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Effects of landscape structure on butterfly species richness and abundance in agricultural landscapes in eastern Ontario, Canada

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ABSTRACT

The conversion of land from natural areas to agricultural land-use results in changes in landscape pattern, which may affect the presence and distribution of species within these landscapes. Agricultural landscapes with more cover types (higher compositional heterogeneity) should provide more species with the resources necessary to survive. Landscapes with more complex spatial patterns (higher configurational heterogeneity) should allow organisms to obtain resources more efficiently. The objective of this study was to test the predictions that butterfly richness and abundance will be higher in more heterogeneous agricultural landscapes, where heterogeneity was measured by the number of patch types (patch richness) and the number of patches (patch density) in the landscape. Butterflies were sampled at the centers of 40 landscapes in eastern Ontario, Canada. The landscape variables patch density, patch richness and the amount of butterfly habitat were measured for each landscape at multiple spatial scales. Butterfly species richness was higher in landscapes with more butterfly habitat and higher patch density. In contrast, butterfly abundance was higher in landscapes with lower patch richness. Our results suggest that agricultural and environmental policies aimed at maintaining butterfly diversity and abundance should provide incentives for farmers to maintain landscapes with higher configurational heterogeneity and more butterfly habitat.

1. Introduction

Biodiversity conservation has become an increasingly important consideration in land-use management. Advances in machinery, genetic research, and chemical compounds have allowed for intensification of agricultural practices worldwide (McLaughlin and Mineau, 1995). A consequence of agricultural intensification has been the alteration and structural simplification of agricultural landscapes (Persson et al., 2010). Agricultural land-use can reduce landscape heterogeneity by reducing the number of natural cover types and/or the number of crop cover types (Fahrig et al., 2011). Agricultural expansion often results in the loss of natural wildlife habitat (Teyssedre and Couvet, 2007). This habitat loss leads to a decrease in the size of habitat patches and an increase in the distance between habitat patches within the landscape (Goodwin and Fahrig, 2002; Ockinger and Smith, 2006). Changes in the amount of habitat and the pattern in which habitat patches occur within the landscape can have major biodiversity implications (Tscharntke et al., 2002; Benton et al., 2003).

In addition to habitat loss, agricultural intensification reduces landscape heterogeneity by specialization of agricultural production in a few major crops (ex. maize, *Zea mays* and soybean, *Glycine max*) (McLaughlin and Mineau, 1995). Crop specialization leads to a reduction in heterogeneity of the landscape because it results in fewer crop types and larger crop fields (Persson et al., 2010). Since some species can use or persist in some crop types, landscapes with a diversity of crop types will harbor more species (Fahrig et al., 2011). Since crop fields are risky environments for some species (Dowdeswell et al., 1940; Dover, 1990; Fry and Main, 1993; Thomas et al., 2002; Schtickzelle et al., 2006), abundance and persistence of these species may be reduced in landscapes with larger crop fields if individuals have to move through them to get from one habitat patch to another. Therefore, maintaining higher heterogeneity in agricultural landscapes may play an important role in maintaining biodiversity in these areas (Benton et al., 2003; Persson et al., 2010).

Landscape heterogeneity is the spatial complexity of the cover types within a landscape, and has two major components: compositional heterogeneity and configurational heterogeneity (Fahrig and Nuttle, 2005; Fahrig et al., 2011). Landscape compositional heterogeneity refers to the number of components (cover types)

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in the landscape and their relative proportions; landscape compositional heterogeneity is higher in landscapes with more cover types that are more equally distributed (high cover type evenness). Configurational heterogeneity refers to the spatial pattern of the landscape; landscapes with many small, irregularly shaped patches have higher configurational heterogeneity than landscapes with large uniformly shaped patches. Agricultural landscapes include a variety of natural and semi-natural cover types (such as grassy field margins, some pastures, forest, wetland and hedgerows), as well as crop cover types, and therefore have the potential to have high landscape heterogeneity.

A landscape with higher compositional heterogeneity should support more different species, since different species specialize on different resources (Benton et al., 2003). In addition, an increase in compositional heterogeneity can benefit species that require two or more resources that are found in different cover types, since landscapes with higher compositional heterogeneity are more likely to contain both necessary resources. Conversely, these species are unlikely to be found in homogeneous landscapes because all their required resources may not be present (Dennis, 2010). The provision of and access to multiple required habitats within a landscape is termed landscape complementation (Dunning et al., 1992). For example, leopard frogs (*Rana pipiens*), which require breeding ponds, grassy meadows for summer foraging, and streams or lakes for overwintering, are more abundant in more heterogeneous landscapes due to landscape complementation (Pope et al., 2000). Ouin et al. (2004) showed that within an agricultural landscape butterflies used different types of patches (road verge, lane way, hedgerow, grazed and ungrazed meadow) for different purposes (foraging, flying, and resting), which supports the resource complementation hypothesis for butterflies, and suggests that butterflies might be more abundant in more heterogeneous landscapes.

Landscape configurational heterogeneity should also increase biodiversity because a complex patterning of the landscape increases the probability that different required resources will be found in close proximity to each other, allowing organisms to obtain resources more efficiently (Dunning et al., 1992). For example, in a landscape that has many small patches (i.e. high configurational heterogeneity), the distances between habitat patches are less than in landscapes with few large patches (i.e. lower configurational heterogeneity) (Ricketts, 2001; Goodwin and Fahrig, 2002; Burel and Baudry, 2005).

Studies of the effects of landscape pattern on biodiversity in agricultural landscapes have generally focused on effects of the amount and heterogeneity of habitat, i.e. of the natural or semi-natural covers, in the landscape. Agricultural landscapes with more natural cover have higher diversities of a range of taxa including birds, bees, butterflies, other invertebrates, and herbaceous plants (Devictor and Jiguet, 2007; Dormann et al., 2007; Dallimer et al., 2010). Landscape-scale studies have also shown that the effectiveness of organic farming in augmenting biodiversity is higher when the landscape surrounding the organic field is heavily dominated by intensive agriculture (low habitat amount) (Rundlof and Smith, 2006; Holzschuh et al., 2007, 2010; Rundlof et al., 2008). In addition, the diversity of natural and semi-natural covers in an agricultural landscape has been shown to increase species diversity (Devictor and Jiguet, 2007; Woodcock et al., 2010), and Hendrickx et al. (2007) showed that increased configurational heterogeneity of natural and semi-natural cover types can have a positive impact on insect diversity in agricultural landscapes.

