

Hedgerow trees and extended-width field margins enhance macro-moth diversity: implications for management

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Summary

1. Improving the effectiveness of agri-environment schemes is essential for reversing declines in farmland biodiversity. Crucial to achieving this is identifying management options that are practical and beneficial to biodiversity, and understanding the influence of the surrounding landscape. We used data on abundance and species richness of farmland macro-moths, many of which are declining, and trait-based analyses on their feeding guild, mobility and conservation status, to explore local- and landscape-scale effects of two farmland features (extended-width field margins and hedgerow trees) and surrounding farmland intensification.

2. Macro-moths were light trapped at 48 fixed sites on 16 farms, over 4 years, within a 1200-km² area of lowland UK farmland. Sites belonged to one of four experimental groups that differed in their combinations of hedgerow tree presence and field margin width.

3. Hedgerow trees and extended-width field margins locally increased species richness, but not abundance, of macro-moths, irrespective of each other's presence. Overall, species richness and abundance were not affected by agricultural intensification, as measured by the amount of arable land in the surrounding landscape.

4. Sedentary moths showed double the species richness, but were half as abundant as mobile moths. Both groups responded positively to extended-width margin and hedgerow tree presence. The effect of hedgerow trees was particularly strong for shrub- and/or tree-feeding species.

5. Analyses based on the conservation status of moths demonstrated that agricultural intensification lowered the species richness of nationally severely declining UK Biodiversity Action Plan priority species and the abundance of both nationally moderately declining and priority species. These effects were most pronounced at the 0.8-km radius scale.

6. *Synthesis and applications.* Our results suggest that the presence of extended-width field margins and hedgerow trees, possibly promoted by agri-environment schemes targeting their implementation at relatively small spatial scales (0.8 km), may help mitigate negative effects of agricultural intensification on macro-moths. A wide range of other taxa feed on macro-moths and may therefore indirectly benefit from these features. Nevertheless, taxa differ widely in their mobility and measures mitigating biodiversity loss may need to be targeted at multiple spatial scales to maximize their effectiveness for multiple taxa.

Key-words: agri-environment schemes, Biodiversity Action Plan priority species, conservation status, farmland biodiversity, farmland restoration ecology, farmland rewilding, feeding guild, Lepidoptera, moth mobility, multiple spatial scales

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Introduction

Farmland covers about half of the world's potentially useable land, and farmed crops feed, dress and, increasingly, fuel the growing human population. However, current agricultural practices are not only detrimental to the replaced ecosystems, but often also reduce ecosystem services from neighbouring ecosystems. Nevertheless, biodiversity on farmland provides significant ecosystem services too, with benefits for society as a whole (Tilman *et al.* 2002). Farmland biodiversity is severely declining due to agricultural intensification (Robinson & Sutherland 2002), and agri-environment schemes (AES) have been introduced, in part at least, in many European countries to reverse these negative trends (Whittingham 2007). However, there is a pressing need to design them so that they actually achieve their goals and are cost-effective (Kleijn *et al.* 2006).

Agri-environment schemes cost-efficiency can be improved by developing effective support payments for targeted low-intensity farming systems (Warren & Bourn 2011), and by identifying farmland features and management options that are both straightforward to integrate within high-intensity farming systems and beneficial to the overall biodiversity levels (Merckx *et al.* 2009a; Raebel *et al.* 2012). The extent to which any overall biodiversity benefit of these farmland features is dependent on the intensification degree of the surrounding landscape (Gabriel *et al.* 2010) is also important. Evidence suggests that AES options may have larger biodiversity benefits with intermediate levels of intensification and homogeneity of surrounding landscapes (Kleijn *et al.* 2011; but see Whittingham 2011).

Here, we test whether and to what degree two farmland features (extended-width field margins and hedgerow trees) are able to increase abundance and species richness levels of macro-moths and whether their effect is modified by the amount of intensively managed agricultural fields in the surrounding landscape. Although an increasing amount of arable land is expected to result in lower overall moth abundance and richness levels, we predict that the positive impact of extended-width field margins and hedgerow trees on both abundance and species richness will be relatively greater with an increasing amount of arable land (Kleijn *et al.* 2011).

However, this general prediction may not hold true for all species, because different species are likely to vary in their response to agricultural intensification (Ekroos, Heliölä & Kuussaari 2010). In addition to analysing effects on overall abundance and species richness, exploring responses to agricultural intensification for species groups with shared life-history traits (Williams *et al.* 2010) may be more revealing. This approach has been successfully applied for several animal taxa (e.g. Bommarco *et al.* 2010; Öckinger *et al.* 2010); however, trait-based analyses on the effect of local- and landscape-scale agricultural intensification on nocturnal macro-moths are lacking.

Significant declines in abundance and distribution have been recorded for the majority of common and widespread macro-moth species that inhabit farmland, in Great Britain and other European countries (Conrad *et al.* 2006; Groenendijk & Ellis 2011). These declines are of concern because the herbivorous macro-moth larvae are significant primary consumers and nutrient recyclers. Macro-moths are also key prey items, in all life-stages, for a wide range of other taxa (e.g. birds, bats, shrews, parasitoids, spiders, beetles). For example, it is estimated that blue tit *Parus caeruleus* chicks alone consume at least 35 billion caterpillars in Britain each year (Fox *et al.* 2006). Another ecosystem service to which they contribute is pollination, with moths dominating both temperate and tropical flower visitor faunas after dark (Devoto, Bailey & Memmott 2011).

The larval feeding niche (hereafter called 'guild') may be a particularly useful life-history trait for understanding benefits of certain farmland elements (Sekar 2012) and, therefore, the effectiveness of certain AES options. For example, although we predict hedgerow trees to benefit all macro-moths as a result of the shelter provided (Merckx *et al.* 2010), we hypothesize that shrub and/or tree-feeders (hereafter called 'high-feeders') will benefit more from the presence of hedgerow trees than will grass and/or herb-feeders (hereafter called 'low-feeders') as hedgerow trees may, for the former group, additionally provide larval feeding resources, female egg-laying sites and/or may more strongly attract high-feeders to roost (Waring & Townsend 2003). Similarly, we hypothesize that low-feeders may show a greater benefit from extended-width margins than do high-feeders.

