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Quantifying trade-offs between butterfly abundance and movement in the management of agricultural set-aside strips

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Abstract. 1. Agri-environment schemes (AES) create small areas of habitat within agricultural landscapes to support biodiversity. Here, we study butterfly flight behaviour within linear AES features and examine whether differences in resource availability affect the speed, linearity, or directionality of local movements, thereby affecting their contribution to landscape connectivity.

2. We surveyed butterflies within three basic (naturally regenerating) and three wildflower-sown linear field margin strips (0.09–0.15 ha) on a farm in North Yorkshire, UK, and mapped butterfly flight paths to quantify local displacement (movement speed), efficiency (linearity, turning angles), directionality (step orientation), and behaviour (time spent flying, nectaring).

3. Butterfly species richness was similar between margin types {estimated asymptotic species richness of 21.9 [confidence interval (CI): 15.0–77.7] for basic margins and 14.2 (CI: 14.0–18.7) for wildflower-sown margins}, but abundance was 78% higher in wildflower-sown margins. For the three most common species [meadow brown, *Maniola jurtina* (L.); ringlet, *Aphantopus hyperantus* (L.); and small white, *Pieris rapae* (L.); $n = 233$ paths], movements within both margin types were highly linear (median turning angle 45°) and generally oriented along the length of the margin strip (median step orientation 27°). Movements in basic margins were slightly more orientated along the length of the margin but we found no differences between margin types in speed, path linearity, turning angles or the proportion of time spent flying or nectaring.

4. We found strong channelling of movements along field margin strips regardless of management type, potentially aiding landscape connectivity. Providing field margin strips with additional foraging resources through wildflower-sowing increases butterfly abundance without impeding local movement rates or efficiency.

Key words. Agri-environment scheme, butterfly, connectivity, corridor, movement.

Introduction

The modern global footprint and intensity of agriculture is a well-known driver of biodiversity declines (Foley *et al*., 2005; Newbold *et al*., 2015; Zabel *et al*., 2019). As well as direct implications of land use changes and intensification for biodiversity, the spatial patterning of remaining habitat is important for determining biodiversity impacts (Chaplin-Kramer *et al*., 2015). Spatial patterning affects landscape connectivity, defined as the extent to which organisms are able to move between habitat patches (Taylor *et al*., 1993). Agricultural land uses are generally considered to be hostile to much of the world's biodiversity, and agricultural land can represent a significant barrier to movement for many species which avoid entering it at boundaries (Stevens *et al*., 2006; Scriven *et al*., 2017). The connectedness of resulting habitat networks has varied implications,

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dependent on the species of interest, and local context. For instance, poor connectivity at the edge of species' current distributions can reduce the ability of species to shift their ranges in response to climate change (Saura *et al*., 2014; Anadon *et al*., 2018). Within a species' range, poor connectivity can reduce gene flow between local populations (Keller & Largiadèr, 2003; Coulon *et al*., 2004; McRae & Beier, 2007), and prevent colonisations necessary to maintain persistent meta-populations (Swart & Lawes, 1996; Hanski & Ovaskainen, 2000). Poor connectivity can also reduce access to necessary resources (e.g. food, breeding sites, suitable microclimates) for survival (Taylor *et al*., 1993; Grundel & Pavlovic, 2007). Whilst connectivity is often thought of as a property of habitats at landscape scales, it is fundamentally dependent on localised movements which contribute to longer-distance dispersal by individuals.

The local movements of individuals which contribute to landscape-scale dispersal can broadly be categorised into two components: movements across habitat boundaries and movements within habitat patches. It has generally been observed that species prefer high-quality habitat, or habitat over non-habitat, at boundaries (Schultz *et al*., 2012; Delattre *et al*., 2013; Kallioniemi *et al*., 2014; Mair *et al*., 2015; Scriven *et al*., 2017), but if subsequent movements through non-habitat (matrix) areas are faster, or more directional than movements through high-quality habitat, the relationship between habitat quality and dispersal may not be straight forward. Low-quality habitat corridors have been shown to be effective at facilitating dispersal (Haddad & Tewksbury, 2005), and movement rates can be higher in areas where habitat quality is lower (Schultz, 1998; Gilliam & Fraser, 2001; Kuefler *et al*., 2010). Examining butterfly movement behaviour, Kuefler *et al*. (2010) identified a negative relationship between the probability of entering habitat and the speed of moving through it. This illustrates that high-quality habitat may attract a greater abundance of individuals, for which movement rates through that habitat may then be limited because individuals engage more in behaviours associated with routine breeding and foraging activities, rather than movement. As a consequence, when habitat patches are introduced into landscapes for the purposes of improved connectivity (e.g. habitat corridors, stepping stones), it would be useful to understand the impacts of habitat quality within these features on local movement patterns.

In response to concerns over the detrimental environmental impacts of agriculture, many countries now operate subsidy schemes which financially incentivise farmers to take small patches of agricultural land out of production for purposes including soil conservation, preventing agricultural runoffs and supporting biodiversity. These agri-environment schemes (AESs) are particularly common within Europe where the European Union (EU) requires all member states to offer some form of AES (Keenleyside *et al*., 2011). By introducing additional habitat into landscapes, many options within AES agreements (e.g. hedgerows, woodland planting, grassland restoration, field margin strips) have the potential to improve functional connectivity. However, it remains unclear the extent to which the habitat quality (e.g. resource provision) of a feature may positively, or negatively, impact its contribution to connectivity by influencing individual movement patterns.