In contrast, while the effects of natural and semi-natural habitat on biodiversity in agricultural landscapes are relatively well studied, there are few studies that have included the effects of compositional and configurational heterogeneity of the crop/production cover types on biodiversity (Fahrig et al., 2011). Gaba et al. (2010) found that weed diversity was greater in landscapes that had many small crop fields (i.e. increased configurational heterogeneity) than in landscapes with a few large fields, and Burel and Baudry (2005) predicted that changes in total cropped area and configuration together could influence landscape connectivity for forest species. In addition to the paucity of studies on the effects of heterogeneity of the crop/production cover types, there are particularly few, if any, studies that clearly separate the effects of the amount of natural and semi-natural covers from the effects of landscape compositional and configurational heterogeneity. To clearly elucidate the effects of landscape heterogeneity on biodiversity it is necessary to control for the known, strong effects of the amount of natural and semi-natural covers on biodiversity in agricultural landscapes.

Butterflies are an ideal species group for studying the effects of landscape heterogeneity on biodiversity in agricultural landscapes (Rossi and Van Halder, 2010). Within a given geographic area, butterfly species can vary greatly in their life history traits, behavioral characteristics and movement capabilities (Dennis et al., 2003). Butterflies commonly use multiple different habitat types to obtain necessary resources. The three most important general habitat types for all butterflies are breeding, foraging and roosting habitats (Ouin et al., 2004). Linear features such as green lanes, roadside ditches, and hedgerows provide resources for oviposition as well as for foraging (Dover and Sparks, 2000; Dover et al., 2000; Croxton et al., 2005), and may also be important in facilitating the movement of butterflies within agricultural landscapes. Low-intensity grazed fields and field margins often contain host plants required by various butterfly species for oviposition and therefore may be considered breeding habitat (Dover and Sparks, 2000). Other cover types such as laneways and road verges have high floral resources and are often associated with foraging (Munguira and Thomas, 1992). Cover types that provide roosting habitat typically contain high grass resources, such as grazed meadows (Ouin et al., 2004). Despite these generalizations, different butterfly species require different resources (i.e. different species of host or nectaring plants) and therefore use cover types differently (Dennis et al., 2003; Schneider et al., 2003; Dover and Settele, 2009). We therefore hypothesize that more heterogeneous agricultural landscapes should offer greater landscape complementation for more butterfly species.

Our objective was to test the prediction that butterfly species richness and abundance should be higher in more heterogeneous landscapes, where heterogeneity is measured as the number of patch types (patch richness; compositional heterogeneity) and the number of individual patches in the landscape (patch density; configurational heterogeneity). To separate the effects of compositional heterogeneity and configurational heterogeneity, we selected our sample sites to minimize the correlation between patch richness and patch density in the surrounding landscapes. We also tested and controlled for the amount of butterfly habitat within each landscape by including it as a third landscape predictor variable.

2. Methods

2.1. Study area and site selection

Our study was conducted in agriculture-dominated landscapes in eastern Ontario, Canada (Fig. 1). We used a focal site study design (Brennan et al., 2002), in which the response variable(s) is estimated at multiple “focal” sites, each of which is at the center of a landscape in which the landscape predictor variables are measured. In our study the responses were butterfly abundance and richness, the focal sites were survey transects in 40 grassy roadside ditches, and the landscapes were circular areas (at multiple spatial scales;

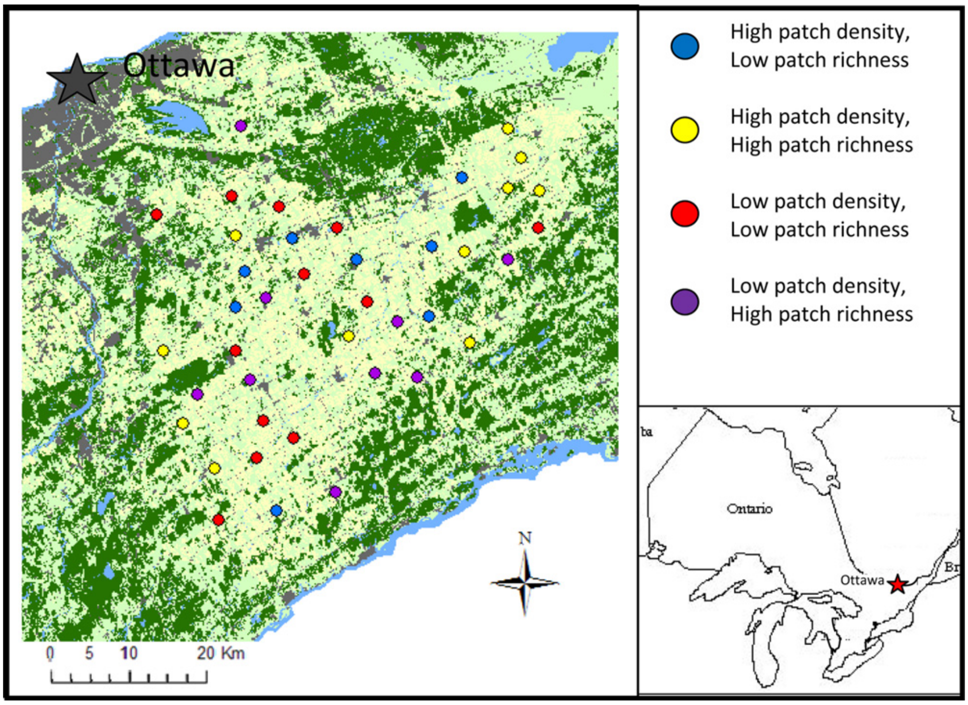

Fig. 1. Map of study region in eastern Ontario, Canada. Dark gray areas are urban development, dark green is forest, light green is grassland and yellow is agricultural crops. The 40 butterfly sample sites are at the centers of the colored circles. The circles represent the type of landscape in which the sample site was imbedded. These landscapes represented gradients in patch density and patch richness, but for the purpose of mapping we grouped them into four categories shown with the different colors. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

see below) around these focal sites (Fig. 1). The focal site design allowed us to select landscapes that varied widely in landscape heterogeneity, while controlling for local site quality by sampling butterflies in a consistent local cover type. It was therefore aimed at elucidating the effects of surrounding landscape structure on the butterfly community in a representative cover type (here, roadside ditches).

The 40 landscapes were selected such that each contained >70% farmed land. The average cover of each cover type was: cereal 4.6%, corn 28.8%, forest 3.9%, hay/pasture 19.3%, hedgerow 0.2%, soy 7.0%, undifferentiated grassy cover 29.3%, urban 6.6%, and wetland/water 0.2% (see Appendix C and Table C1 for individual landscapes). The amount of butterfly habitat within each landscape was estimated as the proportion of the landscape comprised of hay, pasture, hedgerow and undifferentiated grassy cover (Ouin and Burel, 2002; Weibull et al., 2003; Ouin et al., 2004). Hay cutting can negatively affect butterfly abundance (Dover et al., 2010). However, we did not incorporate this in our habitat estimates because we did not have data on hay cutting at sufficient spatio-temporal resolution to adjust the habitat amount estimates for disappearances (and reappearances, with re-growth) of hay in the landscapes. All landscape metrics were calculated using ArcMap 9.3, using data provided by Pasher et al. (submitted for publication).