Species mobility, in particular, appears to be a strong predictor of insect population success (Mattila *et al.* 2006). In general, poor dispersers seem to be more prone to extinction due to human-induced processes such as habitat fragmentation and agricultural intensification (Bommarco *et al.* 2010; Marini *et al.* 2010, 2012a; but see Pereira, Daily & Roughgarden 2004), as these processes may increase the need to move between resource patches. As species mobility is likely to be related to actual dispersal distances, we hypothesize that, for a given spatial scale, landscape intensification will have a stronger negative effect on sedentary compared to mobile species [Burel *et al.* 2004 (coleoptera; diptera); Jennings & Pocock 2009 (arthropods; insectivorous mammals)].

As agricultural intensification is considered to be an important cause of biodiversity declines (Tilman *et al.* 2002), we also test whether the impact of agricultural intensification differs between species with contrasting conservation status (see also Fuentes-Montemayor, Goulson & Park 2011). More specifically, we hypothesize that species with nationally declining populations, and especially so species in severe decline, will be more negatively impacted by agricultural intensification than species that are increasing nationally. Any negative impacts of agricultural intensification on the latter group are likely to be

relatively minor and may be compensated for by positive impacts of other factors, such as encountering an empty niche for recent invaders and/or climate change for cold-restricted generalist species (Conrad *et al.* 2006).

These hypotheses were tested using a 4-year study in which multiple fixed sites were sampled within a lowland agricultural landscape. The aims of this study were to test (i) the effect on macro-moth abundance and species richness of the presence of two prominent farmland features, which either are already popular within national AES (i.e. extended-width field margins) or have the potential to become so (i.e. hedgerow trees); (ii) the effect of amount of arable land cover in the surrounding landscape (as a proxy for agricultural intensification) on macro-moth abundance and species richness at five spatial scales; (iii) to what extent the potential benefit of extended-width field margins and hedgerow trees depends on the degree of landscape intensification at different spatial scales; and (iv) whether the effects of these local and landscape factors differ between high- and low-feeders, between mobile and sedentary species, and between species groups of differing conservation concern.

Materials and methods

STUDY SITES

Macro-moths were sampled during four consecutive years (2006–2009; 240 trap nights; 1920 trap events) using light traps with 48 fixed sampling sites, which were spread over 16 predominantly arable farms (three sampling sites per farm; Fig. 1a). All farms were located within a 1200-km² area of the lowland agricultural landscape of Oxfordshire, UK. In general, these 16 farms had fields characterized by having both standard and extended-width margins, and within each farm, the number of hedgerow trees per field margin varied from zero to one or more hedgerow trees. Nevertheless, the precise locations of all three sampling sites at a given farm were chosen so that they belonged to only one of four experimental groups (4 farms per group), which differed in their combinations of hedgerow tree presence and field margin width: (i) hedgerow tree + extended-width margin; (ii) hedgerow tree + standard margin; (iii) no hedgerow tree + extended-width margin; (iv) no hedgerow tree + standard margin (Fig. 1b). We thus sampled 24 sites characterized by extended-width (6 m) margins (current AES option; Defra 2005) vs. 24 sites with standard

(1 m, cross-compliance) margins, and 24 sites next to a single open-grown hedgerow tree (minimum height: 15 m, usually pedunculate oak *Quercus robur*) vs. 24 sites without any nearby tree. All margins were well-established, tussocky sown perennial grass strips, of variable age, next to hedges, machine-cut once every 2 or 3 years, not grazed, and unfertilized, although fertilizer may have drifted into the margin unintentionally. The four treatment groups were selected to avoid clumping in space of any treatment. The sampling design was factorial, allowing the testing of interactions between the presence/absence of a hedgerow tree and an extended-width margin (Fig. 1). We sampled the farms so as to maximize independence between local and landscape factors.

MOTH SAMPLING

We used heath pattern actinic light traps (6 W). These were operated from dusk until dawn, when the live sample in and on the trap was enumerated, and identified to species-level, except for five species-pair aggregates of essentially cryptic species. Each farm was sampled 40 times between 2006 and 2009, in discrete fortnightly periods from mid-May to mid-October, once in each period, and in random order within the period. Usually three farms (i.e. nine sites) were sampled on any one night. Sampling sites were carefully selected so that the variation in farmland feature characteristics other than the subject variables was minimal throughout. All sites were positioned 1 m away from average-sized hedgerows (2–3 m high, 1.5–2.5 m wide), with both sides bordered by arable land. Sampling sites were at least 50 m away from hedgerow intersections and were minimally 100 m apart, which prevented moth attraction radius interference (Truxa & Fiedler 2012). The sampling protocol controlled for confounding factors between sites and between sampling events. Traps were placed upon a white sheet, which enhanced and equalized trap visibility, and which enabled us to include all individuals resting on the sheet. Sampling was conducted in similar, sufficiently favourable conditions to minimize bias due to differences in weather-related activity levels.

MOTH TRAITS

For each farm, and for each year, the total number of individuals (abundance, N) and species richness (number of species, S) were calculated by combining the data from each farm's three sampling sites over the whole sampling season. As well as these overall values, we also calculated N and S for each farm split by the following species groups:

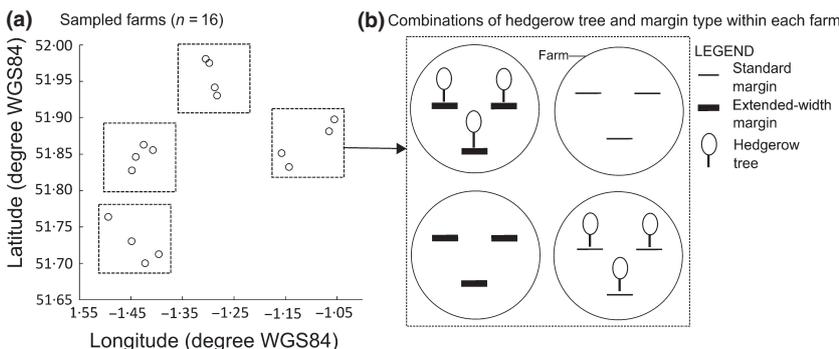


Fig. 1. (a) Distribution of the 16 sampled farms (open circles) and (b) scheme of the sampling design within each farm (range of minimum, mean and maximum distances between the three sites per farm: 60–470 m; 190–1290 m; 280–1930 m, respectively).