AES habitat patches can support biodiversity by successfully providing additional habitat within landscapes, and so we would expect AESs to also have a positive impact on overall landscape connectivity (Threadgill *et al*., 2020). This could come about by various means: e.g. increasing landscape carrying capacity and therefore the production of propagules, functioning as 'stepping stone' habitat patches (Saura *et al*., 2014; Herrera *et al*., 2017), and/or providing resources which reduce rates of dispersal mortality. On a local scale, the physical design of certain linear AES habitat features (including field margin strips, hedgerows, and ditches) may have additional connectivity benefits if they are able to promote and channel movements in particular directions, providing direct linkages (i.e. corridors) between neighbouring habitat sites. Previous studies illustrate that linear AES features can be useful movement conduits for many species (Burel, 1989; Verboom & Huitema, 1997; Joyce *et al*., 1999; Sutcliffe *et al*., 2003; Delattre *et al*., 2013; Guiller *et al*., 2016); however, it remains unclear whether the quality of habitat within linear features influences how organisms move through them. Enhancing the resource availability within AES features has been shown to boost species abundance and/or richness of various insect taxa (Meek *et al*., 2002; Carvell *et al*., 2006; Haaland *et al*., 2011; Pywell *et al*., 2011), but this could come at a cost to movement rates. If land managers wish to deploy linear AES habitat features strategically to facilitate connectivity, it would be useful to know whether resource enhancement involves a trade-off between boosting species abundance/richness and maintaining movement rates.

Here, we examine the effect of habitat quality on butterfly movement behaviour through linear habitat features. Specifically, we examine the extent to which sowing wildflower seed mixes in field margin strips affects, firstly, abundance, and species richness of adult butterflies and, secondly, the speed and efficiency of their movement. We expect that although the additional foraging resources available in wildflower-sown margins may attract greater abundance and diversity of butterflies, this may also affect the speed and efficiency of movements through these features. By comparing basic and wildflower-sown field margins, we test the following hypotheses. Firstly, we predict that wildflower-sowing of field margin strips increases the abundance and species richness of butterflies compared to basic margins. Secondly, we predict that wildflower-sowing impacts local movements by reducing the speed, efficiency (linearity), and directionality of butterfly movements, as well as the proportion of time spent in flight.

Methods

Study site

We surveyed butterflies and recorded their flight paths from June to August 2018 at Askham Bryan College farms (Home Farm and Westfield Farm), near York, in the north of England (Fig. 1; 53.92°N, −1.16°E). At the time of data collection, these farms were managed under an Environmental Stewardship Scheme (ESS) agreement. ESS is an AES operational within England from 2005 to 2025 (closed to new applicants from 2015). The agreement held by Askham Bryan College farms

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Figure 1. Study site at Askham Bryan College farms, near York, UK. Darker shaded areas highlight fields within which data collection occurred. Orange and purple strips represent the basic and wildflower sown field margins respectively which were sampled in this study. [Color figure can be viewed at wileyonlinelibrary.com]

included provision for both 'buffer strips' – naturally regenerating set-aside strips at the edges of arable fields – and 'floristically enhanced buffer strips' – strips sown with a seed mix of grasses and wildflower species and subjected to a restricted cutting regime, with each margin type established 2 years prior to data collection. These margin types are herein referred to as 'basic' and 'wildflower-sown', respectively.

We observed butterflies in six individual field margin strips, three basic and three wildflower-sown margins. These margins were arranged in a paired design across three arable fields, such that each field contained one margin of each type. All margins had a width of 6 m, were adjacent on one side to a non-flowering crop (wheat and potatoes pre-flowering) of height no greater than 1 m (to prevent crops acting as a physical barrier), and on the other a hedgerow in excess of 2 m tall. Within each margin, we established a 100 m × 6 m plot within which butterflies were sampled. The complete length of margins varied from 148 to 246 m (0.09–015 ha).

Surveys of nectar resources

To assess the resource provision in each margin type, we surveyed the nectar resources available for butterflies to feed on. Each margin was sampled once, between 25th June and 9th July 2018. Nectar availability was sampled at six positions 20 m apart along the length of the margin, in five 0.5 × 0.5 m quadrats across the width (centred at 0.25, 1.75, 3, 4.25, 5.25 m). In each quadrat, we recorded the number of single flowers (or capitulum for Asteraceae; flower number estimated to nearest 10 flowers for species with compound umbels) of each flowering species (30 quadrats per margin). From these counts, we calculated the total mass of nectar sugar available in each quadrat using nectar quantity values for each species from published literature (Table S2). We also sampled both general vegetation composition and density (of particular relevance for the availability of larval host plants), summarised in Supplementary Materials Appendix 1.