Each landscape was centered on a butterfly sampling transect in a grassy roadside ditch (Fig. 2). Grassy ditches were selected because they are similar in vegetation structure, they are easy to sample, they can be important sources of butterfly habitat, and they are thought to facilitate butterfly movement within landscapes (Saarinen et al., 2005; Noordijk et al., 2009). The roadside ditches varied in width, but the areas surveyed for butterflies were constant across sample transects. The effect of the larger amount of grassy cover at wider roadsides was accounted for within the habitat amount predictor variable as part of the “undifferentiated grassy cover” class (above). Most of the roadside ditches were mowed at least once during the sampling period. The effects of mowing on our estimates of butterfly richness and abundance were accounted for in the flower abundance and richness local predictor variables (below). In addition, these effects were expected to be independent of the effects of landscape heterogeneity, our primary interest. All sample transects were located adjacent to a crop field, and there was no hedgerow or woody vegetation between the ditch and the field, with the exception of one site. The crop type adjacent to the ditch varied among sites (but was most commonly maize or soybean crops). We note that, while tall maize could potentially provide shelter to butterflies using roadsides adjacent to maize fields, since our sampling was done during the early to mid growing season, maize height varied from low (seedlings) to moderate (<1 m), so was not likely a significant source of shelter for butterflies.

The forty landscapes were selected such that all forty focal transects were separated by at least 4000 m. Landscape metrics were calculated for landscapes of radii 250 m, 500 m, 750 m, 1000 m, 1250 m, 1500 m, 1750 m and 2000 m around each transect (Fig. 2). We used this multi-scale approach because we did not know a priori the scale at which landscape pattern would most strongly affect butterfly richness and abundance, i.e. the scale at which butterflies observed at a local site interact with the surrounding landscape. The forty landscapes were also selected such that correlations between patch richness (compositional heterogeneity) and patch density (configurational heterogeneity) in the surrounding landscapes were minimized at all the scales. The study therefore included landscapes representing all four combinations of high and low configurational and compositional heterogeneity at all scales (Fig. 1). To avoid broad regional spatial trends in landscape predictor variables, which could confound results, landscapes in each of the four categories were selected such that they were distributed as evenly as possible over the entire study region, i.e., sites of each of the four categories were represented in the North, South, East and West areas of the study region (Fig. 1). Thus, there were no significant correlations ($p > 0.1$) between the site coordinates (latitude and longitude) and the landscape variables (patch richness and patch density) across the selected landscapes.

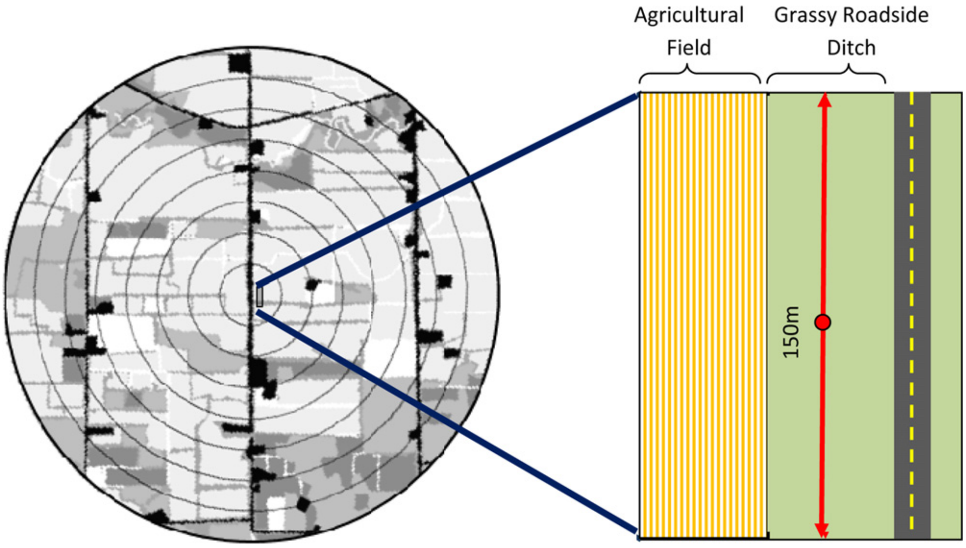

Fig. 2. Example landscape centered on a 150 m butterfly sampling transect (shown as the red arrow). Each butterfly sampling transect was located in a grassy roadside ditch next to an agricultural field. The example landscape is shown with radii of 250 m, 500 m, 750 m, 1000 m, 1250 m, 1500 m, 1750 m and 2000 m around the center of the butterfly sampling transect. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

2.2. *Butterfly sampling*

Butterflies were sampled between May 10th and July 7th 2010, between 8 am and 4 pm. Each site was visited four times, with about two weeks between visits. To remove any potential bias due to seasonality, sites were grouped into 10 groups, each group consisting of four sites representing the four combinations of high and low configurational and compositional heterogeneity, and the groups were then visited in random order during each sampling period. Sampling was carried out on days when the temperature was above 15 °C and there was no rain or strong wind (less than 4 on the Beaufort scale); cloud cover varied among sampling days. Butterflies were sampled along a 150 m linear transect at each sample site, where the transect was oriented along the grassy ditch in the center of the landscape, with the center of the transect as the center point of the landscape (Fig. 2). The transect was walked at a steady pace of 10 m/min and butterflies observed within 5 m to either side and in front of the sampler were visually identified and recorded. Butterflies that flew into the sampling area from all directions (including from behind the observer) were recorded. Double-counting of individuals was avoided by keeping track of those that had already been counted. Butterflies that could not be identified while in flight were caught and identified, and then released after the sample was completed.

We measured two response variables at each site, butterfly species richness and butterfly abundance. Butterfly species richness at a site was the total number of butterfly species observed at that site over all four visits. The total butterfly abundance at a site was the sum of all individual butterflies observed at that site over all four visits.

2.3. *Local predictor variables*

We measured three local predictor variables at the survey transect at the center of each landscape: flower abundance, flower species richness, and traffic intensity on the adjacent road. Floral vegetation was sampled four times along the transect at each study site on the day following butterfly sampling. Flower abundance and species richness were measured in 15 1 × 1 m quadrats placed randomly along the transect. Flower abundance was measured as the number of flowering ramets observed in each quadrat, averaged over the 15 quadrats and then over the four sample dates. Flower species richness was measured as the total number of species in bloom at the time of the survey, observed in the quadrats over all four sample dates. Flowering plants were identified using Newcomb's Wildflower Guide (1977).

