 1). For each capture (i) species, (ii) date, (iii) site, and (iv) individual mark number were recorded. Locations of trap sites were obtained via a GPS receiver (Garmin/etrex).

Distances of movements between captures were measured using a GIS (ArcGIS 9.0). The average distance among all pair-wise

Table 1

Numbers of trapped (N), marked (M), and recaptured individuals (R_{ind}) and recapture events (R_{ev}) of 23 species belonging to grass/herb and shrub/tree-feeding guilds. Recapture percentages ($R\%$) and period between first and last observed individual are given for all species. Observed mean and maximum covered distances are given for species where recaptures were made.

Species	Family	N	M	R_{ev}	R_{ind}	$R\%$	Mean dist. \pm SE (m)	Max. dist. (m)	First–last
Grass/herb									
<i>Apamea anceps</i>	Noctuidae	398	395	44	37	9.4	384 \pm 50	1120	09/6–18/7
<i>Agrotis exclamationis</i>	Noctuidae	293	292	8	8	2.7	505 \pm 154	1130	09/6–18/7
<i>Xestia c-nigrum</i>	Noctuidae	151	148	1	1	0.7	345	345	09/6–14/7
<i>Mythimna conigera</i>	Noctuidae	101	101	10	7	6.9	100 \pm 66	423	25/6–19/7
<i>Apamea sordens</i>	Noctuidae	35	33	0	0	0.0			09/6–04/7
<i>Ochropleura plecta</i>	Noctuidae	32	32	0	0	0.0			09/6–14/7
<i>Euthrix potatoria</i>	Lasiocampidae	14	14	4	4	28.6	264 \pm 152	539	04/7–19/7
<i>Camptogramma bilineata</i>	Geometridae	13	13	0	0	0.0			24/6–18/7
<i>Charanyca trigrammica</i>	Noctuidae	12	11	0	0	0.0			09/6–16/6
<i>Hada plebeja</i>	Noctuidae	7	7	0	0	0.0			09/6–17/6
Total		1056	1046	67	57	5.4			
Shrub/tree									
<i>Horisme tersata</i>	Geometridae	84	78	5	4	5.1	157 \pm 110	468	09/6–17/7
<i>Horisme vitalbata</i>	Geometridae	47	44	1	1	2.3	324	324	09/6–01/7
<i>Crocallis elinguaris</i>	Geometridae	43	43	4	4	9.3	558 \pm 235	1143	02/7–19/7
<i>Campaea margaritata</i>	Geometridae	23	20	1	1	5.0	227	227	17/6–18/7
<i>Opisthograptis luteolata</i>	Geometridae	22	21	0	0	0.0			10/6–19/7
<i>Hemistola chrysoprasaria</i>	Geometridae	16	15	2	2	13.3	0 \pm 0	0	10/7–19/7
<i>Habrosyne pyritoides</i>	Thyatiridae	10	9	0	0	0.0			07/7–18/7
<i>Ligdia adustata</i>	Geometridae	10	10	1	1	10.0	0	0	09/6–17/7
<i>Melanthia procellata</i>	Geometridae	9	9	3	3	33.3	185 \pm 118	404	21/6–18/7
<i>Phalera bucephala</i>	Notodontidae	7	7	1	1	14.3	652	652	20/6–18/7
<i>Ourapteryx sambucaria</i>	Geometridae	4	4	0	0	0.0			28/6–14/7
<i>Acronicta aceris</i>	Noctuidae	3	3	0	0	0.0			30/6–16/7
<i>Malacosoma neustria</i>	Lasiocampidae	1	1	0	0	0.0			10/7–10/7
Total		279	264	18	17	6.4			
Grand total		1335	1310	85	74	5.6			

combinations of all trap sites is 624 ± 25 m (mean \pm SE; $N=210$). The furthest distance between any two traps is 1444 ± 7 m (combined error). As accurate dispersal levels can only be obtained using extensive landscape-scale (>50 km²) studies (Franzén and Nilsson, 2007), this field-scale MRR experiment is not designed to assess dispersal abilities, but is able to compare relative mobility/movement levels among species.