Butterfly surveys and flight path tracking

Butterflies were sampled between 10.00 and 17.00 h on sunny days at temperatures of at least 15°C and when wind speed did not exceed five on the Beaufort scale. Each field margin plot was patrolled on foot along the length of the 100 m plot (along the crop- and hedge-side edges, without venturing into the

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middle of the field margin, one observer each side), and all butterflies of any species observed within the plot were recorded. Owing to relatively low butterfly densities (mean of 8.3 individuals per hour), butterfly occurrences were recorded during and between butterfly movement observations (see below; butterflies observed during flight path observations were noted into an audio recording device). This approach did risk some double-counting of individuals, but we expect this to be relatively rare due to this low average butterfly density and because no repeated observations were made of marked individuals (marked following movement tracking, see below) on subsequent sampling days (see the *Butterfly movement behaviour* section for further details). Sampling times varied slightly between plots due to unsuitable weather conditions in parts of some days (total sampling time per margin plot ranged from 17.0 to 23.8 h). We therefore recorded butterfly abundance as abundance per hour sampled.

To track butterfly flight behaviour, we followed butterflies within field margin strips on foot and recorded their position every 20 s, and every time they landed, in accordance with methodology developed by Turchin *et al*. (1991). Numbered markers were dropped at the edge of the margin alongside a tape measure; this allowed recording of longitudinal position to the nearest 0.1 m. Repeatedly venturing into the centre of the margin on foot was not possible due to trampling of vegetation, therefore the position of butterflies across the width of the margin was classified by eye to the nearest 1.5 m (quarter of total width), by reference to width markers placed in the margin at regular intervals. Due to the coarse resolution of width position data, longitudinal positions were rounded to the nearest 1.5 m for further analysis. Markers were also dropped to mark the positions of exits from and entries into the margin. When individuals exited, they continued to be observed (until they were lost from view) – if the individual returned to the margin the position of re-entry was marked and the observation was continued. Individuals were followed until any of the following criteria were met: (i) 20 markers had been placed, (ii) the individual remained stationary for >10 min, (iii) the butterfly exited the margin and was not seen to return, and (iv) the butterfly was lost into the vegetation of the margin. Timings and behaviours at markers were logged by a voice recording device. Behaviours were characterised as: stationary (nectaring/basking/sitting) or flying. Where possible, butterflies were captured at the end of a flight path and marked to avoid repeated sampling of the same individuals.

Flight path analysis

To analyse movement behaviour, we first summarised each individual flight path as a series of discrete steps between successive numbered markers. From these, we were able to summarise movement speed rate (total flight path distance, divided by total duration) and linearity (ratio of maximum displacement between two markers to total path length – as Ovaskainen *et al*., 2008) for each individual. For each individual step, we were able to calculate its orientation relative to the orientation of the margin (measured as a value between 0° and 90°, corresponding to parallel and perpendicular orientations respectively). Step orientation analysis was limited to those steps ≤6 m in length, because margins were 6 m wide and therefore no steps of longer than 6 m could occur in the perpendicular direction. For each step after the first step, we were able to calculate the turning angle defined as the angle through which a step direction deviated from the direction of the previous step (varying from 0° to 180°, corresponding to continuing to move in the same direction, and an about turn respectively), an additional measure which we use to illustrate the linearity of flight paths.

Statistical analysis

To examine the effect of margin type on butterfly abundance (total number of individuals per hour of observation, irrespective of species identity), we compared a linear model containing the single predictor of margin type (categorical; basic or wildflower-sown) and a response variable of butterfly abundance (each data point represented average abundance per hour for a single sampling day) to a null model using a likelihood ratio test. Although data contained repeated sampling in different field margin plots, a mixed-effects model with a margin identity random intercept term was unsuitable because the random effect variance was close to zero. To compare the species richness of butterflies between margin types, we constructed sampling effort (surveying time)-based accumulation curves and expected asymptotic species richness for each field margin type (*iNEXT* package in *R*; Hsieh *et al*., 2016). To examine the butterfly community composition, we used non-metric multidimensional scaling (NMDS) ordination (*vegan* package in *R*, using Manhattan distance for relative abundances) where sampling units represent single days spent sampling in individual field margin strips, allowing us to compare community composition between margin types.

For our analysis of movement properties, we used a subset of our data which covered the three most commonly sampled species [meadow brown, *Maniola jurtina* (L.), ringlet, *Aphantopus hyperantus* (L.), and small white, *Pieris rapae* (L.)]. To examine the effect of margin type on movement properties across species, we constructed (G)LMMs using the *R* packages *nlme* and *glmmTMB*. For responses of movement speed, step orientation, turning angles, proportion of time flying, and proportion of time nectaring, we first constructed full models with fixed effects of margin type (categorical; basic or wildflower-sown), species (categorical; *M. jurtina*, *A. hyperantus*, or *P. rapae*) and their interaction. For path linearity, we also included a fixed effect for total path length (to account for correlation between path length and linearity – longer paths have greater opportunity for deviation from a straight line). Movement speed was square-root transformed and modelled with a Gaussian family and identity link. Path linearity, step orientation, turning angles, proportion of time flying, and proportion of time nectaring were scaled to [0,1], transformed by $y' = \frac{y(N-1)+0.5}{N}$, where N is the total sample size, so that all values fell in the interval (0,1) (Smithson & Verkuilen, 2006), and then modelled with a beta family and logit link. For all models, we included random intercept terms representing, firstly, the identity of the field within which data were

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collected, and secondly, the day on which data were collected (to account for day-to-day variation in weather conditions). For step orientation and turning angle models, we also included a random intercept term for the identity of individual butterflies because each data point represented one step within an individual's path. For each model, we compared all fixed effects structures nested within our full model and report top models as those for which ΔAICc ≤2, except those with a higher AICc than any simpler nested version.

