

Life-history traits and landscape characteristics predict macro-moth responses to forest fragmentation

ELEANOR M. SLADE,^{1,2,6} THOMAS MERCKX,^{1,3} TERHI RIUTTA,⁴ DANIEL P. BEBBER,⁵ DAVID REDHEAD,¹
PHILIP RIORDAN,¹ AND DAVID W. MACDONALD¹

¹Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, Recanati-Kaplan Centre,
Tubney House, Abingdon Road, Tubney, Abingdon OX13 5QL United Kingdom

²Spatial Foodweb Ecology Group, Department of Applied Biology, P.O. Box 27, Latokartanonkaari 5,
FI-00014 University of Helsinki, Finland

³Behavioural Ecology and Conservation Group, Biodiversity Research Centre, Earth and Life Institute, Université Catholique de
Louvain (UCL), Croix du Sud 4–5, bte L7.07.04, BE-1348 Louvain-la-Neuve, Belgium

⁴Environmental Change Institute, School of Geography and the Environment, University of Oxford,
South Parks Road, Oxford OX1 3QY United Kingdom

⁵Earthwatch Institute, 256 Banbury Road, Oxford OX2 7DE United Kingdom

Abstract. How best to manage forest patches, mitigate the consequences of forest fragmentation, and enable landscape permeability are key questions facing conservation scientists and managers. Many temperate forests have become increasingly fragmented, resulting in reduced interior forest habitat, increased edge habitats, and reduced connectivity. Using a citizen science landscape-scale mark–release–recapture study on 87 macro-moth species, we investigated how both life-history traits and landscape characteristics predicted macro-moth responses to forest fragmentation. Wingspan, wing shape, adult feeding, and larval feeding guild predicted macro-moth mobility, although the predictive power of wingspan and wing shape depended on the species' affinity to the forest. Solitary trees and small fragments functioned as “stepping stones,” especially when their landscape connectivity was increased, by being positioned within hedgerows or within a favorable matrix. Mobile forest specialists were most affected by forest fragmentation: despite their high intrinsic dispersal capability, these species were confined mostly to the largest of the forest patches due to their strong affinity for the forest habitat, and were also heavily dependent on forest connectivity in order to cross the agricultural matrix. Forest fragments need to be larger than five hectares and to have interior forest more than 100 m from the edge in order to sustain populations of forest specialists. Our study provides new insights into the movement patterns of a functionally important insect group, with implications for the landscape-scale management of forest patches within agricultural landscapes.

Key words: agricultural matrix; citizen science; dispersal ability; habitat fragmentation; habitat specificity; landscape connectivity; Lepidoptera; mark–release–recapture; species mobility; temperate woodland.

INTRODUCTION

Functional landscape connectivity refers to the ability of organisms to disperse among habitat resource patches (Baguette and Van Dyck 2007). Landscape connectivity theory is grounded within island biogeography and metapopulation dynamics, which explain species occurrence by probabilities of immigration to, and survival in, habitat patches (MacArthur and Wilson 1967, Hanski 1999). Modeling these processes has taken on increasing practical importance in biological conservation, as habitats become fragmented and isolated, and populations are forced to move in response to climate change (Devictor et al. 2012).

Much of Europe now consists of agricultural land interspersed with plantation forests, urbanized areas, and remnant forest fragments. These fragments are characterized by reduced interior forest areas, increased edge habitat, increased isolation, and reduced connectivity between patches (Dolman et al. 2007, Riutta et al. 2011). In the United Kingdom, forest cover has declined from ~75% 6000 years ago to ~12% today, with three-quarters of forest patches currently <2 ha (Watts 2006). This fragmentation process results in population size reductions and disruptions to dispersal, particularly for forest specialists (Dolman et al. 2007, Callens et al. 2011).

Studies on butterflies have highlighted the importance of landscape connectivity and have provided some classic examples of metapopulation dynamics (e.g., Thomas et al. 1992, Hanski and Kuussaari 1995). They have also been used to document the effects of habitat

Manuscript received 7 August 2012; 11 December 2012;
accepted 31 January 2013. Corresponding Editor: J. A. Jones.

⁶ E-mail: eleanor.slade@helsinki.fi

fragmentation, land-use change, and climate change (e.g., Summerville and Crist 2001, Thomas et al. 2001, Warren et al. 2001). In contrast, and despite their roles in terrestrial ecosystems as pollinators, herbivores, and as prey for birds, bats, and other taxa (Fox 2013), moths remain a relatively understudied group (but see beta-diversity studies in tropical landscapes [e.g., Beck et al. 2012] and in North American forests [e.g., Summerville and Crist 2008]). Habitat destruction, degradation, and fragmentation, along with climate change, are thought to be major drivers of the often severe population declines seen for two-thirds of the United Kingdom's once widespread and common species of moth (Fox 2013). Because of their ecological roles, such widespread declines are likely to cascade through whole ecosystems.

Recent studies at the field and farm scale have highlighted the importance of hedgerow trees and improved agricultural practices through agro-environment schemes (Merckx et al. 2012), and habitat connectivity has been found to be critical for moth movements within agricultural landscapes (Merckx et al. 2010). Several recent meta-analyses have also highlighted the importance of considering species' life-history traits when assessing their dispersal ability and responses to habitat fragmentation (Beck and Kitching 2007, Bommarco et al. 2010, Öckinger et al. 2010, Sekar 2012). However, moth movements have been rarely quantified at the landscape scale (but see Nieminen 1996, Betzholtz and Franzén 2011), and there are only a handful of dispersal-related studies for forest invertebrates, most of which are for ground beetles and butterflies (Brouwers and Newton 2009). Although an estimated 60% of the United Kingdom's moths are reliant on seminatural, broad-leaved lowland forest (Young 1997), the effects of forest fragmentation on moths are relatively unknown, and there have been no attempts to quantify moth movement patterns within and between remaining forest fragments. We believe it is of increasing conservation relevance to do so in order to be able to predict both the distribution of species within fragmented forest landscapes and their movement patterns between forest fragments.

The aim of this study was to detect if moth life-history traits and landscape characteristics affect the distribution and movement patterns of macro-moths among forest fragments set within an agricultural matrix. Specifically, we asked: (1) Are macro-moth life-history traits able to explain movement patterns across a landscape? (2) How do forest fragment size and forest edges affect macro-moth abundance and species composition? (3) Do forest macro-moths use linear landscape features (i.e., hedgerows) and stepping stones (i.e., isolated trees, small forest fragments) to move across the landscape?

METHODS

Experimental design

The study took place in a landscape encompassing 10 forest fragments around Wytham Woods, a 400-ha

seminatural broad-leaved forest in southern England (51°46' N, 01°20' W). Fragments differed in size (0.37–361 ha), but all were characterized by similar soil, topography, tree species composition, and management (see Appendices A and B; see also Butt et al. 2009).

A mark–release–recapture experiment was conducted across the fragments, and at solitary oak trees (either isolated or within a hedgerow) within the matrix. Light traps (heath-type actinic 6 W; Bioquip, Knutsford, Cheshire, UK) were permanently placed at 44 sampling sites, all within a 2 km radius from the center of the largest fragment (study area of 12.6 km²; Appendix A). Eight traps (four edge and four interior traps) were placed in the largest fragment (361 ha), four traps (two edge and two interior traps) in each of the larger fragments (4.8–21.7 ha), and two traps were placed at the edges of smaller fragments (0.3–3.5 ha). These fragments were so small that there was no true interior forest habitat and so we could not distinguish between edge and interior traps (Riutta et al. 2011). Edge traps were placed on the side nearest to neighboring fragments to increase the capture of movements between fragments. Traps were also placed within the agricultural matrix, at the base of 10 similarly sized solitary large oak trees (the study landscape's predominant solitary tree species): five at trees within linear hedgerows and five at isolated trees within fields (Appendices A and B). The average distance among all pairwise trap combinations was 1739 ± 20 m (mean \pm SE; maximum = 4131 m, minimum = 45 m). Actinic 6W traps have an attraction radius of only 10 to 30 m (E. M. Slade and T. Merckx, *unpublished data*), and as such allow for a good representation of real movement patterns.