Since our focal sites were located in grassy roadside ditches, we measured traffic intensity on the adjacent road to account for potential effects of traffic on the butterfly richness and abundance measures. Traffic intensity was the average number of vehicles that passed by the transect during a 15-min period, averaged over twelve sampling events on twelve separate dates for each transect, i.e. the 4 dates of the butterfly sampling, the 4 dates of the flower surveys, and 4 additional dates following the conclusion of the butterfly sampling period. We recorded the number of passing vehicles using a digital audio recorder (Toshiba DMR-850 W Digital Voice Recorder). Digital audio software (NCH Software, WavePad Sound Editor v 4.59) was then used to count the number of vehicles that passed during the recording time. The average traffic count for each site was log transformed to correct for unequal variance before use in the analyses.

2.4. *Analyses*

To determine at what spatial extent the landscape structure most strongly affected butterflies, we ran simple linear regressions of each of the two response variables (butterfly species richness and butterfly abundance) on each of the three landscape predictor variables (patch density, patch richness and amount of butterfly habitat) at each scale. The R^2 values from each of the simple linear regressions were then plotted against scale to determine the spatial extent at which each landscape variable most strongly affected butterfly richness and abundance.

Using the landscape predictor variables calculated at the scales where their effects were strongest, we then performed multimodel selection using all 63 combinations of the three landscape predictors and the three local variables (flower species richness, flower abundance, and ln(average traffic)) to determine their relative effects on butterfly species richness and butterfly abundance. The models were ranked using AIC (Burnham and Anderson, 2002). All analyses were performed using SAS 9.1 (2004).

3. Results

Twenty butterfly species (superfamily Papilinoidea) and 913 individual butterflies were observed (Fig. 3). Six species accounted for 91% of individuals: red admiral (*Vanessa atalanta*, 29%), common ringlet (*Coenonympha tullia*, 23%), clouded sulphur (*Colias philodice*, 16%), cabbage white (*Pieris rapae*, 11%), silvery blue (*Glaucopsyche lygdamus*, 8%) and bronze copper (*Lycaena hyllus*, 4%) (Fig. 3). The highest species richness observed at a single site was 11 species and the average number of species observed per site was 5.7 ± 1.9 (s.d.) species.

The simple linear regressions of butterfly species richness and abundance on the three landscape variables showed that when there was a strong effect of a landscape variable on either species richness or abundance, it occurred at the 250 m scale (Fig. 4). Therefore, all further analyses were conducted using the landscape variables measured within 250 m of the butterfly survey transects. Correlations among the predictors, with the landscape predictors measured at the 250 m scale, are shown in Table 1.

The top 11 (of 63) models for butterfly species richness were within 2 AIC units of the best model (Appendix A). All of these 11 models included habitat amount (positive effect) and 9 of the 11 top models included patch density (positive effect). The R^2 of the top 11 models ranged from 16% to 27%. The top 6 (of 63) models for butterfly abundance were within 2 AIC units of the best model (Appendix B). All of these 6 models included patch richness (negative effect) and 5 of the 6 top models included patch density (positive effect). The R^2 of the top 6 models for butterfly abundance ranged from 18% to 24%.

4. Discussion

The spatial extent at which landscape structure showed the strongest effects on butterflies was relatively small, within 250 m of the butterfly surveys. This is consistent with findings by Krauss et al. (2003) who found that butterfly communities in Germany responded to landscape diversity within 250 m but not at larger extents, and with Marini et al. (2009) who found responses at extents less than 135 m. In general, butterflies make daily movements of between 200 and 600 m and dispersal movements from 1 to 2 km (Davis et al., 2007). Therefore our results suggest that butterfly species may be responding to landscape structure primarily at the spatial extent of their daily movements. Daily movements in butterflies are related to resource acquisition (i.e. feeding, roosting and egg deposition) as well as mate seeking and predator escape (Dennis et al., 2003; Ouin et al., 2004). These behaviors and their associated movements may also be affected by daily weather, where temperature and sun orientation may cause butterflies to move from cooler/shady areas to warmer/sunny areas to maximize resource use and acquisition (Cormont et al., 2011). In an agricultural landscape resources are likely to occur spatially separated from each other (i.e. in different cover types), requiring a butterfly to move between these resources on a daily basis (Dennis et al., 2006). Since butterflies responded to landscape structure at this extent, we can postulate that the mechanism of the observed responses to landscape structure may be the movement between complementary resources within the landscape.

Although we and others have found that butterflies respond to landscape structure at a relatively small extent, some other research has found that butterflies can respond to larger scales. Bergman et al. (2004, 2008) and Berg et al. (2011) found that butterfly abundance was related to the amount of forests and semi-natural grasslands within a radius of 5000 m, with the highest abundances in landscapes with more forests and semi-natural grasslands. Interestingly, Bergman et al. (2008) did not find a significant effect of habitat amount on species richness at this scale, whereas we found that habitat amount at the much smaller spatial extent of 250 m was consistently included in all the top models for butterfly species richness. The discrepancy between the studies may be due to the different ways in which habitat was defined; Bergman et al. (2008) included forest in their measure whereas we did not. On the other hand, Marini et al. (2009) did include forest in their habitat measure and found that butterfly species richness responded to the amount of woody vegetation and grassland within 95–135 m radius. At this point there are too few multi-scale studies, with too many differences among them, to draw conclusions as to the reasons for these disparate results.

Our finding that butterfly species richness was greater in landscapes containing more butterfly habitat (measured as the proportion of the landscape composed of hay, pasture, hedgerow and undifferentiated grassy cover) is consistent with many other findings that the amount of habitat in a landscape generally has a positive effect on biodiversity (Fahrig, 2003). Butterfly species richness was also greater in agricultural landscapes that had many smaller patches (i.e. high patch density; higher configurational heterogeneity). This supports our hypothesis that more heterogeneous landscapes allow for more efficient use of complementary resources within the landscape. Many smaller patches within a landscape should reduce the distances between complementary resources thus facilitating butterfly movement between them. Also, landscapes with many small patches will have higher edge density which may further facilitate butterfly movement because many species are known to move along linear features and patch edges (Heal, 1965; Ries and Sisk, 2008; Rossi and Van Halder, 2010). For example, Fry and Main (1993) and Dover (1990) found that individual butterflies preferentially moved along hedgerows and wood edges and rarely moved into crop fields. Schtickzelle et al. (2006) modeled the movement of female *Proclossiana eunomia* through a fragmented landscape and predicted that butterflies experience greater mortality when moving between habitat patches if they choose linear paths rather than longer routes along edges. Even for species that do not use edges, a butterfly's survival should be higher when crossing small high-risk patches than when crossing large ones (Fahrig, 2007), so movement should be facilitated in landscapes with high configurational heterogeneity.