Results

Nectar resources, and butterfly abundance, and richness in field margin strips

Wildflower-sown margins contained five times more foraging resource than basic field margin strips, measured as nectar sugar availability (Friedman rank sum test with replicated block design, $\chi^2 = 7.70$, d.f. = 1, $P < 0.01$; median nectar availability in basic margins = 21.3 μg m^{-2}, IQR = 38.9 μg m^{-2}, median in wildflower-sown margins = 113.6 μg m^{-2}, IQR = 86.8 μg m^{-2}; Fig. 2). A total of 984 butterflies were observed from 15 species across all six field margin strips and 25 sampling days (Table S4). Total butterfly abundance was 78% greater in wildflower-sown margin strips than basic margins (LRT: $\Delta\chi^2 = 12.99$, d.f. = 1, $P < 0.001$), with an estimated mean abundance (±SE) in basic margins of 5.57 ± 1.10 individuals per hour and in wildflower-sown margins of 9.92 ± 1.14 individuals per hour (Fig. 3a). However, expected asymptotic species richness was similar across basic and wildflower-sown field margin strips (basic: expected = 21.9, CI = 15.0–77.7; wildflower-sown: expected = 14.2, CI = 14.0–18.7; Fig. 3b). Given the relatively limited number of butterfly species found in the UK (~60, and many of which are restricted to the south of England), we would expect the true asymptotic species richness of basic margins to lie at the lower end of this calculated confidence interval. Ordination of butterfly communities (NMDS in three dimensions, stress = 0.12; Fig. S1A) illustrated some separation between community compositions of basic and wildflower-sown field margin strips, although some caution should be applied in the interpretation of this analysis owing to unevenness in sampling effort across sampling units (an individual sample represents all observations within a sampling day; observation duration within a day varied from 3.8 to 6.0 h). Nearly all species were found in higher abundances in wildflower-sown margins (Fig. S1B), but *A. hyperantus* was the only species to exhibit substantially higher abundance in basic margins, whilst common blue (*Polyommatus icarus* Rottemburg) and comma (*Polygonia c-album* L.) were observed only in basic margins, but constituted very small numbers of observations (two and three individuals, respectively).

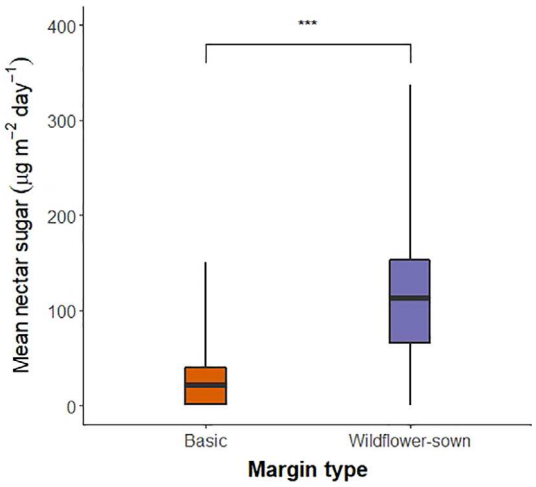

Figure 2. Mean nectar quantity at each position along margin plots (five samples at each position x six positions 20 m apart = 30 quadrats per margin type) for each margin type. Bracket indicates significant difference (***$P < 0.001$) according to Friedman rank sum test with replicated block design (field ID as blocks). Orange represents basic field margins, and purple represents WFS field margins. [Color figure can be viewed at wileyonlinelibrary.com]

Butterfly movement behaviour

For analysis of movement behaviour, we examined flight paths from the three most commonly occurring species, *M. jurtina*, *A. hyperantus*, and *P. rapae*, which together made up 74% of flight paths (43 *M. jurtina*, 68 *A. hyperantus*, and 122 *P. rapae*, out of a total of 313 paths) and 69% of all butterflies observed (112 *M. jurtina*, 172 *A. hyperantus*, and 392 *P. rapae*, out of a total of 984 individuals). Overall, these species moved with a median speed (total flight path length divided by total duration) of 0.25 m s^{-1} (IQR = 0.43 m s^{-1}) and a median displacement (distance between first and last positions divided by total duration) of 0.11 m s^{-1} (IQR = 0.29 m s^{-1}). 30% (94/313) of followed individuals were marked; of these, no individuals were observed again on subsequent sampling days, either in the same or different field margins.