1. *Guild*: all species recorded were divided into two groups: those species feeding on (mainly) grasses and/or low herbs (i.e. 'low-feeders', $N = 134$), vs. shrub- and/or tree-feeders (including lichen-feeders; i.e. 'high-feeders', $N = 177$; Waring & Townsend 2003).

2. *Mobility*: using wing morphology as a proxy for mobility (Sekar 2012), we contrasted recorded species with an average wingspan < 31 mm and rounded wings (i.e. 'sedentary' species, $N = 77$) vs. species with an average wingspan > 44 mm and pointed wings (i.e. 'mobile' species, $N = 34$). Species that did not fall into either of these contrasting categories were not retained.

3. *Conservation status*: each recorded species was classified into one of three classes based on national abundance trend data over 35 years (Conrad *et al.* 2006): (a) decline 70–99% (i.e. nationally severely declining UK Biodiversity Action Plan 'BAP' priority species, $N = 44$); (b) decline 0–69% (i.e. nationally moderately 'Declining' species, $N = 106$); (c) increase $> 0\%$ (i.e. nationally 'Increasing' species, $N = 76$). Species for which the national trend is unknown were not retained.

Although guild and conservation status were weakly correlated (i.e. nationally increasing species tended to be more often high-feeders than low-feeders; $\chi^2 = 4.65$, $P = 0.09$), mobility was not correlated with either conservation status ($\chi^2 = 1.40$, $P = 0.50$) or guild ($\chi^2 = 0.52$, $P = 0.77$).

EXPLANATORY VARIABLES

Using a GIS (ARCMAP 9.2, Esri, Redlands, California, USA), five circles (radii: 200, 400, 800, 1600 and 3200 m) were constructed around each of three sampling sites within each farm. On the basis of recent, high-resolution land-use data (Land Cover Map, CEH, UK), the percentage of arable land within each of these circles was calculated. The five spatial scales were selected to roughly cover the extent of foraging movements for a gradient of sedentary to mobile species (Merckx *et al.* 2009b, 2010), and the variable percentage of arable land was chosen as a proxy for the degree of agricultural intensification (Tschardt *et al.* 2005). Arable land cover was negatively related to the amount of semi-natural habitats in the landscape (Spearman correlation: $r_s = -0.71$, $P < 0.01$, $n = 16$, radius = 0.8 km) as well as to the landscape habitat diversity (i.e. Shannon diversity) ($r_s = -0.90$, $P < 0.01$, $n = 16$, radius = 0.8 km) and can be viewed as the major component in shaping landscape structure in intensive agricultural landscapes (Ekroos, Heliölä & Kuussaari 2010). We tested whether arable land cover at the five spatial scales differed between the two levels of our local factors (presence vs. absence of a hedgerow tree and presence vs. absence of an extended-width margin) using two-way ANOVA. There was no significant association at the 200, 400, 800 and 3200 m scales. At the 1600-m scale, we found a weak difference ($F_{1,13} = 4.44$, $P = 0.055$) in arable land cover between farms with hedgerow tree sampling sites (54.7%) and farms without such sites (46.4%), and a weak difference ($F_{1,13} = 4.78$, $P = 0.048$) between farms with extended-width margin sampling sites (46.2%) and farms without (54.8%). As the collinearity between local and landscape factors was very low, we included both factors in the same models using traditional hypothesis testing based on P -values.

STATISTICAL ANALYSES

First, linear mixed models (LMMs) were run to test the effects of extended-width margin presence, hedgerow tree presence, and

arable land cover in the landscape (and all possible two-way interactions) on overall N and S across the 4 years. N and S were log-transformed in all the models. These two models were run at each of the five spatial scales to test potential scale dependence in the landscape effects. We included 'year' and 'farm' as random factors to account for the fact that the sampling was repeated for 4 years in each farm. Models were simplified using a backward deletion procedure ($P > 0.05$). If the arable land variable was not significant, we removed the main effect and presented the model testing local factors only.

Second, LMMs were run to test the same variables as above, but species life-history traits (mobility, guild, conservation status) were additionally included as a fixed effect (see also Bommarco *et al.* 2010; Öckinger *et al.* 2010; Marini *et al.* 2012b). In these models, traits were entered as categorical fixed factors, while overall abundance and the number of species in each level of the traits were the response variables. A major advantage of this statistical approach was that any collinearity between traits, presence of extended-width margin with or without hedgerow tree and cover of arable land was avoided, allowing tests of interactions and main effects within a factorial design. We ran separate LMMs for each trait to test whether that trait modified the abundance and species richness response to our local and landscape factors. The random structure of the mixed models was similar to the one described above for the overall models:

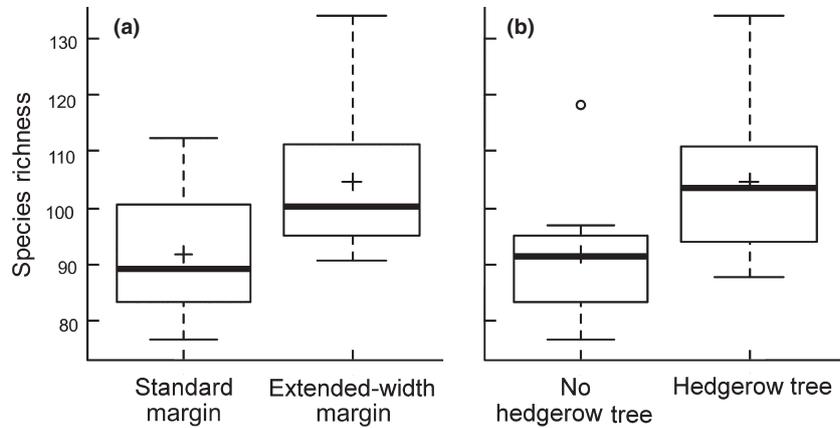
Abundance or Species richness \sim Fixed effects : all main effects
 + tree \times trait_{*i*} + margin \times trait_{*i*} + arable \times trait_{*i*} + arable \times tree
 \times trait_{*i*} + arable \times margin \times trait_{*i*}, Random effects : farm per year

Models were simplified using backward deletion ($P > 0.05$). Models were again run separately at each of the five spatial scales. As suggested by Pinheiro & Bates (2000), we used sequential F-tests to test main effects and interactions in all models using the `lme(nlme)` and `anova.lme(nlme)` functions in R (version 2.8.0; R Development Core Team 2008) with the restricted maximum likelihood (REML) estimation method.