In contrast to the results for species richness, the proportion of butterfly habitat within the landscape was not an important predictor of butterfly abundance. Consistent with this result, Steffan-Dewenter and Tscharntke (2000) found that although the diversity of butterfly species was positively related to habitat amount, butterfly density was not. In fact, they found that densities of polyphagous and oligophagous species (i.e. food plant generalists) were negatively related to habitat amount whereas densities of monophagous (i.e. food plant specialist) butterfly species was positively related to habitat amount, thus averaging out to no overall effect on abundance. It is possible that our measure of habitat amount – the total cover of hay, pasture, hedgerow and undifferentiated grassy cover – is too coarse to represent habitat availability for butterflies. For example, Thomas et al. (2001) found that host plant presence and habitat quality, instead of total habitat amount, were the most important factors in determining the occurrences of three butterfly species (*Melitaea cinxia*, *Polyommatus bellargus*, and *Thymelicus acteon*) and Dover (1996) found that for certain butterfly species the presence of 'sheltered environments' (structural features, such as hedgerows, that protect individuals from wind in open areas) was a primary factor in determining the number of individuals caught in a farmland area in the U.K. We do not have data at a sufficiently fine resolution over the large geographic extent of our study to allow us to test these possibilities.

Our results suggest that butterfly abundance, like butterfly richness, is higher in landscapes with many smaller patches (high

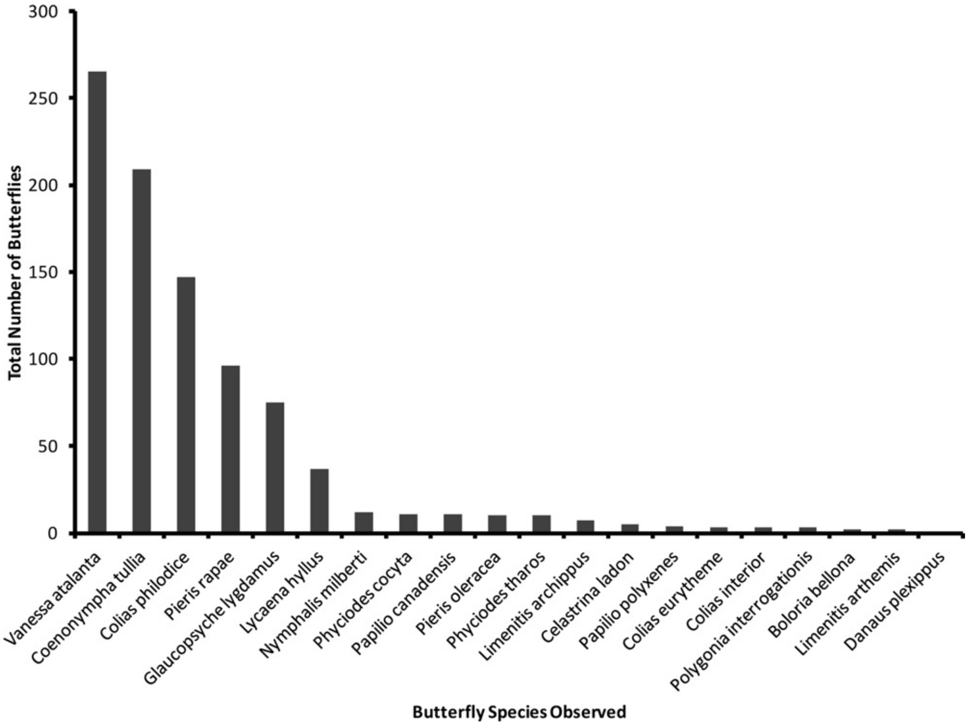

Fig. 3. Total number of individuals of each species observed along the butterfly sampling transects in all 40 landscapes over the entire study period.

configurational heterogeneity) than in landscapes with a few larger patches. As discussed above in the context of species richness, increased patch density may result in higher abundance due to higher movement success between habitat patches (landscape complementation), with associated lower mortality and possibly increased reproduction through increased resource accessibility (Debinski et al., 2001; Ries and Sisk, 2008).

In contrast to our expectations, butterfly abundance was higher in landscapes with fewer patch types (patch richness), i.e., lower compositional heterogeneity. One possible explanation for this result derives from the “intermediate heterogeneity hypothesis” (Fahrig et al., 2011). Landscapes with more patch types necessarily contain smaller amounts of each type. The intermediate heterogeneity hypothesis suggests that abundance and species richness should increase with increasing compositional heterogeneity up to a point, but then beyond this point, decreases in abundance and richness could occur due to limited availability of individual cover types. This could explain our result if the landscapes we studied were in the upper range of compositional heterogeneity (for butterflies), i.e., beyond the peak in the abundance response. However, in a post hoc test we failed to find support for this idea. Since, across our landscapes, the cover of hay/pasture decreases with increasing compositional heterogeneity, we hypothesized that the hay/pasture cover type could be a particular cover type that becomes limiting to butterflies in landscapes with high cover type richness. However, there was no significant correlation between hay/pasture and butterfly abundance, so this suggestion is not supported in our study. Further research will be needed to identify the cause of the negative effect of compositional heterogeneity on butterfly abundance.

We did not find any significant effects of the three local variables measured (flower species richness, flower abundance and traffic) on butterfly richness and abundance. The lack of effects of floral resources may be considered surprising, considering that many studies suggest that nectaring resources are a limiting factor for many species of butterflies (Schneider et al., 2003; Ockinger and Smith, 2006). The most likely explanation for this discrepancy is that our study was not designed to estimate the effects of local habitat quality. In fact, we deliberately selected sites that were as similar as possible, to facilitate detection of effects of landscape structure, our primary objective. Therefore we likely did not have a wide enough range in local floral resources across our sites to measure their effect on butterfly richness and abundance. Regarding traffic intensity, we note that, while butterflies are known to experience mortality due to vehicles (McKenna et al., 2001), Munguira and Thomas (1992) and Saarinen et al. (2005) suggest that butterfly road mortality is likely insignificant on smaller roads with lower speed limits such as the ones in our study.

The overall R^2 values for our top models for butterfly species richness and abundance were 16–27% (Appendix A) and 18–24%

Table 1
Pairwise correlations among the three landscape predictor variables and three local predictor variables. Landscape variables were calculated within 250 m of each of the 40 butterfly survey transects.