The experiment ran from 14 June 2009 until 24 July 2009 on 31 nights. Traps were divided across the landscape (i.e., 25 in the southern part, and 19 in the northern part). These two sets of traps were run on alternate nights, with traps lit before dusk and visited at dawn. Using data from Merckx et al. (2009, 2010) and Waring and Townsend (2009), a subset of 92 macro-moth species was selected based on their forest habitat use, flight period, common presence, identification ease, and ease of marking. Every individual from the selected species was marked at first capture by writing a unique number on the left forewing, using a fine (0.4 mm) nontoxic, waterproof, permanent marker pen (Lumocolor; Staedtler, Nurnberg, Germany). Three separate teams were needed to check all traps, and so three different pen colors (i.e., red, green, black) were used. After marking, moths were released in situ into nearby tall vegetation. For each capture, date, species, trap, and individual mark number were recorded. Recaptured individuals on which the mark could not be read reliably (22 individuals) were not included in analyses. All 31 nights met the sampling criteria of a minimum night temperature of 10°C, maximum wind speed of 20 km/h, and maximum precipitation risk of 50% (data from the Wytham Woods weather station of the Environmental

Change Network, Center for Ecology and Hydrology [CEH], UK, 2009).

Analyses

The data were split into two themes to analyze (1) the effect of life-history traits on movements and (2) the effects of landscape characteristics and forest fragmentation on movements, species richness, and abundance.

Life-history traits.—Each species was classified using Manley (2008) and Waring and Townsend (2009) for the following traits: (1) forest affinity (weak [i.e., ubiquitous species], medium [i.e., associated with forest, but not exclusively so], and strong [i.e., broad-leaved forest specialists]), (2) larval feeding guild (grass/herb feeders or shrub/tree feeders), (3) larval diet breadth (monophagous, oligophagous, polyphagous), (4) adult feeding (yes or no), (5) average wingspan (mm), and (6) wing shape (i.e., wing aspect ratio as broad or pointed). All species were also classified in terms of conservation status based on national population trends measured over 35 years: severely declining (i.e., declines >69%), moderately declining (i.e., declines 0–69%), increasing, unknown (Conrad et al. 2006) (see Appendix C).

A sound phylogeny is not yet established for Eurasian moths (Betzholtz and Franzén 2011), and we were therefore unable to use a phylogenetic tree to control for trait evolution (see Sekar 2012). Instead, we controlled for phylogenetic relatedness by fitting models with “family,” “subfamily,” and “subfamily nested within family” as random effects (Nieminen et al. 1999). Their effect was assessed using likelihood ratio tests comparing models with and without these error terms. “Family” was not included as a fixed effect in models as we were interested in the specific life-history traits that describe moth dispersal ability at the species level.

To answer the question of whether macro-moth life-history traits were able to explain movement patterns across a landscape, the effect of the trait variables on the total distance moved across the landscape for each recaptured individual was analyzed. Linear mixed effects and generalized least squares (GLS) models were used, including the trait variables as fixed effects and “days since marking” as an additional continuous variable. “Species” was fitted as a random factor in the models, both alone and nested within “subfamily” and “family.” Different variances among forest affinity classes were modeled using the *varIdent* weights function (Zuur et al. 2009). All two-way interactions were fitted and nonsignificant interaction terms and variables dropped from the model until the minimal adequate model was obtained, using AIC scores and likelihood ratio tests (LRT). Fixed effects of model parameters were also estimated using LRTs to assess the differences between models after sequentially deleting significant terms from the minimal model and adding nonsignificant terms (Zuur et al. 2009). Variables were log- or square-root-transformed where necessary to meet the assumptions of parametric testing, and continuous variables were

standardized using a z-transformation so that the magnitude of the coefficients were directly comparable (Schielzeth 2010). *P* values were calculated using adjusted sums of squares as models contained both categorical and continuous variables.

Movement distances between captures were calculated using GIS (ESRI 2008). Coefficients from the final model were then used to predict the mean distance traveled over seven days for all moth species, using their trait values.

Landscape characteristics.—A series of landscape variables was calculated for each trap site using GIS (ESRI 2008): (1) fragment area, (2) distance to fragment edge (for within-fragment sites) or to nearest fragment edge (for sites outside fragments), (3) fragment perimeter, (4) number of hedgerow connections/fragment perimeter, (5) hedge density (i.e., total hedgerow length/1 km radius around each fragment or tree), (6, 7) number and area of fragments within a 1 km radius, (8) fragment shape (calculated as $R = 0.282P/\sqrt{A}$ where *P* is perimeter, *A* is area, and 0.282 is the factor that ensures $R = 1$ for circular fragments; *R* values increase as fragments become more elongate [Usher and Keiller 1998]), (9) isolation (calculated as

$$I = 1 / \left[\sum_{i=1}^n (A_i/d_i^2) \right]$$

where *I* is calculated as *n* other fragments within a distance of 1 km of the study fragment, each of which has an area *A_i* and is separated by a margin to margin distance *d_i* from the study fragment [Usher and Keiller 1998]), and (10) dominant surrounding matrix type around fragment or tree (arable, A; short-grass pasture, SP; and long-grass pasture, LP).

A correlation matrix of the variables was constructed to check for collinearity. “Fragment area” and “distance to edge” were highly correlated (Pearson’s correlation coefficient = 0.9), which is unavoidable as the largest distances to the edge occur within the large fragments, and the smallest distances are from solitary oak sites (negative values), which have the smallest areas (see Appendix B). Consequently, we split the data set in two. To answer the question of how forest fragment size and forest edges affect macro-moth abundance and species composition, we considered only trap sites within fragments (“fragments-only” data set). To answer the question of whether forest macro-moths use linear landscape features (i.e., hedgerows) and stepping stones (i.e., isolated trees) to move across the landscape, we considered only solitary oak trap sites (“oaks-only” data set).

In the “fragments-only” data set there was also significant correlation among several of the continuous variables (fragment perimeter, number of hedgerow connections/fragment perimeter, area of fragments within a 1 km radius, fragment shape) and area (Pearson correlation values > 0.55). We therefore excluded these

TABLE 1. Minimum adequate model for distance moved with wingspan and wing shape as wing morphology traits and adult feeding, larval feeding guild, and forest affinity as life-history traits for the 87 moth species marked in this study in Wytham Woods, UK.

Trait	df	F	P
Intercept	1, 645	22.65	<0.0001
Days since marking	1, 645	23.24	<0.0001
Wingspan	1, 645	7.43	0.0066
Wing shape	1, 645	0.02	0.8905
Forest affinity	2, 645	6.46	0.0017
Larval feeding guild	1, 645	4.05	0.0446
Adult feeding	1, 645	4.77	0.0293
Wingspan \times forest affinity	2, 645	8.32	0.0003
Wing shape \times forest affinity	2, 645	8.81	0.0002

Note: Wing shape was described as broad or pointed using the wing aspect ratio; forest affinity was defined as weak (i.e., ubiquitous species), medium (i.e., associated with forest, but not exclusively so), or strong (i.e., broad-leaved forest specialists); larval feeding guild was described as grass/herb feeders or shrub/tree feeders; and adult feeding was described as yes or no.

continuous variables from the models. The fragments-only data set displayed only a marginal correlation between “area” and “distance to edge” (Pearson correlation coefficient = 0.4), and so both variables were included for analysis. For the oaks-only data set, only “distance to nearest forest edge” was included, as “area” was similar for all oak trees used in the study.