The orientation of individual steps was highly biased towards moves parallel to, rather than perpendicular to, the orientation of the margin (median standardised step orientation = 27°, IQR = 63°; Fig. 4a). Flight paths were generally linear, with turning angles biased towards movements in a similar direction to that of the previous step (median turning angle = 45°, IQR = 76°; Fig. 4b). Results from our top GLMMs (Table 1) indicate significant bias from random in both step orientation and turning angles (intercept terms significantly less than zero; Table 2). Individuals spent a median of 54.4% of time in flight (IQR = 68.8%). 46.9% of individuals engaged in nectaring behaviour during their recorded movement path, of which the median proportion of time spent nectaring was 34.9%.

Comparison of movement behaviour between margin types and species

Across all movement metric (G)LMMs, margin type featured as a predictor in the top model of the step orientation model only.

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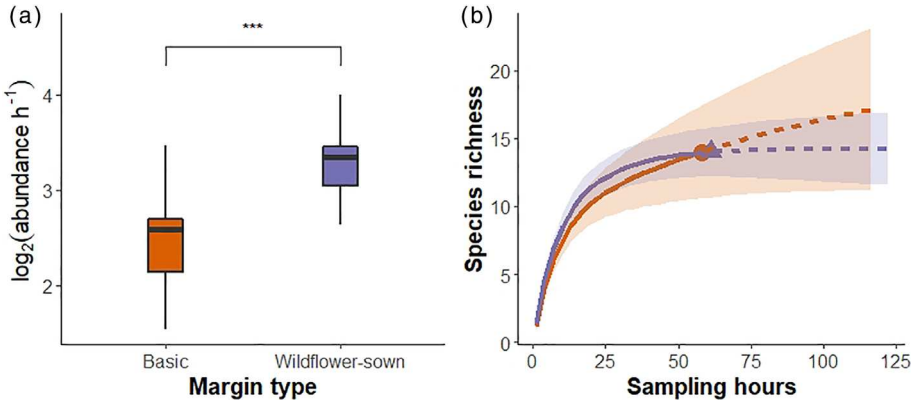

Figure 3. Butterfly abundance and species richness in basic field margins (orange) and wildflower-sown field margins (purple). (a) Per-hour butterfly abundance in basic and wildflower-sown field margins (log2 transformed). Bracket indicates significant difference in abundance between margin types (LRT: $\Delta\chi^2 = 12.99$, d.f. $= 1$, $P < 0.001$). (b) Sampling effort (surveying time)-based species accumulation curves in basic and wildflower-sown field margins. Solid lines indicate species accumulation up to the total sampling duration in this study, with dashed lines extrapolating expected species accumulation up to twice the total sampling duration for each margin type. Error bands indicate 95% confidence interval. [Color figure can be viewed at wileyonlinelibrary.com]

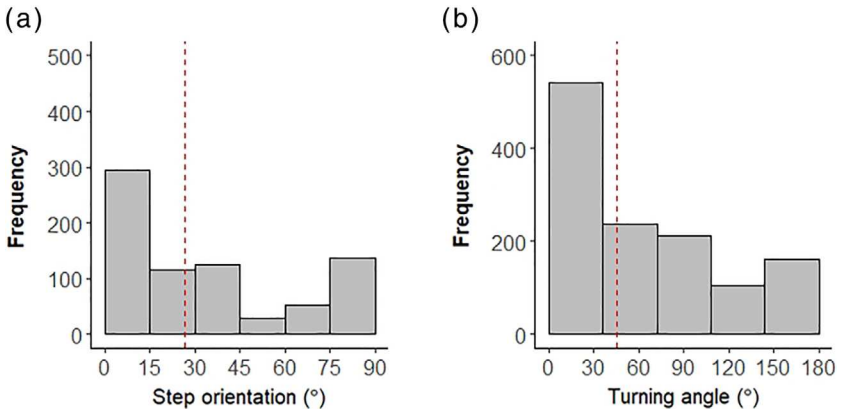

Figure 4. Frequency distributions of (a) step orientations and (b) turning angles for flight paths of *M. jurtina*, *A. hyperantus*, and *P. rapae* (pooled for all species). Red dashed lines indicate median values. Step orientation is measured as the angle between a step and the orientation of a field margin, scaled to [0°, 90°] where 0° represents a step parallel to, and 90° represents a step perpendicular to, the orientation of the margin. Turning angles are measured as the change in direction between one step and the next, scaled to [0°, 180°] where 0° represents a step in the same direction as the previous step, and 180° represents a step in the opposite direction to the previous step. [Color figure can be viewed at wileyonlinelibrary.com]

Butterflies in basic margins exhibited moves which were closer to the orientation of the margin than in wildflower-sown margins but this effect was very small (mean difference in orientation = 6°; $P < 0.003$; Table 2). Even though nectar resources differed considerably between margin types (see above), margin type did not appear as a predictor in top models for movement speed, linearity, turning angle, proportion of time spent flying, or proportion of time spent nectaring (Table 2; Fig. 5). Species identity was an important predictor for the top models of overall movement speed and proportion of time nectaring, but not linearity, step orientation, or turning angles (Table 2; Fig. 5). For movement speed, a post hoc Tukey test illustrated that *A. hyperantus* moved significantly slower than *M. jurtina* (by 0.025 m s^{-1}, $P < 0.01$) and *P. rapae* (by 0.044 m s^{-1}, $P < 0.001$), but that there was no significant difference in movement speeds between *M. jurtina* and *P. rapae* (difference in mean speed = 0.003 m s^{-1}, n.s.). For the proportion of time nectaring, a post hoc Tukey test illustrated that *P. rapae* spent a significantly greater proportion of time nectaring than either *M. jurtina* (mean difference = 12.6% of time, $P < 0.01$) or *A. hyperantus* (mean difference = 8.5% of time, $P < 0.05$), but no significant difference between *M. jurtina* and *A. hyperantus*. For the proportion of time spent flying, the species-only and null models had similar support (ΔAICc = 1.04; Table 1). Thus, we find no support for our hypotheses that wildflower-sowing reduces speed or efficiency (measured as linearity or turning angles) of movement, or the proportion of time spent in flight. We do find evidence for step orientations differing between margin types, although the size of this effect is very small.