2.2. Analyses

For each moth species the number of individuals (excluding any recaptures) sampled at each of the twenty sites was totalled. These numbers were \log_{10} -transformed, as they are multiplicative. The Information Theoretic (IT) approach (Burnham and Anderson, 2002; Richards, 2005) was used to compare 15 alternative and biologically plausible models that capture key elements of the system under study. This IT approach aspires to find the best of a suite of models, with the fewest parameters absolutely necessary (Johnson and Omland, 2004; Boyce et al., 2007). The additive models were generalised linear models (GLM) that contrast the effects of three independent class variables (i.e. fixed effects) on moth numbers: 'margin' (standard vs. wide); 'hedgerow tree' (absent vs. present); 'guild' (shrub/tree vs. grass/herb-feeder); and all two- and three-way interactions of the three main effects. All possible combinations of these fixed effects give a total of 15 different models. The parameters 'species' nested within 'guild' and 'site' were included as random effects in all models. Akaike's Information Criterion (AIC; Akaike, 1974) corrected for small sample sizes (AICc) was used to determine Akaike's weights of evidence for each model given the other models considered. Using the COMP MIX macro (Russell D. Wolfinger; SAS 9.1), the model with the lowest AICc was selected. Degrees of freedom were calculated using the Satterthwaite option (Littell et al., 1996). Differences of least squares means (DLSM) were calculated.

We used the distance covered between first capture and first recapture as a proxy to contrast the mobility of the two guilds. Calculations include all 13 species with at least one recaptured individual. In case of multiple recaptures, only the first movement was taken into account, so that all data points are independent (i.e. different individuals). An IT approach similar to the one above was used to select the best GLM with 'guild' and 'days' and their interaction as possible fixed effects.

3. Results

A total of 1335 individuals from 23 pre-selected species were captured throughout the trapping period. Numbers varied greatly among species and among guilds [13 shrub/tree-feeders ($N=279$) vs. 10 grass/herb-feeders ($N=1056$); Table 1].

We arbitrarily chose to exclude eight species with abundances of 10 or smaller, as doing so results in considerably more degrees of freedom and hence more statistical power, while only reducing the number of individuals by 51 to $N=1284$ (Table 1). Anyway, the IT approach selected the same 'habitat preference' model as being the best for both the restricted and complete dataset, though the residuals of the model with all 23 species were only marginally normally distributed ($N=460$; Shapiro-Wilk, $W=0.93$), whereas the same model that excluded eight species where $N \leq 10$ had normally distributed residuals ($N=300$; $W=0.95$). The Akaike's weight of this best model (0.40) was much larger than the second and third best model (0.19; 0.17, respectively), and the Akaike's difference between the top-ranked model and these other models was 1.45 and 1.70, respectively. As these differences are not larger than 2.0, all three models were considered (see Burnham and Anderson, 2002, 2004). However, the additionally retained two-way interaction effects in the more complex second and third best models were never significant. Hence, there is substantial evidence to support the top-ranked and less complex model, and this model has

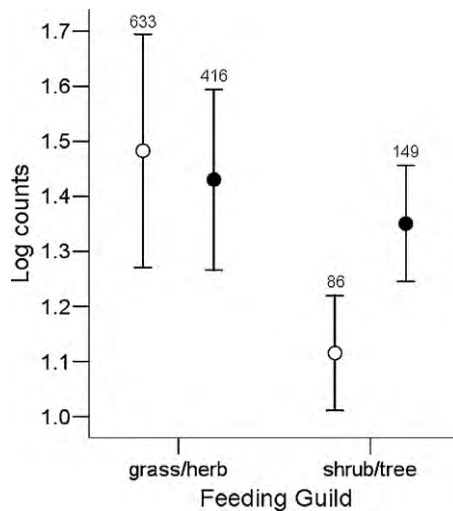


Fig. 1. Hedgerow trees and moth guild numbers. Log-transformed total counts (\pm SE) of individual moths at sites with (●) and without (○) a hedgerow tree for nine grass/herb and six shrub/tree-feeding species. Non-transformed individual counts are given on top of each error bar.

considerably more support than all other models tested (see also Richards, 2008). Therefore, only this one selected generalised linear model was used and interpreted (Proc Mixed, SAS 9.1).