Linear mixed-effects and GLS models were used to model abundance and a measure of species richness as a function of forest affinity and the landscape variables. As we had preselected the species we marked, we could not use species richness per se, so instead, we used the proportion of species of the preselected species found in each trap for each forest affinity class (PropS). Abundances and PropS were summed across trap nights for each affinity class in each trap to avoid issues of temporal autocorrelation, and because we were not interested in the effects of date or weather conditions.

Thus, of the original variables calculated, only “hedge density,” “number of fragments within a 1-km radius,” “isolation,” “area,” and “distance to edge” were not correlated for the fragments-only data set, and hence were included as fixed effects, along with the categorical variables “matrix type” and “forest affinity.” For the oaks-only data set, “distance to nearest fragment edge,” “hedge density,” “number of fragments within a 1 km radius,” and “isolation” were not correlated, and hence were included as fixed effects. “Position” (i.e., hedgerow oak/isolated oak), “forest affinity,” and “matrix type” were included as the categorical variables.

Variables were log- or square-root-transformed where necessary, and continuous variables were standardized using a z-transformation as above in the subsection *Life-history traits*. For the fragments-only data set, “trap nested within site” was modeled as a random effect for both the abundance and PropS models. For the oaks-only data set, “site” fitted as a random factor did not

significantly improve the fit of the abundance model (LRT, $P > 0.05$), and hence was only included in the PropS model. Different variances among affinity classes were modeled using the *varIdent* weights function where necessary. The interactions between each main effect and “forest affinity,” and “position” (for the oaks-only data set), were modeled using LRTs and AIC values as above in the subsection *Life-history traits*. Coefficients from the final models were used to predict the abundance and PropS of moth species associated with different landscape characteristics. Spatial autocorrelation among sites was tested for abundance and species richness by calculating Moran’s I index using GIS (ESRI 2008).

The *lme*-function of the *nlme* package for R 2.10.1 (R Development Core Team 2006, Pinheiro et al. 2008) was used for all of the analyses.

RESULTS

A total of 14 719 individuals from 87 of the 92 preselected species were sampled, with 679 recaptures of 657 individuals comprising 41 species, resulting in a recapture rate of 5.17% (see Appendix D). There was no evidence of spatial autocorrelation between traps ($P > 0.05$ in all cases). The simplest model, without any phylogenetic component, was found to be the best (likelihood ratio tests, $P > 0.05$). In all cases, the variance explained by family, subfamily, and species (0.002, 0.872, and 1.29, respectively) was low compared to the residual variance (15.06), and the coefficient estimates changed little between the models.

Life-history traits

Overall, species with strong and medium forest affinity had nearly double the recapture rate of species with weak forest affinity (strong, 6.4%; medium, 6.7%; weak, 3.5%). There was a large variation in movements (overall mean = 348 m, overall median = 52 m). On average, species with weak forest affinity moved larger distances than species with strong and medium forest affinity (weak, 430 ± 52 m [$n = 220$]; medium, 314 ± 34 m [$n = 375$]; and strong, 261 ± 65 m [$n = 62$]).

Moths with pointed wings moved further than moths with broad wings, although this was only the case for species with either weak or strong forest affinity (Table 1, Fig. 1a). An increase in wingspan accounted for larger distances moved overall, but this was only significant for species with a strong forest affinity (Fig. 1a; Appendix E). Among all single traits considered, adult feeding was the strongest predictor of movement rate for moth species regardless of forest affinity (Appendix E). Moths that fed as adults and moths with shrub/tree-feeding larvae had larger predicted movement rates than those that did not feed as adults or with grass/herb-feeding larvae, and this pattern was similar among all forest affinity classes (Table 1, Fig. 1b, c; Appendix C). The predictive power of wingspan and wing shape was low, except for species with a strong forest affinity (Appendix E). The majority of species were predicted to move <500

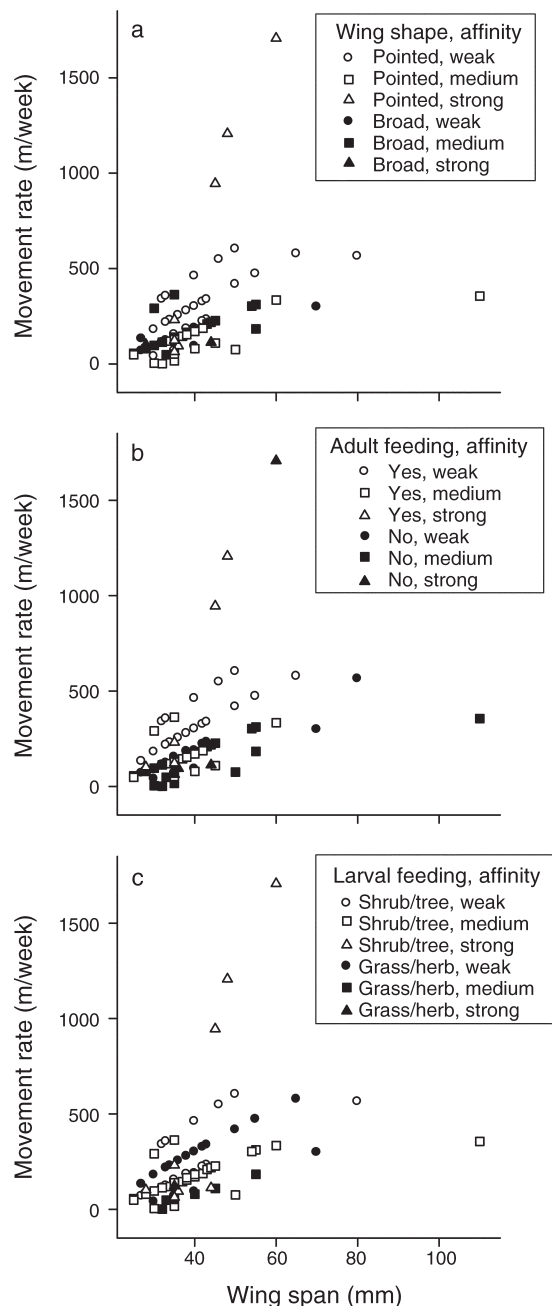


FIG. 1. Model-predicted movement rates for the 87 moth species marked in this study in Wytham Woods, UK. Movements are given for each forest affinity class (weak [i.e., ubiquitous species], medium [i.e., associated with forest, but not exclusively so], and strong [i.e., broad-leaved forest specialists]) as a function of wingspan and (a) wing shape (i.e., wing aspect ratio as pointed or broad), (b) adult feeding (yes or no), and (c) larval feeding guild (shrub/tree or grass/herb feeders).

m in a week, with the range increasing with wingspan. The three species with the largest predicted movement rates, i.e., lobster moth *Stauropus fagi*, green arches *Anaplectoides prasina*, and scarce silver-lines *Bena bicolorana*, were all forest species with pointed wings

(Fig. 1a; Appendix C). Species with medium forest affinity tended to have the smallest predicted movement rate for a given wingspan.

Landscape characteristics

Most individuals moved relatively small distances and were recaptured within the same fragment. However, for isolated oaks, only 27% of recaptured individuals were marked and re-caught again at an isolated oak compared to 61% of individuals at hedgerow oaks and around 80% for small and large fragments. Hedgerow trees “captured” more marked individuals than did isolated trees (mean = 14 vs. 3 individuals/trap, respectively).

Most individuals of species with a weak forest affinity were recaptured at hedgerow trees, while most recaptures of medium affinity species were in small fragments. The majority of species with a strong forest affinity were captured in the large fragments (>5 ha; 94% of individuals and 89% of species), and were only recaptured in the largest fragments, or rarely at hedgerow trees, and never in smaller fragments or at isolated trees.