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Table 1. Top models for movement property (G)LMMs. Models reported are those for which ΔAICc ≤ 2 except those with a higher AICc than any simpler nested version.

Response	Full model	Top model structure	d.f.	logLik	AICc	Δ_i	w_i
Speed*	margin type + species + margin type:species	Species	8	−16.080	48.8	-	0.683
Linearity†	margin type + species + margin type:species + path length	Path length	5	116.140	−222.0	-	0.537
Step orientation†	margin type + species + margin type:species	Margin type	6	1187.496	−2362.9	-	0.656
Turning angle†	margin type + species + margin type:species	-	5	572.910	−1135.8	-	0.516
Proportion of time flying†	margin type + species + margin type:species	Species	6	75.155	−137.9	-	0.311
		-	4	72.531	−136.9	1.04	0.184
Proportion of time nectaring†,‡	margin type + species + margin type:species	Species	8	357.865	−699.1	-	0.034

*Gaussian response with identity link function, square-root transformed. Fitted with a species-wise variance structure to account for heteroscedasticity across species groups.
†Beta response with logit link, transformed to (0,1) by $y' = [y(N - 1) + 0.5]/N$ (Smithson & Verkuilen, 2006).
‡Fitted with dispersion parameter varying by species to account for heteroscedasticity across species groups.

Table 2. Parameter estimates for movement property (G)LMMs based on top models specified in Table 1. All coefficients are reported on the scale of the link function.

Response	*n*	Model structure	Parameter	Coefficient	SE	*t*-value	*P*-value
Speed†	219	Species	Intercept [species (*M. jurtina*)]	0.555	0.054	10.236	<0.001***
			species (*A. hyperantus*)	−0.152	0.044	−3.473	<0.001***
			species (*P. rapae*)	0.050	0.046	1.093	0.276
Response	*n*	Model structure	Parameter	Coefficient	SE	*z*-value	*P*-value
Linearity‡	219	path length	Intercept	1.521	0.193	7.899	<0.001***
			path length	−0.009	0.002	−4.554	<0.001***
Step orientation‡	752	Margin type	Intercept [margin type (basic)]	−0.494	0.071	−6.975	<0.001***
			margin type (WFS)	0.293	0.098	2.971	0.003**
Turning angle‡	1259	-	Intercept	−0.482	0.075	−6.441	<0.001***
Proportion of time flying‡	226	Species	Intercept [species (*M. jurtina*)]	0.718	0.229	3.140	0.002**
			species (*A. hyperantus*)	−0.539	0.268	−2.009	0.045*
			species (*P. rapae*)	−0.540	0.253	−2.132	0.033*
		-	Intercept	0.273	0.115	2.37	0.018*
Proportion of time nectaring‡,§	226	Species	Intercept [species (*M. jurtina*)]	−2.257	0.262	−8.628	<0.001***
			species (*A. hyperantus*)	0.407	0.334	1.219	0.223
			species (*P. rapae*)	0.994	0.293	3.394	<0.001***

†Gaussian response with identity link function, square-root transformed. Fitted with a species-wise variance structure to account for heteroscedasticity across species groups.
‡Beta response with logit link, transformed to (0,1) by $y' = [y(N - 1) + 0.5]/N$ (Smithson & Verkuilen, 2006).
§Fitted with dispersion parameter varying by species to account for heteroscedasticity.
*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Discussion

Since their adoption by the EU in the 1980s, AESs have become the principle means of conservation on farmland across Europe and, if designed appropriately, have the potential to provide considerable biodiversity benefits (Batáry *et al*., 2015). Previous studies have shown that, in highly fragmented landscapes with relatively low habitat cover, linear AES habitat features can benefit biodiversity by facilitating functional connectivity across otherwise hostile matrix environments (Burel, 1989; Verboom & Huitema, 1997; Joyce *et al*., 1999; Sutcliffe *et al*., 2003; Guiller *et al*., 2016; Threadgill