	Flower abundance	Flower species richness	ln(Average traffic)	Patch density (250 m)	Patch richness (250 m)	Habitat amount (250 m)
Flower abundance	1					
Flower species richness	0.127	1				
ln(Average traffic)	0.096	−0.038	1			
Patch density (250 m)	0.096	0.032	0.132	1		
Patch richness (250 m)	0.131	0.055	0.081	0.434	1	
Habitat amount (250 m)	0.267	−0.008	0.001	0.254	−0.104	1

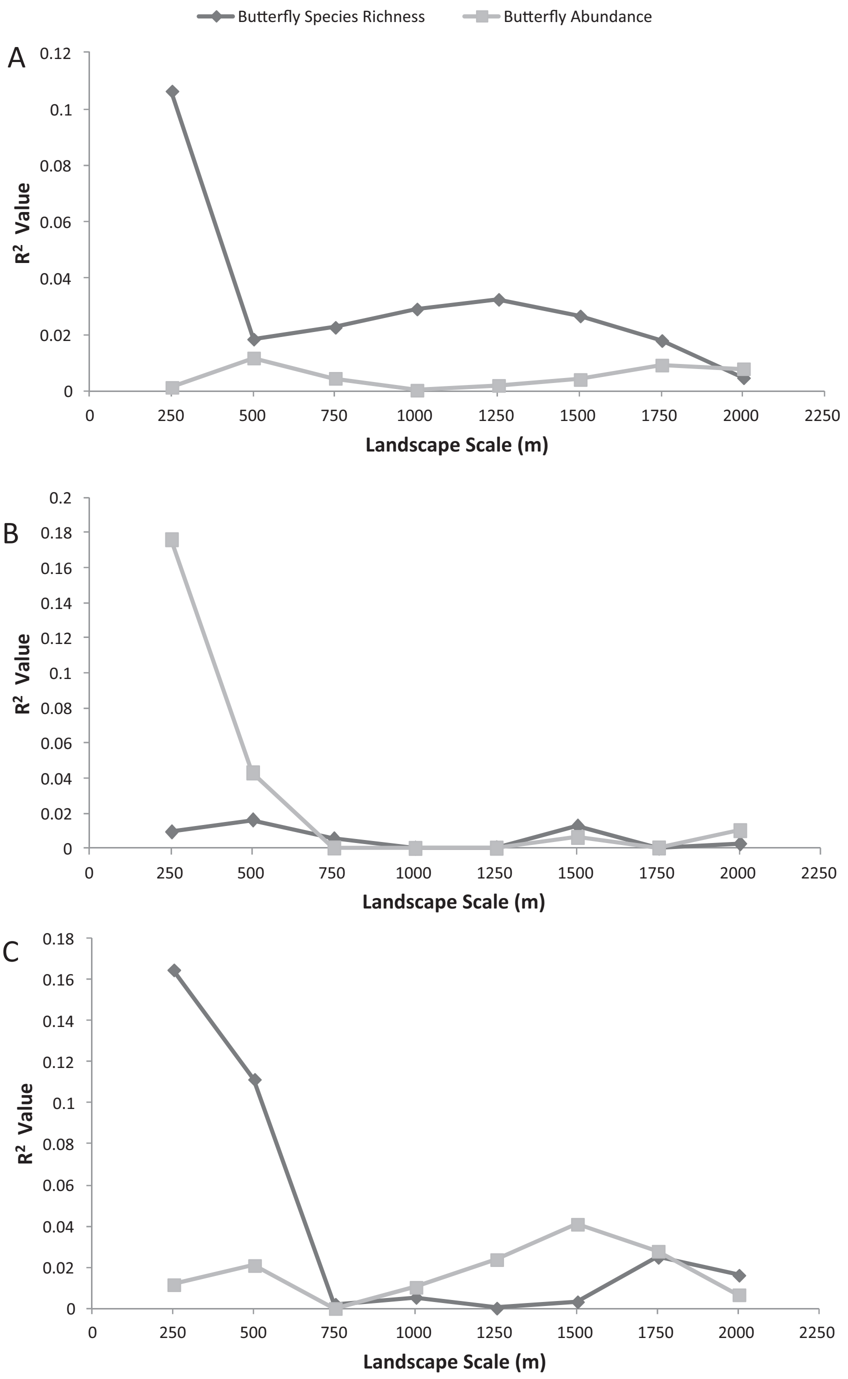

Fig. 4. R^2 values for simple linear regressions of butterfly species richness and butterfly abundance on (A) patch density, (B) patch richness and (C) habitat amount at multiple landscape scales. The landscape scale is the radius of the landscape area surrounding each transect, within which the three landscape predictor variables were measured.

(Appendix B) respectively. These values are comparable to the R^2 values (16–41%) Rossi and Van Halder (2010) report for their models of butterfly species richness in landscapes dominated by pine plantations. While these values seem low, they are not surprising given the large number of uncontrolled factors influencing the relationships. It is likely that a very large proportion of the variance in observed butterfly richness and abundance is due to short-term, small scale environmental variability causing random variability in the butterfly estimates. Many factors will determine whether a butterfly present in a landscape flew into our transects at the time of the surveys, including gusts of wind, passing clouds, the presence of a predator, the presence of a particular host plant, etc. An additional important reason for unexplained variability is likely imprecision in the land cover data. For example, the undifferentiated grassy cover class contains a variety of cover types that likely vary in the resources they offer to butterflies. Also, as stated above, the quality of hay fields in the landscapes will vary temporally with cutting and re-growth. All of these and many more such factors work together to create a large proportion of unexplained variation in the relationships between butterfly richness/abundance and landscape structure. Given this, we suggest it is remarkable that we detected effects of landscape heterogeneity on butterflies. The positive effect of configurational heterogeneity on both butterfly richness and abundance is particularly noteworthy.

Based on our results for species richness, we can conclude that agricultural and environmental policies aimed at

Table A1
All possible models relating butterfly species richness to the three landscape predictor variables and the three local predictor variables, in order of increasing AIC. A "–" indicates the variable was not included in the model.