Effect of fragment size and distance to the edge: fragments-only data set.—“Distance to edge,” rather than “fragment area” was the most important predictor of moth abundance (Table 2, Fig. 2a, b). Predicted abundance increased with increasing distance to the edge, although this effect differed with forest affinity. The abundance of species with strong forest affinity significantly increased with distance to the edge, while there was no such effect for species with weak to medium forest affinity. Low numbers of forest specialists were found outside forests, and the edge effect was particularly pronounced up to 100 m from the edge (Fig. 2b). Moth numbers increased with increasing fragment area, but this was only marginally significant (Table 2, Fig. 2a).

This pattern for abundance was reversed for species richness (PropS). The predicted PropS differed among forest affinity classes only for fragment area (Table 2). The proportion of species captured increased with area

TABLE 2. Minimum adequate model for the abundance and proportion of species (PropS) of moths captured in the fragments.

Trait	df	F	P
Abundance			
Intercept	1, 64	725.73	<0.0001
log(area)	1, 8	4.67	0.0626
Distance to edge	1, 23	0.1	0.7538
Forest affinity	2, 64	213.49	<0.0001
Distance to edge × forest affinity	2, 64	9.2	0.0003
PropS			
Intercept	1, 62	594.05	<0.0001
log(area)	1, 8	1.01	0.3432
Distance to edge	1, 23	3.04	0.0946
Forest affinity	2, 62	0.29	0.7476
log(area) × forest affinity	2, 62	12.03	<0.0001
Distance to edge × forest affinity	2, 62	2.9	0.0593

Note: See Table 1 for a description of the traits.

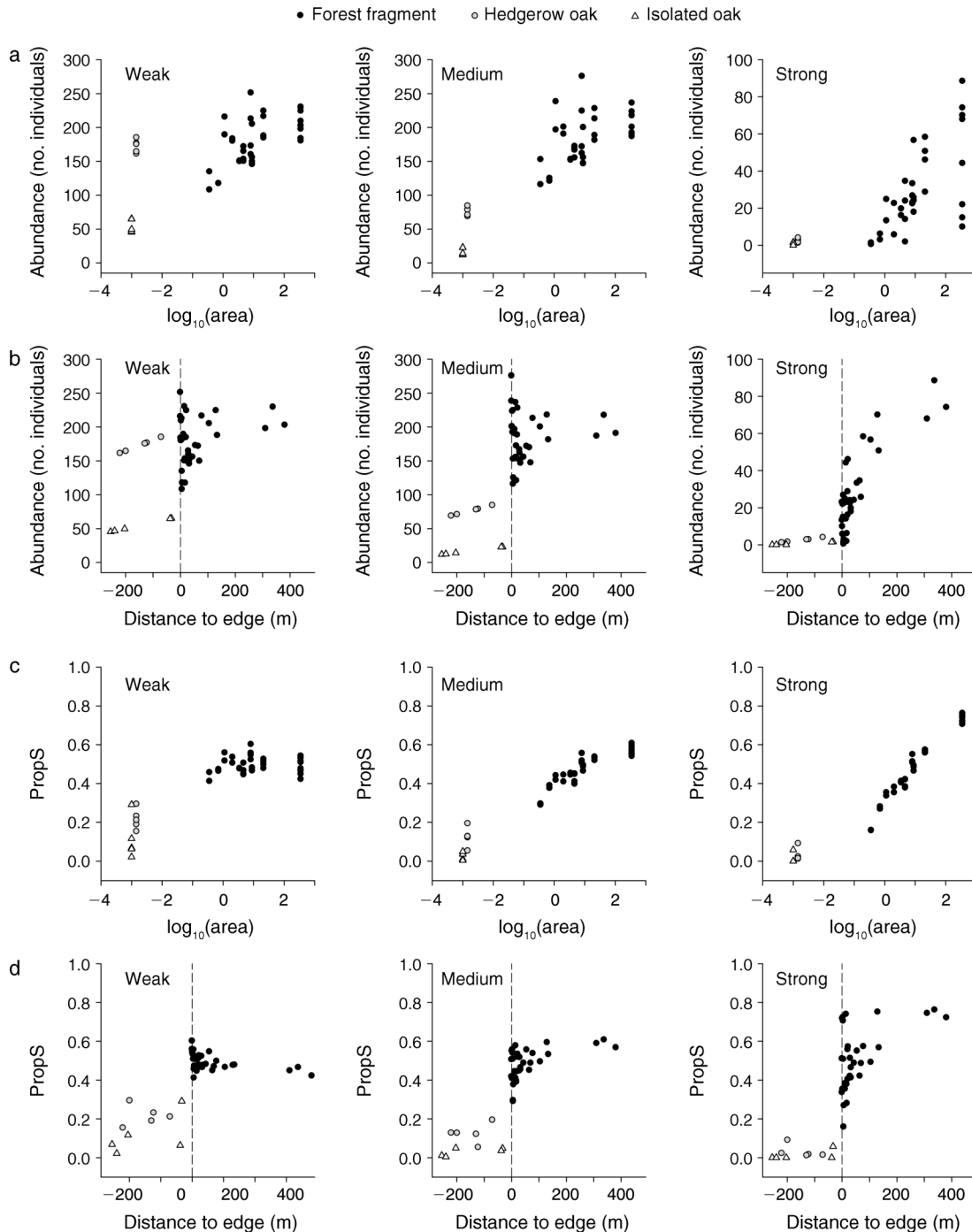


FIG. 2. Model predicted moth abundance and a species richness measure (PropS; see subsection *Landscape characteristics* in *Methods: Analyses* for details) of moths for the three forest affinity classes (weak, medium, and strong), in relation to (a, c) forest area (\log -transformed; originally measured in hectares; hedgerow and isolated oaks were given a value of 0.0015 ha and 0.001 ha, respectively) and (b, d) distance from forest edge. Note that in panels (a) and (b), the y-axis has a different range for the strong forest affinity class. In panels (b) and (d), positive values are the distance from within (i.e., trap is placed inside the forest), and negative values are the distance from outside (i.e., trap is outside the forest at solitary oak trees).

for species with a medium or strong forest affinity, with a minimum fragment size of ~ 5 ha (0.7 at \log_{10} scale) needed for 50% of the species in those affinity classes to be present (Table 2, Fig. 2c). However, an increasing distance to edge only gave a marginally significant increase in the proportion of these species (Table 2, Fig. 2d). None of the other variables was found to affect moth abundance or PropS at within-fragment sites.

Linear landscape features and “stepping stones”: oaks-only data set.—Moth abundance at isolated and hedgerow oaks differed among forest affinity classes. Very few moths with strong forest affinity were caught at either type of oak overall, and species with weak to medium affinity were more abundant at hedgerow oaks than at isolated oaks (Table 3, Fig. 3a). This was also true for the species richness measure (PropS; Table 3, Fig. 3b). Abundance, though not the PropS of species with weak forest affinity, was similar at hedgerow oaks and in many of the fragments (Fig. 2a, c). As distance to edge of the nearest fragment decreased, overall moth abundance increased, both for isolated and hedgerow oaks, with no significant difference between the forest affinity classes (Table 3, Fig. 2b). None of the other variables measured was found to affect moth abundance at isolated and hedgerow oak trees.

The type of matrix surrounding solitary oak trees, as well as the density of hedgerows in the surrounding area, affected the species richness (PropS) of some affinity classes, and the effect was the same regardless of whether the solitary oak was an isolated oak or a hedgerow oak (Table 3). There were significantly more species with weak or strong forest affinity at an oak when it was surrounded by long-grass pasture, rather than either arable or short-grass pasture (Table 3, Fig. 3c). However, only the PropS of species with strong forest affinity increased significantly with an increased density of hedgerows surrounding the oak, with the strongest effects being seen with increases in hedgerow densities above 4 km/km² (Fig. 3d). Distance to nearest forest edge had no effect on the PropS of any affinity class caught at oak trees.