Numbers of shrub/tree-feeders, but not grass/herb-feeders, were higher at sites with hedgerow trees (tree: $F_{1,17.5} = 0.65$; $P = 0.43$; tree \times guild: $F_{1,265} = 11.58$; $P = 0.0008$; DLSM grass/herb guild: 0.07 ± 0.06 ; $t_{25.4} = 1.08$; $P = 0.29$; DLSM shrub/tree guild: -0.15 ± 0.07 ; $t_{37.8} = -2.30$; $P = 0.027$) (Fig. 1). This effect for the shrub/tree-feeders was present for the five species that were able to use the variety of hedgerow trees on offer in this study, as well as for the eight species using other shrubs/trees (mean number of individuals/trap ($N = 10$) \pm SE: 5.3 ± 1.1 vs. 2.4 ± 1.0 and 12.1 ± 3.4 vs. 8.2 ± 2.5 , respectively). Overall, and within both guilds, numbers of individuals did not differ between sites with wide compared to standard field margins ($F_{1,17} = 0.44$; $P = 0.52$).

The Akaike's weight of the best 'mobility' model (0.47) was considerably larger than the second best model (0.30), but the Akaike's difference between these models was smaller than 2 ($\Delta = 0.89$), which means that there is evidence to support both models, and that these models have considerably more support than the other models tested (Burnham and Anderson, 2002, 2004). Therefore, these two selected GLMs (Proc Mixed, SAS 9.1) were used, one of which only included 'group' and the other only included 'days' as a fixed effect.

Overall, 5.6% of individuals ($N = 74$) were recaptured at least once. As some individuals flew away before marking, this calculation only took marked individuals ($N = 1310$) into account. Some individuals were recaptured twice or three times (85 events in total), but the focus is on first recaptures only (see Section 2.2). There was no correlation between covered distance and number of days between captures ($F_{1,72} = 0.07$; $P = 0.80$).

Overall, the shrub/tree-feeders guild ($N = 17$) covered smaller distances than the 30% more mobile guild of grass/herb-feeders ($N = 57$), but not significantly so (272 ± 78 m vs. 357 ± 43 m, respectively; $F_{1,72} = 0.92$; $P = 0.34$) (Fig. 2). A posteriori tests showed that although the presence of a hedgerow tree had a significantly positive effect on the shrub/tree-feeders' guild as a whole (see above), the same parameter had no significant effect on the abundance of *Crocallis elinguaris* and *Phalera bucephala* ($F_{1,18} = 2.90$; $F_{1,18} = 4.41$; $P > 0.05$, respectively), which also appear to be the most mobile species within this group of shrub/tree-feeders (Table 1 and Fig. 2).

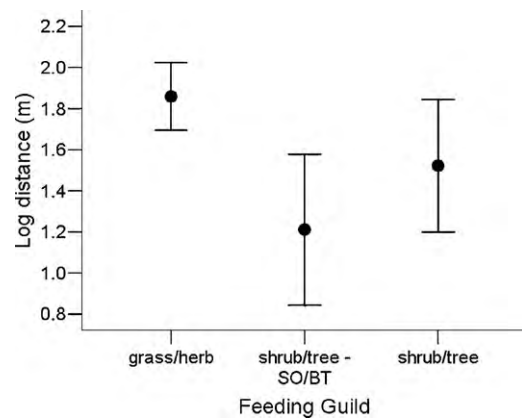


Fig. 2. Moth guild movements. Average log-transformed distances (\pm SE) between capture and first recapture for five grass/herb ($N = 57$) vs. six and eight shrub/tree-feeding species ($N = 12$; $N = 17$, resp.) as two of the latter species (*C. elinguaris* 'SO'; *P. bucephala* 'BT') did not respond to hedgerow tree presence.

4. Discussion

We show that the benefits of wide grassy field margins on macro-moth abundance at the field-scale are smaller than the hedgerow trees' impact. This result contrasts with the popularity of the implementation of these margins as an AES option within European AES (Kleijn and Sutherland, 2003; DEFRA/NE, 2008), and the apparent unpopularity of AES options for hedgerow trees. The planting of new hedgerow trees and the marking of saplings within hedges with easy-to-see tags, in order to avoid cutting them back while flailing, could function as proactive conservation measures (Stokes and Hand, 2002). However, specific hedgerow tree management measures are currently lacking in all EU countries' AES options, though some have recently been added to the English AES (DEFRA/NE, 2009).