AIC	R^2	Habitat amount (250 m)	Patch richness (250 m)	Patch density (250 m)	ln(Average traffic)	Flower abundance	Flower species richness
45.81	0.22	0.0604	–	0.0231	–	–	–
45.96	0.25	0.0517	−0.3851	0.0334	–	–	–
46.45	0.16	0.0709	–	–	–	–	–
46.62	0.24	0.0675	–	0.0236	–	−0.0215	–
46.81	0.24	0.0595	–	0.0250	−0.2781	–	–
46.96	0.27	0.0510	−0.3797	0.0351	−0.2708	–	–
47.17	0.27	0.0585	−0.3417	0.0326	–	−0.0174	–
47.39	0.23	0.0606	–	0.0228	–	–	0.0357
47.42	0.26	0.0518	−0.3940	0.0333	–	–	0.0389
47.44	0.19	0.0779	–	–	–	−0.0205	–
47.78	0.26	0.0662	–	0.0252	−0.2512	−0.0198	–
47.89	0.18	–	−0.5247	0.0439	–	–	–
47.90	0.18	0.0710	–	–	−0.2109	–	–
47.95	0.25	0.0685	–	0.0232	–	−0.0236	0.0443
47.97	0.17	0.0711	–	–	–	–	0.0388
48.31	0.17	0.0699	−0.0984	–	–	–	–
48.31	0.28	0.0572	−0.3410	0.0342	−0.2502	−0.0157	–
48.43	0.28	0.0594	−0.3468	0.0324	–	−0.0196	0.0457
48.43	0.24	0.0598	–	0.0247	−0.2707	–	0.0334
48.48	0.28	0.0511	−0.3882	0.0349	−0.2625	–	0.0367
48.73	0.20	0.0789	–	–	–	−0.0228	0.0472
48.88	0.20	–	−0.5170	0.0456	−0.2859	–	–
49.01	0.19	0.0775	–	–	−0.1842	−0.0192	–
49.15	0.11	–	–	0.0316	–	–	–
49.18	0.27	0.0672	–	0.0248	−0.2392	−0.0219	0.0417
49.39	0.19	0.0771	−0.0569	–	–	−0.0197	–
49.42	0.19	–	−0.5337	0.0438	–	–	0.0383
49.46	0.19	0.0711	–	–	−0.2037	–	0.0373
49.64	0.30	0.0581	−0.3458	0.0339	−0.2378	−0.0178	0.0431
49.80	0.18	0.0700	−0.1086	–	–	–	0.0401
49.80	0.18	0.0701	−0.0833	–	−0.2033	–	–
49.82	0.18	–	−0.5175	0.0441	–	−0.0050	–
50.13	0.13	–	–	0.0335	−0.3001	–	–
50.35	0.21	0.0785	–	–	−0.1723	−0.0215	0.0454
50.46	0.21	–	−0.5257	0.0454	−0.2779	–	0.0359
50.66	0.20	0.0780	−0.0643	–	–	−0.0219	0.0477
50.82	0.11	–	–	0.0313	–	–	0.0335
50.85	0.20	–	−0.5122	0.0457	−0.2819	−0.0034	–
50.97	0.11	–	–	0.0322	–	−0.0086	–
50.98	0.19	0.0768	−0.0458	–	−0.1809	−0.0186	–
51.30	0.19	–	−0.5245	0.0441	–	−0.0067	0.0406
51.33	0.19	0.0701	−0.0936	–	−0.1950	–	0.0385
51.84	0.14	–	–	0.0332	−0.2933	–	0.0310
52.01	0.13	–	–	0.0339	−0.2916	−0.0069	–
52.31	0.21	0.0777	−0.0537	–	−0.1683	−0.0208	0.0459
52.39	0.21	–	−0.5189	0.0456	−0.2714	−0.0051	0.0377
52.57	0.12	–	–	0.0320	–	−0.0102	0.0371
53.20	0.01	–	–	–	−0.2098	–	–
53.27	0.01	–	−0.1729	–	–	–	–
53.28	0.01	–	–	–	–	–	0.0375
53.61	0.00	–	–	–	–	−0.0042	–
53.67	0.14	–	–	0.0337	−0.2823	−0.0084	0.0341
54.85	0.02	–	–	–	−0.2029	–	0.0360
54.86	0.02	–	−0.1830	–	–	–	0.0397
54.88	0.02	–	−0.1585	–	−0.1955	–	–
55.18	0.01	–	–	–	−0.2059	−0.0029	–
55.20	0.01	–	–	–	–	−0.0060	0.0397
55.26	0.01	–	−0.1686	–	–	−0.0025	–
56.49	0.03	–	−0.1688	–	−0.1872	–	0.0382
56.81	0.02	–	–	–	−0.1962	−0.0046	0.0377
56.82	0.02	–	−0.1760	–	–	−0.0043	0.0412
56.88	0.02	–	−0.1563	–	−0.1938	−0.0014	–
58.47	0.03	–	−0.1641	–	−0.1831	−0.0031	0.0393

maintaining or increasing butterfly diversity within agricultural landscapes should provide incentives for farmers to maintain landscapes with higher configurational heterogeneity (many smaller patches) and more butterfly habitat. These conclusions may be useful for the design and implementation of effective agri-environmental schemes, which provide financial incentives to farmers who participate (Ohl et al., 2008). Since our results suggest that butterfly species richness and abundance can be higher in more heterogeneous farmlands, agri-environmental schemes that are directed towards increasing configurational heterogeneity by, for example, increasing edge density and decreasing patch sizes, may be valuable methods for achieving higher butterfly diversity and abundance (Ohl et al., 2008; Delattre et al., 2011). Our results also support recent suggestions that the effectiveness of certain agri-environmental schemes for increasing biodiversity may be heavily dependent on the degree to which they increase configurational

Table B1
All possible models relating butterfly species abundance to the three landscape predictor variables and the three local predictor variables, in order of increasing AIC. A "–" indicates the variable was not included in the model.