DISCUSSION

How best to manage existing forest patches, mitigate the consequences of forest fragmentation, and enable landscape permeability so that biodiversity can adapt to climate change are key questions for conservation (Sutherland et al. 2006, Maclean 2010). Moreover, research specifically aimed at understanding the decline of the United Kingdom's moths and the action necessary to mitigate such declines was listed in the top 100 most important research priorities for informing conservation policy in Britain (Sutherland et al. 2006) and more recently listed in the top 25 key questions in ecology (Maclean 2010).

Understanding the widespread, and often severe declines, of once-common moth species requires a better understanding of the functional connectivity of land-

TABLE 3. Minimum adequate model for the abundance and proportion of species (PropS) of moths captured at oaks.

Trait	df	F	P
Abundance			
Intercept	1, 23	158.2	<0.0001
Distance to edge	1, 23	4.47	0.0456
Position	1, 23	15.1	0.0007
Forest affinity	2, 23	76.66	<0.0001
Position \times forest affinity	2, 23	7.74	0.0027
PropS			
Intercept	1, 10	45.77	<0.0001
Hedge density	1, 5	1.76	0.2423
Position	1, 5	5.15	0.0726
Forest affinity	2, 10	43.7	<0.0001
Matrix	2, 5	4.28	0.0825
Hedge density \times forest affinity	2, 10	4.93	0.0324
Position \times forest affinity	2, 10	6.2	0.0177
Matrix \times forest affinity	4, 10	7.99	0.0037

Note: Position was defined as an isolated oak or oak within a hedgerow; forest affinity was weak, medium, strong; hedge density was defined as total hedgerow length/1 km radius around each tree; matrix was the dominant surrounding matrix type around fragment or tree, described as arable (A), short-grass pasture (SP), or long-grass pasture (LP).

scapes, and how this connectivity is defined by species-specific dispersal propensity (i.e., willingness to leave a patch) and dispersal ability (i.e., matrix crossing and settlement) (Van Dyck and Baguette 2005). Previous studies have considered moth movements at the field scale (Merckx et al. 2009, 2010) and highlighted the importance of considering species' life-history traits (Beck and Kitching 2007, Bommarco et al. 2010, Öckinger et al. 2010, Sekar 2012). However, this study is the first to quantify moth movement patterns for a large number of species at a landscape scale. As most macro-moths show a continuous mode of dispersal during their adult life, their movement rates can be used as a measure of dispersal ability and potential dispersal success (Brouwers and Newton 2009). Such species-specific movement rates are important for modeling the impacts of land use and climate change on species distribution patterns (e.g., Walters et al. 2006).

Mobile forest specialists are most at risk from forest fragmentation

As has been found for other forest invertebrate groups (Brouwers and Newton 2009), in general, species with weak forest affinity moved larger distances than species with strong and medium forest affinity. However, our results also showed that species with a strong forest affinity and with large, pointed wings have a greater ability to disperse than similarly shaped species with medium to weak forest affinity. For instance, individuals of the forest specialist lobster moth *Stauropus fagi* are predicted to move a weekly mean distance of 1707 m, whereas roughly similarly sized and similarly shaped buff-tip *Phalera bucephala* and poplar hawk-moth *Laothoe populi* individuals, species with medium and weak forest affinity, respectively, are predicted to move

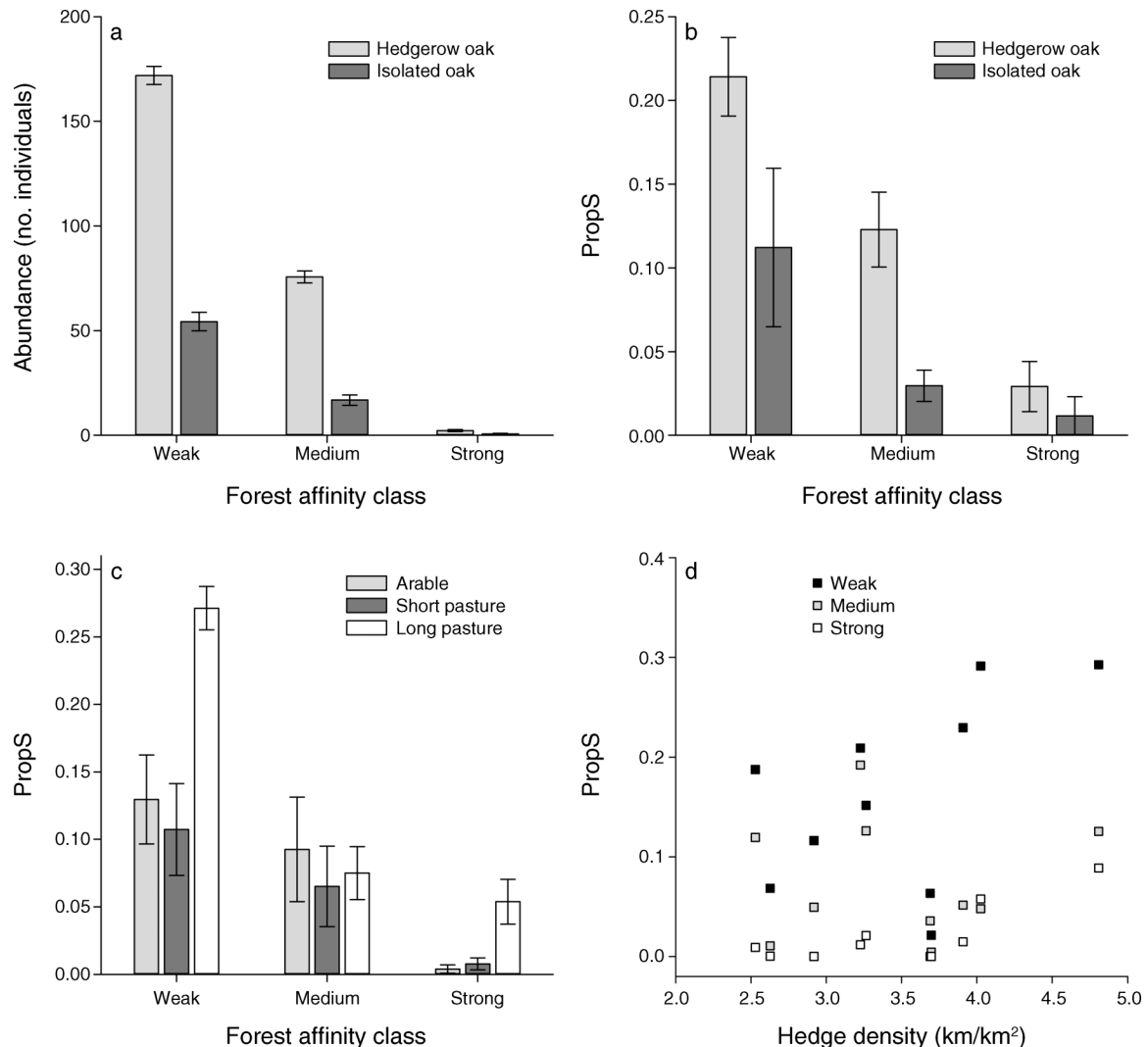


FIG. 3. Model predicted mean (\pm SE) moth (a) abundance and (b) species richness measure (PropS; see subsection *Landscape characteristics* in *Methods: Analyses* for details) in each forest affinity class (weak, medium, and strong) at hedgerow and isolated oaks. (c) Species richness (PropS) for each affinity class in relation to the matrix surrounding all solitary oak trees (hedgerow and isolated oaks combined as the final model showed no effect of position of the oak on PropS captured in the different matrices). (d) Model-predicted species richness (PropS) at all solitary oak trees (hedgerow and isolated oaks are not separated as the final model showed no effect of position of the oak on PropS) for each forest affinity class in relation to hedge density.

only 76 m and 563 m in the same amount of time. The observed high mobility of some macro-moth forest specialists may be a result of these forest specialists being exposed to stronger selection pressures for increased dispersal ability between remnant forest fragments due to the long history of forest fragmentation in the United Kingdom (Bergerot et al. 2012). Selection is predicted to switch direction from increasing to decreasing dispersal ability once species are unable to keep track with the pace of forest fragmentation (Bergerot et al. 2012). Thus, selection working in the opposite direction may currently be at work for those forest specialists that display low mobility. Such species would be predicted to have short movement rates and according flight-related morpholo-

gy. For example, the relatively small and round-winged black arches *Lymantria monacha* and maiden's blush *Cyclophora punctaria* have predicted mean weekly movement rates of 113 m and 102 m, respectively.