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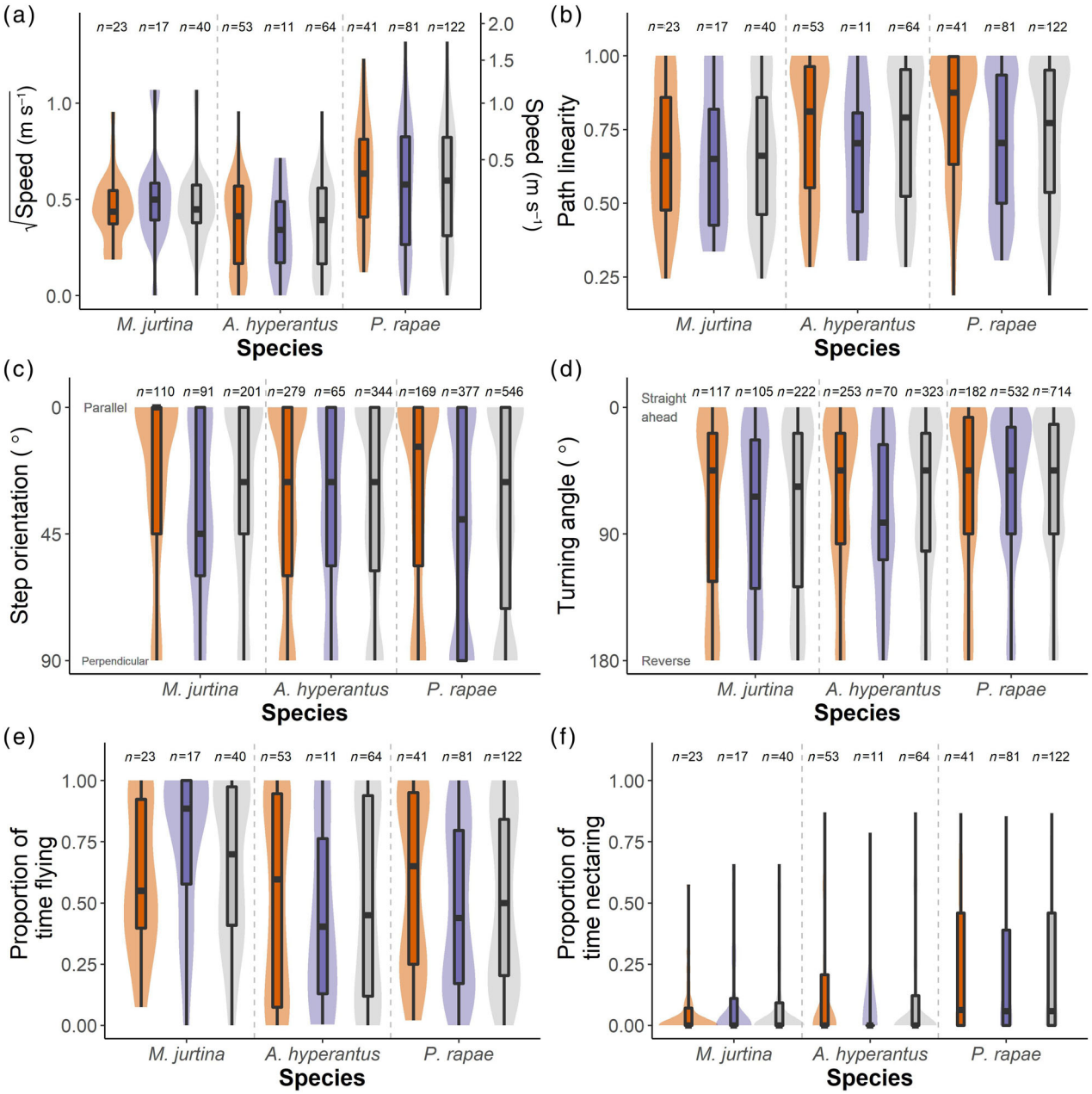

Figure 5. Butterfly movement properties in basic and wildflower-sown field margins for the three most common species. (a) Movement speed, measured as total path length divided by path duration. (b) Path linearity, measured as the ratio between the maximum displacement between any two markers and the total path length. (c) Step orientation, measured as the angle between the orientation of the field margin and the direction of an individual step (0° = step parallel to field margin orientation; 90° = step perpendicular to field margin orientation). (d) Turning angles, measured as the angle between the direction of a step and its previous step (0° = movement continues straight ahead; 180° = movement in reverse direction). Orange represents basic field margins, purple represents wildflower-sown field margins, and grey represents both margin types combined. Shaded 'violins' illustrate smoothed density estimates. For (a), (b), (e), and (f), data points represent individual flight paths. For (c) and (d), data points represent individual movement steps. Sample sizes are illustrated above each plot. [Color figure can be viewed at wileyonlinelibrary.com]

et al., 2020). Here, in agreement with previous research (Delattre *et al.*, 2013), we show that field margin strips are effective at funnelling butterfly movements in linear directions, illustrated by considerable bias in turning angles and step orientations towards parallel, linear movements through margins (Figure 4). However in contrast to our predictions, we found that wildflower-sowing of field margin strips did not affect movement patterns within them in terms of speed or

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efficiency, although it did enhance butterfly abundance by 78%, in line with previous studies on various insect taxa showing elevated abundance for wildflower-sown margin strips (Meek *et al*., 2002; Carvell *et al*., 2006; Haaland *et al*., 2011; Pywell *et al*., 2011).