Results

We sampled a total of 71 751 individuals, from a total of 311 macro-moth species. Average yearly abundance and species richness varied considerably between farms (range, mean \pm SE, respectively: N : 799–1667, 1121 ± 58 ; S : 77–134, 98 ± 3.7). Overall, species richness of macro-moths was higher at sites with extended-width margins (Fig. 2a; $F_{1,13} = 6.03$, $P = 0.029$), and at sites with hedgerow trees (Fig. 2b; $F_{1,13} = 5.81$, $P = 0.031$), compared to sites without these farmland elements. Hedgerow tree sites did not differ in macro-moth abundance compared to sites without trees ($F_{1,13} = 0.75$, $P = 0.40$), and the abundance of macro-moths at sites with extended-width compared to standard margins was not significantly different ($F_{1,13} = 0.83$, $P = 0.38$). We found no interaction between the presence of hedgerow trees and extended-width margins on both abundance and species richness. The amount of arable land cover in the surrounding landscape did not affect the overall species richness and abundance at any

Fig. 2. Main effects ($P < 0.05$) of (a) extended-width margin presence and (b) hedgerow tree presence on overall macro-moth species richness at the local scale only, as the variable arable land cover was not retained in the linear mixed models at any of the five spatial scales tested (200, 400, 800, 1600 and 3200 m). ‘Year’ and ‘farm’ were included as random factors. A solid line in the boxplots indicates the median, whereas a cross line indicates the mean.



of the five spatial scales and did not modify the effect of the local factors (i.e. there was no significant interaction with hedgerow tree and extended-width margin).

Overall, the high-feeders guild was significantly less abundant and less species rich than the low-feeders guild (mean \pm SE: N_{high} : 208 ± 15.3 ; N_{low} : 913 ± 54.7 ; S_{high} : 44 ± 1.7 ; S_{low} : 54 ± 1.2). Guild did not modify the effect of either landscape (arable land cover) or local factors (farmland elements: hedgerow trees and extended-width margins) on moth abundance (i.e. no interaction with guild was significant), although we found a significant interaction between guild and hedgerow tree presence on species richness (Guild \times Tree: $F_{1,62} = 9.32$, $P = 0.003$). The overall positive influence of hedgerow tree presence on species richness, as described above, was consistently greater for high-feeders than for low-feeders (Fig. 3).

Overall, the mobile group was twice as abundant, although less than half as species rich, compared to the sedentary group (mean \pm SE: N_{mobile} : 143 ± 11.3 ; $N_{\text{sedentary}}$: 69 ± 4.9 ; S_{mobile} : 8 ± 0.4 ; $S_{\text{sedentary}}$: 18 ± 0.7). Both sedentary and mobile species reacted positively to extended-width margin and hedgerow tree presence, in terms of abundance and species richness (no significant interactions), whilst neither group responded to the amount of

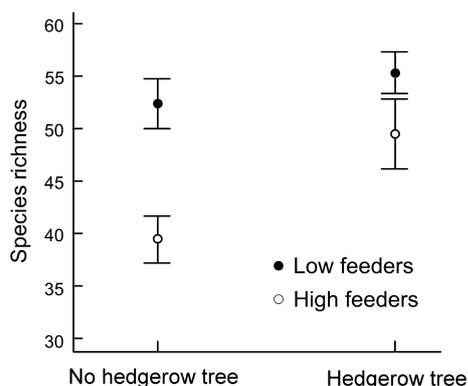


Fig. 3. Mean (\pm SE) macro-moth species richness on farms where sampling occurred near a hedgerow tree vs. farms where such trees were absent near sampling sites, separately for low and high-feeders.

arable land cover in the surrounding landscape, at any of the spatial scales tested.

With regard to conservation status, the nationally moderately ‘declining’ species group was the most abundant and most species rich, followed by the nationally ‘increasing’ group, whereas the nationally severely declining ‘BAP’ priority group was the least abundant and least species rich (mean \pm SE: $N_{\text{declining}}$: 483 ± 28.9 ; $N_{\text{increasing}}$: 380 ± 25.4 ; N_{BAP} : 121 ± 9.8 ; $S_{\text{declining}}$: 43 ± 1.0 ; $S_{\text{increasing}}$: 28 ± 0.8 ; S_{BAP} : 14 ± 0.5). All three groups reacted positively to extended-width margin and hedgerow tree presence, in terms of abundance and species richness. At the 0.8-km radius spatial scale, the nationally severely declining ‘BAP’ priority group declines in species richness, while the nationally moderately ‘declining’ and nationally ‘increasing’ group slightly increased in species richness with increasing amount of arable land cover (Status \times Arable_{0.8 km}: $F_{2,124} = 5.968$, $P = 0.003$; Fig. 4a). This interaction was apparent also at the 0.4-km scale but the model fit was lower than at 0.8 km. For abundance, and also at the 0.8-km radius spatial scale, both the nationally severely declining ‘BAP’ priority and nationally moderately ‘declining’ groups decline in abundance, while the nationally ‘increasing’ group slightly increased in abundance with increasing amount of arable land cover (Status \times Arable_{0.8 km}: $F_{2,124} = 8.09$, $P < 0.001$; Fig. 4b). This interaction was apparent also at smaller and larger spatial scales but the model fit was generally lower than the fit at 0.8 km.

Discussion

Our 4-year study showed that both hedgerow trees and extended-width field margins locally increased overall species richness of macro-moths on farmland, and they did so irrespective of each other’s presence. The positive effect of hedgerow trees is likely to be due largely to the shelter they provide in typically exposed agricultural landscapes (Merckx *et al.* 2008, 2009a). Contrary to our expectation that AES options would have larger biodiversity effects with increasing landscape intensification (Tscharntke *et al.* 2005), the positive impacts of extended-width margins and