Despite the relative high mobility of some forest specialists, they were only rarely found within the matrix at hedgerow oaks and isolated oaks. However, the density of hedgerows in the vicinity of an oak tree (whether hedgerow or isolated oak) was found to increase the species richness of forest specialists at that tree, suggesting that forest specialists are heavily dependent on forest connectivity in order to cross the agricultural matrix. Thus, despite their potentially high dispersal capability, the most mobile species of these forest

specialists appear to be confined mostly to the largest of the forest patches due to their strong forest affinity. Together, these findings contradict the ideas that species with a high degree of habitat specialization are necessarily poor dispersers and that species with low mobility are most likely to be affected by habitat fragmentation and lack of connectivity (Brouwers and Newton 2009, Öckinger et al. 2010). We suggest that forest specialists are the most vulnerable to forest fragmentation, not because of their low mobility, but rather because of their high habitat affinity. Indeed, abundance and species richness of forest specialists increased linearly with fragment area and distance from the edge. As wingspan is generally related to body size, and body size inversely related to population size (Nieminen et al. 1999), viable populations of small-bodied, sedentary forest specialists, such as maiden's blush *Cyclophora punctaria* and nut-tree tussock *Colocasia coryli* could be maintained, even within relatively small fragments, without direct need for rescue by a wider meta-population. However, it is the more mobile, larger species, such as lobster moth *Stauropus fagi* that are at risk from local extinction in smaller fragments, particularly if hedgerow connectivity in the landscape is reduced. This study suggests that fragments need to be larger than five hectares and need to have interior forest >100 m from the edge, in order to sustain populations of mobile forest specialist species (Fig. 2; see also Usher and Keiller 1998).

*Small forest fragments and solitary oaks act
as "stepping stones"*

The lower affinity to forest of weak and medium forest affinity species allows them to move more freely into and out of smaller fragments and through the matrix. These species seemed to be particularly associated with the smaller fragments, perhaps also using them as "stepping stones" to cross the landscape. Isolation was not a significant factor for any of the forest affinity classes and this may in part be due to the "stepping-stone" effect of smaller fragments, hedgerows, and isolated trees in the landscape (Usher and Keiller 1998). Previous studies have also highlighted the importance of small patches of forest and the amount of forest cover (within a 1–1.4 km radius), for several taxa including moths (Ricketts et al. 2001, Summer-ville and Crist 2004, Dolman et al. 2007, Fuentes-Montemayor et al. 2011). Many farm woodland schemes conserve small patches of forest (i.e., <2 ha) within the agricultural landscape. While such schemes may not benefit true forest specialists, this study suggests that small forest fragments may provide key habitat resources for many other species, such as blood-vein *Timandra comae*, lackey *Malacosoma neustria*, and pretty chalk carpet *Melanthia procellata*, all of which are severely declining in Britain (Conrad et al. 2006).

Ubiquitous species, such as the nationally declining bright-line brown-eye *Lacanobia oleracea*, heart and dart *Agrotis exclamationis*, flame shoulder *Ochropleura plecta*,

and flame *Axylia putris*, were relatively abundant at hedgerow oak trees in particular, suggesting that they are using hedgerows as corridors when crossing the agricultural landscape. In fact, hedgerow oaks approached small fragments in terms of abundance and species richness of species with weak to medium forest affinity. Species with weak to medium forest affinity were also frequently captured at isolated oaks, and low recapture rates at the same tree suggest that they were being used as "stepping stones," enabling movement across the landscape. The land use of the surrounding matrix was also found to have an effect on the number of both ubiquitous and forest specialist species using oak trees. Long-grass pastures were associated with higher moth numbers than short-grass pastures and intensively managed arable crops. Reduced vegetation structure and plant species composition, with fewer nectar sources and reduced shelter in grazed and arable fields, have been shown to be detrimental to many moth species (Littlewood 2008).

A previous study found that hedgerow trees were only effective in increasing the abundance of less mobile moth species (Merckx et al. 2010). However, as that study was conducted at the field scale only, the absence of an effect for the more mobile species was probably due to these species moving at a larger scale than the study could capture. The current study provides evidence that hedgerow trees are important for the movement of moths through agricultural landscapes at a large spatial scale, and that this is true for species of all mobility and forest affinity classes. Moreover, we show that for some moth species general landscape characteristics, such as the hedgerow density and the matrix surrounding solitary trees, may be almost as important as whether an individual tree is isolated or directly connected to a hedgerow.

Predicting moth dispersal from species life-history traits

Phylogenetic relatedness was not found to be causing the differences in the life-history traits and mobility between species measured in the study. Similarly, Nieminen et al. (1999) found that phylogenetic relatedness did not qualitatively affect the outcome of their studies on moth migration rates. Thus, both these studies suggest that dispersal in moths evolves independently of phylogeny, but is dependent instead on the ecological and life-history traits of the species.

Wingspan is often used as a surrogate for body size and as a proxy for dispersal ability (Nieminen et al. 1999, Beck and Kitching 2007, Öckinger et al. 2010, Sekar 2012). However, as has been found for butterflies (Sekar 2012) and sphingid moths (Beck and Kitching 2007), the overall predictive power of wingspan and wing shape for dispersal ability in this study was low, as it was dependent on forest affinity, and thus should be interpreted cautiously. However, the true distance travelled was probably underestimated as we used the minimum straight-line distance travelled between mark-release and recaptures. Also, some large and partly

migratory moths, such as *Noctua* species, were probably moving at a greater scale than this study, and were hardly ever recaptured, despite large numbers being marked, which indicates an underestimation of their dispersal ability. These moths, and other migratory moth species, such as the silver Y *Autographa gamma*, have been recorded to move distances of several hundred kilometers in a night (Chapman et al. 2010, 2012). The largest recorded movement in this study was for a broad-bordered yellow underwing *Noctua fimbriata*, which was recaptured outside the study area, having moved 13.7 km in two months (see also Betzholtz and Franzén 2011).

The importance of considering wing shape as well as wingspan is also highlighted, as the most mobile species were those with pointed wings, rather than those with the largest wingspan (e.g., the weekly movement rate of green arches *Anaplectoides prasina* [48 mm wingspan, pointed wings] was 1207 m whereas that of the garden tiger *Arctia caja* [70 mm wingspan, rounded wings] was 297 m). We have, however, no clear explanation why this pattern was most prevalent in forest specialists and to a lesser extent in ubiquitous species, while species with a medium forest affinity showed no difference in distance moved with wing shape or wingspan. In contrast to the extensively studied butterflies, the mobility of the majority of moth species is largely unknown, and for many species these data represent some of the first records of their dispersal ability.

Larval host plant, adult habitat specificity, and adult feeding have been shown to affect Lepidoptera dispersal ability (Nieminen et al. 1999, Beck and Kitching 2007, Betzholtz and Franzén 2011, Sekar 2012). In contrast to these studies, adult feeding rather than larval food plant specificity was the strongest predictor of mobility. Moths that feed as adults and moths with larvae that feed on shrubs and/or trees were more mobile than those that do not feed as adults or with grass/herb-feeding larvae (e.g., the weekly movement rate of scorched wing *Plagodis dolabraria* [adult feeder with shrub/tree feeding larvae] was 363 m whereas that of the white ermine *Spilosoma lubricipeda* [adults do not feed and larvae are grass/herb-feeders] was 92 m). Adult moths dependent on nectar resources may need to be more mobile in order to locate enough of these energy resources, while the adults of shrub/tree-feeding larvae may be more mobile than grass/herb-feeding species in order to locate sufficient host plants because shrubs and trees are generally more dispersed within a landscape than the more ubiquitous grasses and herbs. Similarly, it has been suggested for tropical hawk-moths that adult feeders are typically longer lived and therefore may disperse further and be less habitat specific (Beck et al. 2006, Beck and Kitching 2007).