Whilst hedgerow trees – in landscapes targeted for increased AES uptake – conferred a considerable positive effect on overall moth abundance, only a trend towards higher abundances in wide compared to standard grassy field margins could be detected (Merckx et al., 2009a). Other studies have shown the highly significant impacts on invertebrates, such as bumblebees and Lepidoptera, of improving the floristic and structural diversity of arable field margins (e.g. Feber et al., 1996; Pywell et al., 2006; Carvell et al., 2007).

The present field-scale study sheds more light on the mechanism underlying the observed, positive effect of hedgerow trees, and is able to show that hedgerow trees are associated with increased adult moth numbers mainly because they provide additional shelter in typically exposed agricultural landscapes, rather than merely being larval food resources. In line with the hypothesis, it is shown that (i) numbers of adult shrub/tree-feeders were similar at wide vs. standard margins, notwithstanding the likely adverse impacts of agrochemical drift at narrow margins on hedgerow food-plants and larvae, and (ii) hedgerow trees were associated with increased adult moth numbers, even for the eight species using different hostplants than the variety of hedgerow trees on offer. This evidence in favour of shelter was further corroborated by the observation, in line with the other hypothesis, that the effect was strongest for less mobile species. These species are believed to be more prone to convective cooling in typically exposed agricultural landscapes (Dover and Sparks, 2000; Pywell et al., 2004), and were hence predicted to benefit most from the additional shelter provided by trees, even if hedgerows alone do already provide some degree of shelter in these landscapes (Dover and Sparks, 2000; Maudsley, 2000). In line with this prediction, it is shown that

hedgerow tree presence (i) did not significantly affect the two most mobile species of the shrub/tree guild, (ii) nor the 30% more mobile group of grass/herb-feeders.

Although this 30% difference in mobility between guilds was not statistically significant because of considerable within-guild variation (Table 1 and Fig. 2), this may have been a conservative result: (i) Merckx et al. (2009b)'s data from 2007 on nine grass/herb-feeding moth species within a similar MRR set-up at the same fields, revealed higher mean distances covered for the grass/herb-feeders *Apamea anceps*, *Mythimna conigera* and *Xestia c-nigrum*, which were also studied in the current MRR experiment in 2008, though it is not known whether movement intensity may generally have been higher in 2007 due to different weather conditions between years; (ii) given the relatively high number of marked individuals, the zero recapture rates for the grass/herb-feeding species *A. sordens* and *Ochropleura plecta* point to a high level of mobility (Table 1); (iii) the overall difference in mobility between the two guilds is reflected in their functional wing morphology: a majority of species are geometrids in the shrub/tree-feeding guild and noctuids in the grass/herb-feeding guild.

It would be good if national AES would include options for the retention and establishment of hedgerow trees so as to increase both the field- and landscape-scale supply of these prominent, shelter-providing structures. A significant increase of hedgerow trees at both scales will address the European-wide problem of the current hostile levels of exposedness of intensive agricultural landscapes, without having to decrease the intensity of agricultural production.

Positive effects of field margins on invertebrate abundance and species richness are most likely to be achieved when these strips provide improved habitat quality (e.g. a diverse mixture of native pollen/nectar-rich wildflowers; Carvell et al., 2007), and when they are implemented in heterogeneous landscapes resulting in improved functional connectivity at the landscape-scale (e.g. Rundlöf et al., 2008). As with hedgerow trees, differences in mobility among species (groups) did have an impact on the effect of wide field margins (Merckx et al., 2009b). It is hence likely this applies to other AES options as well. Thus, in order to avoid that the success of AES options is dependent on species-specific mobility, AES options should be implemented at a landscape-scale, larger than the current, and standard, field-scale. On such a larger scale, AES options should not only benefit less mobile species, as they do now, but also the remainder of more mobile species, as this group of species is more strongly affected by the total amount of suitable habitat in the landscape (Hambäck et al., 2007). Similarly, Thomas (2000) and Rundlöf et al. (2008) concluded that butterfly and bumblebee species of intermediate mobility are more affected than those of low mobility in fragmented landscapes (although species at the very high end of the mobility spectrum are generally surviving well). Hence, a landscape-scale approach to the implementation of AES, and a stronger focus on the shelter resource, may deliver significant biodiversity gains, and make AES more cost-efficient.

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