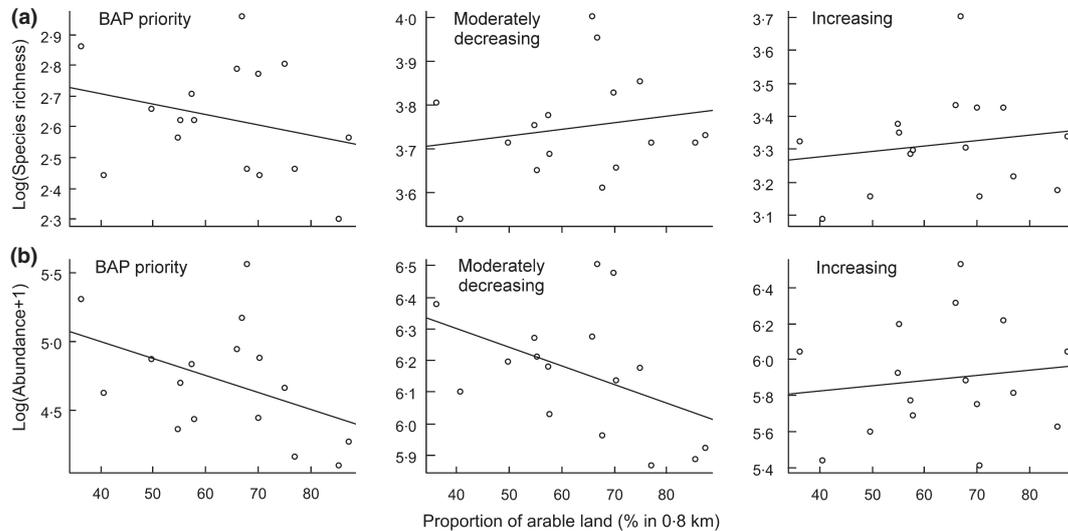


Fig. 4. Effects of arable land cover (% within 0.8-km radius) on macro-moth (a) species richness and (b) abundance, separately for nationally severely declining UK Biodiversity Action Plan priority species ('BAP priority'), nationally moderately declining species ('Moderately decreasing'), and nationally increasing species ('Increasing').

hedgerow trees were not relatively greater with an increasing amount of arable land in the surrounding landscape. Moreover, agricultural intensification, as indicated by the amount of arable land, did not result in lower overall levels of macro-moth abundance and species richness at any of the five spatial scales tested. This result contrasts with the observations for diurnal Lepidoptera, which generally decrease with increasing agricultural intensity, especially so when arable field cover exceeds 60% (Ekroos, Heliölä & Kuussaari 2010).

We then grouped the species according to certain life-history traits, and compared how these groups differed in their response to both farmland elements and the amount of agricultural intensification at multiple spatial scales. In line with our predictions, we showed that high-feeders benefitted more than low-feeders from the presence of hedgerow trees at the local scale, in terms of species richness. In addition to their general shelter effect, hedgerow trees provide larval feeding and female egg-laying resources, at least for some of the 'high-feeding' species, whereas they do not for low-feeders (Waring & Townsend 2003). Also, it is likely that they exhibit a stronger attraction to high-feeders in terms of providing adequate roosting sites compared to low-feeders, as the latter may be more likely to roost in vegetation close to the ground (e.g. the highly abundant large yellow underwing *Noctua pro-nuba* and other common *Noctua*, *Agrotis*, *Xestia*, *Mythimna*, *Apamea* and *Hoplodrina* spp.). In contrast to the stronger benefit for high-feeders vs. low-feeders of hedgerow tree presence, low-feeders did not benefit more strongly than high-feeders from the presence of extended-width margins. This suggests that both guilds benefitted equally from extended-width margin presence. The positive effect of extended-width margins can be explained by the fact they provide a relatively undisturbed breeding

habitat and can act as buffer zones against the impact of agricultural chemicals on moth larvae and their host plants (Pywell *et al.* 2004). As such, this result indicates that extended-width margins may improve larval habitat quality, both for low-feeding larvae within the margins and for high-feeding larvae in adjacent hedgerows and lower parts of hedgerow trees, by reducing exposure to pesticides and fertilizers. Another (complementary) explanation may be that floral resources are providing nectar to adults of both guilds. Increasing plant species richness of margins, and optimizing availability of resources through appropriate management, may have benefits for both larval and adult macro-moths, as is the case for other farmland Lepidoptera (Feber, Smith & Macdonald 1996). Although typically less abundant, high-feeders make up a significant part of the total macro-moth fauna (e.g. 57% of all species recorded during our study) and were represented by an additional 43 species compared to low-feeders. At the local scale, however, they were almost 20% less species rich than low-feeders. These contrasting findings suggest that high-feeders, despite having a lower α -diversity, are characterized by a higher β -diversity than low-feeders.

Contrary to the hypothesis that landscape intensification would have a more negative effect for sedentary than for mobile species (Jennings & Pocock 2009), such an interaction was absent. This unexpected result may be due to limited intensification gradients, although we expect this may only have been an issue for the largest spatial scale (0.2 km: 10–100%; 0.4 km: 19–100%; 0.8 km: 30–91%; 1.6 km: 35–78%; 3.2 km: 34–59%). Another explanation may be that our proxy for mobility, being a proxy, may have failed (see also Summerville *et al.* 2006). Several life-history traits may interact to determine species mobility (Sekar 2012). For example, some very small

species (e.g. diamondback moth *Plutella xylostella*, a micro-moth) may actually be very mobile if they undertake high-altitude and high-velocity migration (Chapman *et al.* 2002), although this probably only applies to a small number of small macro-moth species as most migrating macro-moth species would fall in our mobile species group based on their wing morphology. Due to the absence of mobility data for the majority of species in our study, we chose wingspan (combined with wing shape) as a plausible proxy, and currently the best available (Sekar 2012). Moreover, we opted to contrast two extremes – that is, very small and round-winged moths vs. very large and sharp-winged moths – to ensure that we contrasted two species groups that differed considerably in terms of mobility (Marini *et al.* 2010).

Broadly in line with our initial prediction, our study showed that nationally declining species became less abundant with increasing levels of agricultural intensification in the surrounding landscape, especially so at the intermediate spatial scale of 0.8-km radius. We observed no difference in the extent of this negative effect between nationally severely declining species (i.e. BAP priority species) and nationally moderately declining species. Our study is the first to show that these negative correlations may be the result of direct negative impacts of landscape intensification on these nocturnal insects and indicate that agricultural intensification may be the factor that explains most of the extensive declines of many macro-moths, such as dusky thorn *Ennomos fuscantaria*, lackey *Malacosoma neustria* and garden tiger *Arctia caja* (98%, 90% and 89% declines over 35 years in Britain, respectively), seen over the last few decades (Conrad *et al.* 2006; Groenendijk & Ellis 2011). The negative effects observed here of agricultural intensification on the abundance of both nationally severely and moderately declining species did translate into a negative effect with regard to species richness for the nationally severely declining species group only, which may be due to considerable time-lags between population declines and resulting local extinctions. The observed negative effects on macro-moths corroborate earlier observations by Wickramasinghe *et al.* (2004), who compared land under conventional vs. organic farm systems, suggesting that agricultural intensification has a profound negative impact on nocturnal insect communities. The group of species that are nationally on the increase is positively impacted with increasing levels of agricultural intensification, which may be a result of reduced competition with species that are declining or going extinct as a result of agricultural intensification.