Citizen science in action

We believe that this is the largest ever mark–release–recapture experiment, in terms of species involved, individuals released, and area covered. One reason that a study such as this has not been conducted before is the

large workforce it takes to monitor such large numbers of light traps and moths across a landscape. Our study was unique in that it involved teams of citizen scientists, allowing large quantities of data on a large number of moth species to be collected on a landscape scale. However, the use of volunteers to carry out scientifically sound research is not easy and studies need to be designed so that volunteers can make a meaningful contribution or enable research that would otherwise be unfeasible (Lovell et al. 2009). Many invertebrates are difficult to sample at large scales or across long time periods and these issues have been identified as particular challenges to invertebrate conservation (Lovell et al. 2009).

Monitoring of butterflies through citizen science based programs within Europe has enabled large amounts of data to be collected on their distributions, making butterflies useful indicators of biodiversity change and flagships for conservation (Kuhn et al. 2008, van Swaay et al. 2008). Recently, moths were also proposed as an excellent group to engage citizen scientists, as they occur in large numbers and are relatively easy to trap and identify in temperate regions (Fox et al. 2010). Moreover, because of their high species richness and ecological diversity, they are thought to represent terrestrial insects as a whole better than butterflies (Fox et al. 2010). This large-scale mark–release–recapture study serves as an example of labor-intensive and time-consuming research where the use of volunteers greatly increased the numbers of individuals and species recorded and the spatial scale sampled.

Conservation implications

Both forest size and forest connectivity are important when considering how to conserve moth diversity in fragmented landscapes. Different groups of forest-associated species will require different degrees of habitat connectivity, and it has been suggested that physical links, such as corridors, may be important both for forest specialists (Bailey 2007) and for generalists (Dolman et al. 2007). This study highlights that even small fragments and isolated trees have a fundamental role to play, and act as crucial “stepping stones” for moths as they move through the landscape. Furthermore, the higher the landscape connectivity surrounding trees, through their positioning within hedgerows or within a favorable matrix, the higher their “stepping-stone” capacity, both for forest specialist and ubiquitous moth species. Such connectivity is particularly important in light of climate change, which means that species are moving, and will need to move, in order to stay within their climatic envelopes (Devictor et al. 2012). We suggest that increasing the landscape connectivity between patches of remaining forest should be a key priority (e.g., for national agro-environment schemes). The extent of forest cover in the United Kingdom is now increasing (Mason 2007), and agro-environmental schemes, combined with farm business models that

include sustainable forest revenue streams, have the potential to be used to increase connectivity and create forest networks at the landscape level leading to ecologically functional landscapes. However, in order to maintain the full complement of species within the landscape, and forest specialists in particular, it is necessary to maintain both connectivity and large patches of suitable forest habitat. Our results thus have important implications for the landscape-scale management of forest patches and their connectivity within agricultural landscapes.

ACKNOWLEDGMENTS

We thank Marc Botham, Rita Gries, Darren Mann, Claire McLaughlan, Alison Slade, Richard Sylvester, Chloe Wells, and the Earthwatch/HSBC Climate Champions for help with data collection. Richard Lewington gave us permission to use his plates from Waring and Townsend (2009). Martin Harvey, Darren Mann, and Martin Townsend provided advice on species selection and identification, and Richard Comont provided advice on data analyses. Nigel Fisher and Phil Smith provided support and access to forest fragments. The Food Animal Initiative and Mr. Barnett allowed us access to their fields. We thank Darren Mann and two anonymous reviewers for their comments on earlier versions of the manuscript. The study was funded by the HSBC Climate Partnership Programme through the Earthwatch Institute. The manuscript was in part written while E. M. Slade was funded by an Academy of Finland grant: number 138346. E. M. Slade, T. Merckx, and T. Riutta designed the experiment. E. M. Slade was responsible for coordinating the research, and E. M. Slade, T. Merckx, T. Riutta, and D. Redhead were responsible for data collection. E. M. Slade, T. Merckx, T. Riutta, and D. P. Bebbler analyzed the results. D. W. Macdonald and P. Riordan conceived the research program within which this work fits. E. M. Slade wrote the first draft of the paper, and all authors contributed to revisions.

LITERATURE CITED

- Baguette, M., and H. Van Dyck. 2007. Landscape connectivity and animal behavior: functional grain as a key determinant for dispersal. *Landscape Ecology* 22:1117–1129.
- Bailey, S. 2007. Increasing connectivity in fragmented landscapes: An investigation of evidence for biodiversity gain in woodlands. *Forest Ecology and Management* 238:7–23.
- Beck, J., J. D. Holloway, C. V. Khen, and I. J. Kitching. 2012. Diversity partitioning confirms the importance of beta components in tropical rainforest Lepidoptera. *American Naturalist* 180:E64–E74.
- Beck, J., and I. J. Kitching. 2007. Correlates of range size and dispersal ability: a comparative analysis of sphingid moths from the Indo-Australian tropics. *Global Ecology and Biogeography* 16:341–349.
- Beck, J., I. J. Kitching, and K. E. Linsenmair. 2006. Effects of habitat disturbance can be subtle yet significant: Biodiversity of hawkmoth-assemblages (Lepidoptera: Sphingidae) in Southeast-Asia. *Biodiversity and Conservation* 15:465–486.
- Bergerot, B., T. Merckx, H. Van Dyck, and M. Baguette. 2012. Habitat fragmentation impacts mobility in a common and widespread woodland butterfly: do sexes respond differently? *BMC Ecology* 12:5.
- Betzholdt, P.-E., and M. Franzén. 2011. Mobility is related to species traits in noctuid moths. *Ecological Entomology* 36: 369–376.
- Bommarco, R., J. C. Biesmeijer, B. Meyer, S. G. Potts, J. Pöry, S. P. M. Roberts, I. Steffan-Dewenter, and E. Öckinger. 2010. Dispersal capacity and diet breadth modify the response of wild bees to habitat loss. *Proceedings of the Royal Society B* 277:2075–2082.
- Brouwers, N. C., and A. C. Newton. 2009. Movement rates of woodland invertebrates: a systematic review of empirical evidence. *Insect Conservation and Diversity* 2:10–22.
- Butt, N., G. Campbell, Y. Malhi, M. Morecroft, K. Fenn, and M. Thomas. 2009. Initial results from establishment of a long-term broadleaf monitoring plot at Wytham Woods, Oxford, UK. University of Oxford Report. University of Oxford, Oxford, UK.
- Callens, T. O. M., P. Galbusera, E. Matthysen, E. Y. Durand, M. Githiru, J. R. Huyghe, and L. U. C. Lens. 2011. Genetic signature of population fragmentation varies with mobility in seven bird species of a fragmented Kenyan cloud forest. *Molecular Ecology* 20:1829–1844.
- Chapman, J. W., J. R. Bell, L. E. Burgin, D. R. Reynolds, L. B. Pettersson, J. K. Hill, M. B. Bonsall, and J. A. Thomas. 2012. Seasonal migration to high latitudes results in major reproductive benefits in an insect. *Proceedings of the National Academy of Sciences USA* 109:14924–14929.
- Chapman, J. W., R. L. Nesbit, L. E. Burgin, D. R. Reynolds, A. D. Smith, D. R. Middleton, and J. K. Hill. 2010. Flight orientation behaviors promote optimal migration trajectories in high-flying insects. *Science* 327:682–685.
- Conrad, K. F., M. S. Warren, R. Fox, M. S. Parsons, and I. P. Woiwod. 2006. Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. *Biological Conservation* 132:279–291.
- Devictor, V., et al. 2012. Differences in the climatic debts of birds and butterflies at a continental scale. *Nature Climate Change* 2:121–124.
- Dolman, P. M., S. A. Hinsley, P. E. Bellamy, and K. Watts. 2007. Woodland birds in patchy landscapes: the evidence base for strategic networks. *Ibis* 149:146–160.
- ESRI. 2008. ArcMap 9.3. Environmental Systems Research Institute, Redlands, California, USA.
- Fox, R. 2013. The decline of moths in Great Britain: a review of possible causes. *Insect Conservation and Diversity* 6:5–19.
- Fox, R., Z. Randle, L. Hill, S. Anders, L. Wiffen, and M. Parsons. 2010. Moths count: recording moths for conservation in the UK. *Journal of Insect Conservation* 15:55–68.
- Fuentes-Montemayor, E., D. Goulson, and K. J. Park. 2011. Pipistrelle bats and their prey do not benefit from four widely applied agri-environment management prescriptions. *Biological Conservation* 144:2233–2246.
- Hanski, I. 1999. *Metapopulation ecology*. Oxford University Press, Oxford, UK.
- Hanski, I., and M. Kuussaari. 1995. Butterfly metapopulation dynamics. Pages 149–171 in N. Cappuccino and P. W. Price, editors. *Population dynamics: New approaches and synthesis*. Academic Press, San Diego, California, USA.
- Kuhn, E., R. Feldmann, A. Harpke, N. Hirneisen, M. L. P. Musche, and J. Settele. 2008. Getting the public involved in butterfly conservation: Lessons learned from a new monitoring in Germany. *Israel Journal of Ecology and Evolution* 54: 89–103.
- Littlewood, N. A. 2008. Grazing impacts on moth diversity and abundance on a Scottish upland estate. *Insect Conservation and Diversity* 1:151–160.
- Lovell, S., M. Hamer, R. Slotow, and D. Herbert. 2009. An assessment of the use of volunteers for terrestrial invertebrate biodiversity surveys. *Biodiversity and Conservation* 18:3295–3307.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey, USA.
- Maclean, N. 2010. Twenty-five key questions in ecology. Pages 156–163 in N. Maclean, editor. *Silent summer: the state of wildlife in Britain and Ireland*. Cambridge University Press, Cambridge, UK.
- Manley, C. 2008. *British moths and butterflies: a photographic guide*. A and C Black, London, UK.