Local movements in AES field margin strips

Our results show that investment in additional foraging resources within our field margin strips, measured in terms of nectar sugar availability, provided substantial abundance benefits without affecting local movements. Of the movement metrics examined, only one (step orientation) showed significant differences between treatments. However, the scale of this difference (steps in basic margins were 6° closer to the orientation of the field margin) is small, especially when considered in relation to the relatively coarse spatial resolution of butterfly positional data (1.5 m in each direction). We therefore found no substantial evidence of a trade-off for margin management between boosting abundance/richness, and maintaining movement rates. Contrasts in abundance between margin types may be explained either by wildflower-sown margin strips being more attractive than basic margins to individuals dispersing through the wider landscape, or by wildflower-sown margins supporting greater numbers of resident individuals.

The absence of a trade-off in land management between increasing abundance/richness and increasing movement rates was counter to our initial predictions. A number of studies provide evidence for reduced movement speeds of butterflies in higher quality habitats (Schultz, 1998; Kuefler *et al*., 2010; Schultz *et al*., 2017), and yet we find no evidence for this effect within these highly linear habitat features. One reason for this could be that movement rates within field margin strips of all types are elevated by the linear nature of these features. Inherent in their design, field margin strips have large edge-to-area ratios, and we expect that within our plots (6 m wide) both long edges are within an individual's perceptual range at all times. Therefore, this may limit the extent to which individuals capitalise on the higher nectar provision within wildflower-sown margins. Habitat edges may be perceived as risky, making butterflies more reluctant to engage in long periods of foraging behaviours which could leave them vulnerable to threats such as predation. Alternatively, similar movement and nectaring behaviours between margin types could be explained by both treatments providing sufficient resource for maximal foraging. Although additional resources were provided in wildflower-sown margins, if these were not required because individuals were able to be satiated under either treatment, we would not expect them to behave differently to individuals within basic margins.

The role of species traits in local movement and dispersal

Whilst our results illustrate similar movement patterns through each margin type, the value of these types of habitat patches within landscapes, in terms of their impact on dispersal and long-term persistence, is likely to vary across species. Species which are good, but not excellent, dispersers/reproducers are likely to reap the greatest connectivity benefits from the addition of small habitat patches into landscapes (Threadgill *et al*., 2020). The relative isolation experienced by species within fragmented landscapes is a function of both geographic separation and species' traits (such as dispersal: Dennis *et al*., 2012; Flantua *et al*., 2020), and species with intermediate generalism are likely to be those most reliant on inter-patch movements to maintain genetic diversity (Habel & Schmitt, 2012), and may be particularly susceptible to environmental change (Dapporto & Dennis, 2013). Previous work on UK butterflies has shown that food availability–abundance relationships can be mediated by traits including mobility and generalism (Curtis *et al*., 2015) and generalism can be critical to predicting distributional changes, at least in so much as it affects habitat availability (Platts *et al*., 2019). Further, relationships between traits such as mobility and species occurrence and population trends have been quantitatively examined through the study of UK island butterfly communities (Dennis *et al*., 2012). It may be that the separation of community composition observed in our NMDS analysis is driven by consistent patterns of species' preferences for one margin type in accordance with species traits (e.g. larval host plant availability). Our study provides insufficient total species richness (a total of 15 species recorded, for which good movement data were available for only three species) to carry out a robust trait-based analysis to explore differences between species in abundance or movement. Further work in this area could provide useful insights to develop mechanistic understanding of inter-specific differences in the use of field margin habitat, and understand consequences for species in the wider landscape. Species traits such as mobility and habitat generalism are likely to be key predictors of the magnitude of field margin effects on connectivity and population trends. Wider role of field margin strips for butterflies in agricultural landscapes.

Facilitating movement is not the only way in which habitat can contribute to functional connectivity. Patches of breeding habitat are also essential to produce future generations of propagules. We recorded no incidences of egg laying behaviour during our observations for either margin type, although it is difficult to determine whether this is explained by a true absence of breeding, or difficulties in observing this kind of behaviour, especially at distances of up to three metres (distance from the centre of a margin to its edge, from which observations were taken). Egg laying may have occurred deep in vegetation or directly into the air (as is the egg laying behaviour of *A. hyperantus*) making it difficult to detect. Nevertheless, for *P. rapae* we found no larval host plants in our surveys (Supplementary Material Appendix S1). It may be that more targeted seed mixes focusing on key larval host plants, or management techniques aimed to optimise vegetation structure for breeding, could increase rates of reproduction within these features and further contribute to landscape connectivity.

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Conservation implications of linear AES habitat features

Field margin strips which take land out of production at the edges of arable fields can provide significant quantities of additional biodiversity to otherwise biodiversity-poor farmland environments without reducing yields (Pywell *et al.*, 2015). We have shown that movements of butterflies within these features can be highly directional and that enhancement with nectar resources, which can boost abundance, does not necessarily impede movement rates or efficiency. A lack of clear trade-off between abundance/richness and movement rates in the management of field margin strips suggests that wildflower-sowing is a reasonable strategy when using field margins to facilitate dispersal across landscapes.

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Data availability statement

The data that support the findings of this study are openly available in Dryad at https://doi.org/10.5061/dryad.7m0cfxptf

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1: Supplementary Information

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