IMPLICATIONS FOR MANAGEMENT

Our results may provide valuable insights for the design of more effective AES, especially because the abundant, species rich and ecologically diverse group of macro-moths may act as an indicator for many other flying invertebrates in particular, and as an indicator of environ-

mental change in general (Thomas 2005). We showed that extended-width field margins and hedgerow trees locally increased the number of macro-moth species, and we therefore recommend straightforward creation and management options for these farmland elements to be integrated within national AES.

We suggest that extended-width field margins and hedgerow trees are particularly useful farmland features to include as options in general AES, for several reasons. Largest numbers of macro-moths were found at sites characterized by both extended-width margins and hedgerow trees, which was the result of an additive rather than an interactive effect. As there was no evidence of a margin \times tree interaction, this suggests that AES do not necessarily need to integrate both farmland elements to be effective, as one element's effect is not relatively larger due to the other element's presence. Moreover, their overall benefit was dependent neither on the degree of landscape intensification nor on spatial scale. We also showed that these features were beneficial to both nationally increasing and declining species groups, sedentary and mobile species, and high-feeders and low-feeders. General AES are intended to combat the negative overall effects of agricultural intensification on wider biodiversity, as opposed to AES options that are designed to target key species for conservation.

Our study is the first to demonstrate that landscape intensification lowers the abundance of both nationally moderately declining and nationally severely declining (i.e. BAP priority) macro-moth species. Because this effect was most pronounced at the 0.8-km radius scale, we suggest that conservation and AES measures mitigating agricultural intensification will be most effective when implemented at this spatial scale (see also Pöyri *et al.* 2009). In practice, this means that efforts to increase hedgerow tree density, for example, may be more effective when targeted at 0.8-km radii landscapes than hedgerow tree implementation over smaller or larger areas. However, our result contrasts to some extent with the findings of Fuentes-Montemayor, Goulson & Park (2011), who suggested that increasing the percentage cover of semi-natural biotopes to benefit macro-moth populations would best be done at a 0.25-km radius scale, rather than at larger scales (0.5/1.0-km radii). Nevertheless, we emphasize that although 0.8 km may be the best scale for nationally declining macro-moths, this scale is not necessarily the best one for other taxa. Indeed, we predict mitigation measures to work best when implemented at a larger spatial scale for generally more mobile taxa, and at smaller scales for less mobile taxa (e.g. 0.25 km for micro-moths: Fuentes-Montemayor, Goulson & Park 2011). As a result, measures to mitigate effects of agricultural intensification may need to be targeted at multiple spatial scales to maximize their effectiveness for multiple taxa (Gabriel *et al.* 2010).

Encouraging farmer participation in AES across landscapes further increases their effectiveness, as areas with a relatively larger amount of land under AES management

show larger positive effects of these AES on farm biodiversity (Gabriel *et al.* 2010). This scale-effect has also been shown for the effect of hedgerow tree presence on macro-moths, as it was only in areas where the amount of land under AES (which comprised a mix of AES measures) was experimentally increased, by targeting farmers, that the presence of hedgerow trees resulted in a significantly higher abundance (+60%) and diversity (+38%) of moths compared to sites without hedgerow trees (Merckx *et al.* 2009a).

In addition to the landscape-scale targeting of farmers and multi-scale management of farmland elements, awareness that the provision and adequate management of simple farmland elements do not only provide biodiversity *per se*, but are able to increase a range of ecosystem services that buffer against the combined threats of further agricultural intensification and climate change should improve public perception, uptake and hence cost-effectiveness of AES. AES are able to improve ecosystem services (Whittingham 2011), such as pollination (Power & Stout 2011), biological control (Winqvist *et al.* 2011) and carbon storage and/or soil quality (Lin *et al.* 2011). Although the locally increased macro-moth species richness observed here due to the presence of hedgerow trees and extended-width field margins is, by itself, not a measure of ecosystem functioning, evidence suggests that they are positively related (Hector & Bagchi 2007), and the increased macro-moth richness is likely to provide a number of economically valuable ecosystem services. First, pollination success and resilience are likely to be facilitated due to higher numbers of pollinating moth species (Devoto, Bailey & Memmott 2011), and possible other pollinating taxa benefitting from the presence of these farmland elements (Power & Stout 2011). Higher pollination success should not only benefit populations of wild plant species, but also increase fruit set and yields of insect-pollinated crops. Secondly, moths are an important prey base for various taxa (Conrad *et al.* 2006), which may result in larger, and more stable populations of species at these higher trophic levels. In turn, this may provide better and cheaper crop pest control (Winqvist *et al.* 2011). The resulting increase in functional diversity of field margins and hedgerows will feed back into an improved ecosystem functioning of farmland as a whole via the affected ecosystem services (Cadotte 2011).

Given that most of Europe's intensive agricultural land was once dominated by forest, hedgerow trees are often the only remaining farmland element referring to this natural climax biotope. As such, it is not surprising that they make a large contribution to the ecological resilience of farmed landscapes, similar to the function of shade trees within tropical agroforestry landscapes (Tscharntke *et al.* 2011) and scattered trees within silvopastoral systems (Fischer, Stott & Law 2010). It is hence likely that hedgerow trees are keystone structures, with a disproportionate effect on ecosystem functioning given the small area occupied by any individual tree.

Given the relentless decline of the biodiversity value of many agricultural landscapes, further detailed research is needed on the biodiversity and ecosystem services effects of hedgerow trees, extended-width field margins, and other farmland elements. In addition to knowing which specific farmland elements are valuable, land managers and policy makers also need research that will lead to precise recommendations as to how to implement and manage these farmland elements, and in what numbers, within AES (e.g. Woodcock *et al.* 2007; Staley *et al.* 2012). The shared aim should be to design optimized AES as a powerful tool to combat the adverse effects of agricultural intensification.