- Mason, W. L. 2007. Changes in the management of British forests between 1945 and 2000 and possible future trends. *Ibis* 149:41–52.
- Merckx, T., R. E. Feber, R. L. Dulieu, M. C. Townsend, M. S. Parsons, N. A. D. Bourn, P. Riordan, and D. W. Macdonald. 2009. 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., R. E. Feber, C. McLaughlan, N. A. D. Bourn, M. S. Parsons, M. C. Townsend, P. Riordan, and D. W. Macdonald. 2010. Shelter benefits less mobile moth species: The field-scale effect of hedgerow trees. *Agriculture, Ecosystems and Environment* 138:147–151.
- Merckx, T., L. Marini, R. E. Feber, and D. W. Macdonald. 2012. Hedgerow trees and extended-width field margins enhance macro-moth diversity: implications for management. *Journal of Applied Ecology* 49:1396–1404.
- Nieminen, M. 1996. Migration of moth species in a network of small islands. *Oecologia* 108:643–651.
- Nieminen, M., H. Rita, and P. Uuvana. 1999. Body size and migration rate in moths. *Ecography* 22:697–707.
- Öckinger, E., et al. 2010. Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. *Ecology Letters* 13:969–979.
- Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and the R Core Team. 2008. nlme: linear and nonlinear mixed effects models. R package version 3.1–89. R Foundation for Statistical Computing, Vienna, Austria.
- R Development Core Team. 2006. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ricketts, T. H., G. C. Daily, P. R. Ehrlich, and J. P. Fay. 2001. Countryside biogeography of moths in a fragmented landscape: biodiversity in native and agricultural habitats. *Conservation Biology* 15:378–388.
- Riutta, T., E. M. Slade, Y. Malhi, and M. D. Morecroft. 2011. Living on the edge: Quantifying the structure of fragmented woodland landscapes in England. Pages 31–32 in M. D. Morecroft, S. J. Duffield, C. Margerison, and E. Wayman, editors. *Adapting conservation to a changing climate*. Charles Darwin House, London, UK.
- Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution* 1:103–113.
- 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* 81:174–118.
- Summerville, K. S., and T. O. Crist. 2001. Effects of experimental habitat fragmentation on patch use by butterflies and skippers (Lepidoptera). *Ecology* 82:1360–1370.
- Summerville, K. S., and T. O. Crist. 2004. Contrasting effects of habitat quantity and quality on moth communities in fragmented landscapes. *Ecography* 27:3–12.
- Summerville, K. S., and T. O. Crist. 2008. Structure and conservation of lepidopteran communities in managed forests of northeastern North America: a review. *Canadian Entomologist* 140:475–494.
- Sutherland, W. J., et al. 2006. The identification of 100 ecological questions of high policy relevance in the UK. *Journal of Applied Ecology* 43:617–627.
- Thomas, C. D., J. A. Thomas, and M. S. Warren. 1992. Distributions of occupied and vacant butterfly habitats in fragmented landscapes. *Oecologia* 92:563–567.
- Thomas, J. A., N. A. D. Bourn, R. T. Clarke, K. E. Stewart, D. J. Simcox, G. S. Pearman, R. Curtis, and B. Goodger. 2001. The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. *Proceedings of the Royal Society London B* 268:1791–1796.
- Usher, M. B., and S. W. J. Keiller. 1998. The macrolepidoptera of farm woodlands: determinants of diversity and community structure. *Biodiversity and Conservation* 7:725–748.
- Van Dyck, H., and M. Baguette. 2005. Dispersal behaviour in fragmented landscapes: Routine or special movements? *Basic and Applied Ecology* 6:535–545.
- van Swaay, C., P. Nowicki, J. Settele, and A. van Strien. 2008. Butterfly monitoring in Europe: methods, applications and perspectives. *Biodiversity and Conservation* 17:3455–3469.
- Walters, R. J., M. Hassall, M. G. Telfer, G. M. Hewitt, and J. P. Palutikof. 2006. Modelling dispersal of a temperate insect in a changing climate. *Proceedings of the Royal Society London B* 273:2017–2023.
- Waring, P., and M. C. Townsend. 2009. Field guide to the moths of Great Britain and Ireland. British Wildlife Publishing, Totnes, Devon, UK.
- Warren, M. S., et al. 2001. Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* 414:65–69.
- Watts, K. 2006. British forest landscapes: the legacy of woodland fragmentation. *Quarterly Journal of Forestry* 100:273–279.
- Young, M. 1997. The natural history of moths. Poyser Natural History, London, UK.
- Zuur, A. F., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York, New York, USA.

SUPPLEMENTAL MATERIAL

Appendix A

Study landscape with trap locations ([Ecological Archives E094-138-A1](#)).

Appendix B

Trap and site details ([Ecological Archives E094-138-A2](#)).

Appendix C

Life-history traits for the 87 species marked in the study ([Ecological Archives E094-138-A3](#)).

Appendix D

Recapture rates and distances moved for 41 recaptured species ([Ecological Archives E094-138-A4](#)).

Appendix E

Coefficients table for distance moved with wingspan and wing shape as wing morphology traits and adult feeding, larval feeding guild, and forest affinity as life-history traits ([Ecological Archives E094-138-A5](#)).