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References

- Bommarco, R., Biesmeijer, J.C., Meyer, B., Potts, S.G., Pöyry, J., Roberts, S.P.M., Steffan-Dewenter, I. & Öckinger, E. (2010) Dispersal capacity and diet breadth modify the response of wild bees to habitat loss. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **277**, 2075–2082.
- Burel, F., Butet, A., Delettre, Y.R. & de la Pena, N.M. (2004) Differential response of selected taxa to landscape context and agricultural intensification. *Landscape and Urban Planning*, **67**, 195–204.
- Cadotte, M.W. (2011) The new diversity: management gains through insights into the functional diversity of communities. *Journal of Applied Ecology*, **48**, 1067–1069.
- Chapman, J.W., Reynolds, D.R., Smith, A.D., Riley, J.R., Pedgley, D.E. & Woiwod, I.P. (2002) High-altitude migration of the diamondback moth, *Plutella xylostella*, to the UK: a study using radar, aerial netting and ground trapping. *Ecological Entomology*, **27**, 641–650.
- Conrad, K.F., Warren, M.S., Fox, R., Parsons, M.S. & Woiwod, I.P. (2006) Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. *Biological Conservation*, **132**, 279–291.
- Defra (2005) *Entry Level Stewardship Handbook*. UK Government Department for the Environment, Food and Rural Affairs, DEFRA Publications, London, UK. http://webarchive.nationalarchives.gov.uk/20100429120916/http://www.naturalengland.org.uk/Images/elshandbook2005_tcm6-6506.pdf.
- Devoto, M., Bailey, S. & Memmott, J. (2011) The 'night shift': nocturnal pollen-transport networks in a boreal pine forest. *Ecological Entomology*, **36**, 25–35.
- Ekroos, J., Heliölä, J. & Kuussaari, M. (2010) Homogenization of lepidopteran communities in intensively cultivated agricultural landscapes. *Journal of Applied Ecology*, **47**, 459–467.
- Feber, R.E., Smith, H. & Macdonald, D.W. (1996) The effects of management of uncropped edges of arable fields on butterfly abundance. *Journal of Applied Ecology*, **33**, 1191–1205.
- Fischer, J., Stott, J. & Law, B.S. (2010) The disproportionate value of scattered trees. *Biological Conservation*, **143**, 1564–1567.
- Fox, R., Conrad, K.F., Parsons, M.S., Warren, M.S. & Woiwod, I.P. (2006) *The State of Britain's Larger Moths*. Butterfly Conservation & Rothamsted Research, Wareham, Dorset, UK.
- Fuentes-Montemayor, E., Goulson, D. & Park, K.J. (2011) The effectiveness of agri-environment schemes for the conservation of farmland moths: assessing the importance of a landscape-scale management approach. *Journal of Applied Ecology*, **48**, 532–542.

- Gabriel, D., Sait, S.M., Hodgson, J.A., Schmutz, U., Kunin, W.E. & Benton, T.G. (2010) Scale matters: the impact of organic farming on biodiversity at different spatial scales. *Ecology Letters*, **13**, 858–869.
- Groenendijk, D. & Ellis, W. (2011) The state of the Dutch larger moth fauna. *Journal of Insect Conservation*, **15**, 95–101.
- Hector, A. & Bagchi, R. (2007) Biodiversity and ecosystem multifunctionality. *Nature*, **448**, 188–191.
- Jennings, N. & Pocock, M.J.O. (2009) Relationships between sensitivity to agricultural intensification and ecological traits of insectivorous mammals and arthropods. *Conservation Biology*, **23**, 1195–1203.
- Kleijn, D., Baquero, R.A., Clough, Y., Diaz, M., De Esteban, J., Fernandez, F., Gabriel, D., Herzog, F., Holzschuh, A., Johl, R., Knop, E., Kruess, A., Marshall, E.J.P., Steffan-Dewenter, I., Tschirntke, T., Verhulst, J., West, T.M. & Yela, J.L. (2006) Mixed biodiversity benefits of agri-environment schemes in five European countries. *Ecology Letters*, **9**, 243–254.
- Kleijn, D., Rundlöf, M., Scheper, J., Smith, H.G. & Tschirntke, T. (2011) Does conservation on farmland contribute to halting the biodiversity decline? *Trends in Ecology & Evolution*, **28**, 474–481.
- Lin, B.B., Flynn, D.F.B., Bunker, D.E., Uriarte, M. & Naeem, S. (2011) The effect of agricultural diversity and crop choice on functional capacity change in grassland conversions. *Journal of Applied Ecology*, **48**, 609–618.
- Marini, L., Bommarco, R., Fontana, P. & Battisti, A. (2010) Disentangling area and habitat diversity effects on orthopteran species with contrasting mobility. *Biological Conservation*, **143**, 2164–2171.
- Marini, L., Öckinger, E., Battisti, A. & Bommarco, R. (2012a) High mobility reduces beta-diversity among orthopteran communities – implications for conservation. *Insect Conservation and Diversity*, **5**, 37–45.
- Marini, L., Bruun, H.H., Heikkinen, R.K., Helm, A., Honnay, O., Krauss, J., Kühn, I., Lindborg, R., Pärtel, M. & Bommarco, R. (2012b) Traits related to species persistence and dispersal explain changes in plant communities subjected to habitat loss. *Diversity and Distributions*, **18**, 898–908.
- Mattila, N., Kaitala, V., Komonen, A., Kotiaho, J.S. & Paivinen, J. (2006) Ecological determinants of distribution decline and risk of extinction in moths. *Conservation Biology*, **20**, 1161–1168.
- Merckx, T., Van Dongen, S., Matthysen, E. & Van Dyck, H. (2008) Thermal flight budget of a woodland butterfly in woodland versus agricultural landscapes: an experimental assessment. *Basic and Applied Ecology*, **9**, 433–442.
- Merckx, T., Feber, R.E., Riordan, P., Townsend, M.C., Bourn, N.A.D., Parsons, M.S. & Macdonald, D.W. (2009a) Optimizing the biodiversity gain from agri-environment schemes. *Agriculture, Ecosystems and Environment*, **130**, 177–182.
- Merckx, T., Feber, R.E., Dulieu, R.L., Townsend, M.C., Parsons, M.S., Bourn, N.A.D., Riordan, P. & Macdonald, D.W. (2009b) Effect of field margins on moths depends on species mobility: field-based evidence for landscape-scale conservation. *Agriculture, Ecosystems and Environment*, **129**, 302–309.
- Merckx, T., Feber, R.E., Mclaughlan, C., Bourn, N.A.D., Parsons, M.S., Townsend, M.C., Riordan, P. & Macdonald, D.W. (2010) Shelter benefits less mobile moth species: the field-scale effect of hedgerow trees. *Agriculture, Ecosystems and Environment*, **138**, 147–151.
- Öckinger, E., Schweiger, O., Crist, T.O., Debinski, D.M., Krauss, J., Kuussaari, M., Petersen, J.D., Pöyry, J., Settele, J., Summerville, K.S. & Bommarco, R. (2010) Life-history traits predict species responses to habitat area and isolation – a cross-continental synthesis. *Ecology Letters*, **13**, 969–979.
- Pereira, H.M., Daily, G.C. & Roughgarden, J. (2004) A framework for assessing the relative vulnerability of species to land-use change. *Ecological Applications*, **14**, 730–742.
- Pinheiro, J.C. & Bates, D.M. (2000) *Mixed-Effects Models in S and S-PLUS*. Springer-Verlag, Inc., New York.
- Power, E.F. & Stout, J.C. (2011) Organic dairy farming: impacts on insect-flower interactions and pollination. *Journal of Applied Ecology*, **48**, 561–569.
- Pöyry, J., Paukkunen, J., Heliölä, J. & Kuussaari, M. (2009) Relative contributions of local and regional factors to species richness and total density of butterflies and moths in semi-natural grasslands. *Oecologia*, **160**, 577–587.
- Pywell, R.F., Warman, E.A., Sparks, T.H., Greatorex-Davies, J.N., Walker, K.J., Meek, W.R., Carvell, C., Petit, S. & Firbank, L.G. (2004) Assessing habitat quality for butterflies on intensively managed arable farmland. *Biological Conservation*, **118**, 313–325.
- R Development Core Team (2008) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria, <http://www.R-project.org>.
- Raebel, E., Merckx, T., Feber, R., Riordan, P., Macdonald, D. & Thompson, D. (2012) Identifying high-quality pond habitats for Odonata in lowland England: implications for agri-environment schemes. *Insect Conservation and Diversity*, **5**, DOI: 10.1111/j.1752-4598.2011.00178.x.
- Robinson, R.A. & Sutherland, W.J. (2002) Post-war changes in arable farming and biodiversity in Great Britain. *Journal of Applied Ecology*, **39**, 157–176.
- Sekar, S. (2012) A meta-analysis of the traits affecting dispersal ability in butterflies: can wingspan be used as a proxy? *Journal of Animal Ecology*, **81**, 174–184.
- Staley, J.T., Sparks, T.H., Croxton, P.J., Baldock, K.C.R., Heard, M.S., Hulmes, S., Hulmes, L., Peyton, J., Amya, S.R. & Pywell, R.F. (2012) Long-term effects of hedgerow management policies on resource provision for wildlife. *Biological Conservation*, **145**, 24–29.
- Summerville, K.S., Wilson, T.D., Veech, J.A. & Crist, T.O. (2006) Do body size and diet breadth affect partitioning of species diversity? A test with forest Lepidoptera. *Diversity and Distributions*, **12**, 91–99.
- Thomas, J.A. (2005) Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **360**, 339–357.
- Tilman, D., Cassman, K.G., Matson, P.A., Naylor, R. & Polasky, S. (2002) Agricultural sustainability and intensive production practices. *Nature*, **418**, 671–677.
- Truxa, C. & Fiedler, K. (2012) Attraction to light – from how far do moths (Lepidoptera) return to weak artificial sources of light? *European Journal of Entomology*, **109**, 77–84.
- Tschirntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I. & Thies, C. (2005) Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecology Letters*, **8**, 857–874.
- Tschirntke, T., Clough, Y., Bhagwat, S.A., Buchori, D., Faust, H., Hertel, D., Hölscher, D., Jührbandt, J., Kessler, M., Perfecto, I., Scherber, C., Schroth, G., Veldkamp, E. & Wanger, T.C. (2011) Multi-functional shade-tree management in tropical agroforestry landscapes – a review. *Journal of Applied Ecology*, **48**, 619–629.
- Waring, P. & Townsend, M.C. (2003) *Field Guide to the Moths of Great Britain and Ireland*. British Wildlife Publishing, Rotherwick, Hampshire, UK.
- Warren, M.S. & Bourn, N.A.D. (2011) Ten challenges for 2010 and beyond to conserve Lepidoptera in Europe. *Journal of Insect Conservation*, **15**, 321–326.
- Whittingham, M.J. (2007) Will agri-environment schemes deliver substantial biodiversity gain, and if not why not? *Journal of Applied Ecology*, **44**, 1–5.
- Whittingham, M.J. (2011) The future of agri-environment schemes: biodiversity gains and ecosystem service delivery? *Journal of Applied Ecology*, **48**, 509–513.
- Wickramasinghe, L.P., Harris, S., Jones, G. & Vaughan Jennings, N. (2004) Abundance and species richness of nocturnal insects on organic and conventional farms: effects of agricultural intensification on bat foraging. *Conservation Biology*, **18**, 1283–1292.
- Williams, N.M., Crone, E.E., Roulston, T.H., Minckley, R.L., Packer, L. & Potts, S.G. (2010) Ecological and life-history traits predict bee species responses to environmental disturbances. *Biological Conservation*, **143**, 2280–2291.
- Winqvist, C., Bengtsson, J., Aavik, T., Berendse, F., Clement, L.W., Eggers, S., Fischer, C., Flohre, A., Geiger, F., Liira, J., Part, T., Thies, C., Tschirntke, T., Weisser, W.W. & Bommarco, R. (2011) Mixed effects of organic farming and landscape complexity on farmland biodiversity and biological control potential across Europe. *Journal of Applied Ecology*, **48**, 570–579.
- Woodcock, B.A., Potts, S.G., Pilgrim, E., Ramsay, A.J., Tscheulin, T., Parkinson, A., Smith, R.E.N., Gundrey, A.L., Brown, V.K. & Tallowin, J.R. (2007) The potential of grass field margin management for enhancing beetle diversity in intensive livestock farms. *Journal of Applied Ecology*, **44**, 60–69.

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