AIC	R^2	Habitat amount (250 m)	Patch richness (250 m)	Patch density (250 m)	ln(Average traffic)	Flower abundance	Flower species richness
188.78	0.23	–	−5.7766	0.1567	–	–	–
189.71	0.18	–	−4.5216	–	–	–	–
190.53	0.24	–	−5.7990	0.1518	0.8290	–	–
190.71	0.24	–	−5.7331	0.1577	–	−0.0302	–
190.75	0.23	–	−5.7876	0.1565	–	–	0.0467
190.76	0.23	−0.0195	−5.8294	0.1606	–	–	–
191.28	0.18	–	−4.6047	–	1.1302	–	–
191.51	0.18	0.0681	−4.4491	–	–	–	–
191.68	0.18	–	−4.4850	–	–	−0.0213	–
191.69	0.18	–	−4.5347	–	–	–	0.0517
192.43	0.24	–	−5.7494	0.1528	0.8710	−0.0351	–
192.50	0.24	–	−5.8120	0.1516	0.8411	–	0.0539
192.51	0.24	−0.0174	−5.8459	0.1554	0.8239	–	–
192.68	0.24	–	−5.7431	0.1576	–	−0.0327	0.0579
192.70	0.24	−0.0085	−5.7587	0.1594	–	−0.0284	–
192.74	0.23	−0.0194	−5.8399	0.1605	–	–	0.0465
193.08	0.19	0.0671	−04.5327	–	1.1228	–	–
193.22	0.19	–	−04.5587	–	1.1655	−0.0283	–
193.25	0.19	–	−04.6212	–	1.1436	–	0.0614
193.41	0.18	0.0825	−04.3655	–	–	−0.0397	–
193.49	0.18	0.0681	−04.4622	–	–	–	0.0521
193.65	0.18	–	−04.4959	–	–	−0.0238	0.0599
194.39	0.24	–	−05.7614	0.1526	0.8896	−0.0381	0.0674
194.43	0.24	−0.0040	−05.7614	0.1536	0.8687	−0.0343	–
194.49	0.24	−0.0172	−05.8583	0.1552	0.8360	–	0.0537
194.67	0.24	−0.0073	−05.7650	0.1591	–	−0.0311	0.0572
194.94	0.19	0.0842	−04.4376	–	1.1797	−0.0471	–
195.05	0.19	0.0672	−04.5492	–	1.1361	–	0.0617
195.18	0.19	–	−04.5730	–	1.1852	−0.0315	0.0725
195.37	0.18	0.0837	−04.3759	–	–	−0.0428	0.0668
196.39	0.24	−0.0025	−05.7689	0.1531	0.8881	−0.0376	0.0671
196.88	0.19	0.0856	−04.4513	–	1.2016	−0.0510	0.0798
196.99	0.01	0.1134	–	–	–	–	–
197.19	0.01	–	–	–	–	−0.0663	–
197.31	0.00	–	–	–	0.7145	–	–
197.40	0.00	–	–	0.0208	–	–	–
197.45	0.00	–	–	–	–	–	−0.0033
198.47	0.02	0.1466	–	–	–	−0.0969	–
198.84	0.02	0.1134	–	–	0.7129	–	–
198.99	0.01	0.1111	–	0.0052	–	–	–
198.99	0.01	0.1134	–	–	–	–	−0.0013
199.01	0.01	–	–	–	0.8145	−0.0717	–
199.12	0.01	–	–	0.0255	–	−0.0698	–
199.19	0.01	–	–	–	–	−0.0672	0.0211
199.28	0.00	–	–	0.0165	0.6702	–	–
199.31	0.00	–	–	–	0.7149	–	0.0021
199.40	0.00	–	–	0.0208	–	–	−0.0060
200.26	0.03	0.1485	–	–	0.8559	−0.1030	–
200.46	0.02	0.1473	–	–	–	−0.0986	0.0351
200.46	0.02	0.1433	–	0.0073	–	−0.0972	–
200.84	0.02	0.1134	–	–	0.7137	–	0.0041
200.84	0.02	0.1132	–	0.0003	0.7121	–	–
200.96	0.01		–	0.0209	0.7616	−0.0742	–
200.99	0.01	0.1111	–	0.0052	–	–	−0.0020
201.00	0.01	–	–	–	0.8220	−0.0731	0.0293
201.12	0.01	–	–	0.0254	–	−0.0706	0.0190
201.28	0.00	–	–	0.0165	0.6701	–	−0.0004
202.24	0.03	0.1495	–	–	0.8675	−0.1052	0.0440
202.26	0.03	0.1478	–	0.0016	0.8518	−0.1030	–
202.45	0.02	0.1441	–	0.0070	–	−0.0988	0.0342
202.84	0.02	0.1133	–	0.0002	0.7130	–	0.0041
202.95	0.01	–	–	0.0208	0.7690	−0.0754	0.0271
204.24	0.03	0.1489	–	0.0011	0.8645	−0.1052	0.0439

heterogeneity in agricultural landscapes (Concepcion et al., 2008). In addition, the relatively small scale of effect of the landscape on butterfly richness and abundance, i.e., within 250 m of the sampling transect, suggests that butterfly conservation can be effective on the scale of single land holdings, making agri-environmental schemes more cost effective and improving success rates, because changes made by a single land owner can have positive effects (Ohl et al., 2008).

Table C1
Landscape predictor variables (butterfly habitat amount, patch density and patch richness) and the proportion of each cover type in each of the forty landscapes, measured within 250 m of the butterfly sampling transect at the center of the landscape. Landscapes are sorted by increasing habitat amount.

Habitat amount (250 m)	Patch richness (250 m)	Patch density (250 m)	Proportion of landscape in:								
			Cereal	Corn	Forest	Hay/pasture	Hedgerow	Soy	Undifferentiated Grasses	Urban	Water/wetland
26.12	5	50.91	0.0	41.9	0.0	11.0	0.0	26.5	15.1	5.5	0.0
28.98	6	76.37	2.4	48.8	0.0	4.5	0.0	14.5	24.5	5.3	0.0
32.99	5	76.37	0.0	45.6	0.0	1.0	0.0	13.6	32.0	7.8	0.0
34.25	6	76.37	0.0	39.5	14.8	10.8	0.0	6.0	23.5	5.5	0.0
34.71	7	101.82	3.4	52.3	3.8	6.9	2.2	0.0	25.7	5.7	0.0
36.43	5	71.27	0.0	38.4	0.0	3.2	0.0	19.5	33.2	5.7	0.0
37.11	5	61.09	4.0	53.4	0.0	5.2	0.0	0.0	32.0	5.5	0.0
39.29	7	76.37	0.0	49.1	2.7	10.3	0.3	3.3	28.6	5.5	0.0
40.44	5	61.09	11.7	26.1	0.0	0.0	0.0	12.4	40.4	9.4	0.0
41.01	6	106.91	45.5	0.0	0.0	10.2	2.1	6.9	28.8	6.6	0.0
41.92	7	76.37	14.7	26.9	1.3	12.1	0.0	9.9	29.8	5.4	0.0
42.50	5	101.82	0.0	38.1	13.7	24.4	0.0	0.0	18.1	5.6	0.0
43.76	5	61.09	13.3	37.2	0.0	18.6	0.0	0.0	25.2	5.7	0.0
46.74	5	81.46	13.5	34.1	0.0	18.9	0.0	0.0	27.8	5.6	0.0
46.85	7	96.73	16.6	11.7	3.8	15.3	0.0	13.2	31.5	7.9	0.0
46.96	6	50.91	0.5	34.5	0.0	14.7	0.0	12.8	32.3	5.3	0.0
46.96	6	91.64	0.0	36.9	8.1	3.6	0.0	2.4	43.4	5.6	0.0
47.08	8	81.46	17.5	4.5	8.4	20.4	1.5	17.1	25.2	5.5	0.0
47.42	6	71.27	0.0	13.5	3.3	25.4	0.0	30.0	22.0	5.7	0.0
47.54	4	96.73	0.0	47.0	0.0	25.3	0.0	0.0	22.2	5.5	0.0
48.34	6	71.27	0.0	40.7	5.4	10.1	0.0	0.1	38.3	5.5	0.0
49.03	4	45.82	0.0	45.5	0.0	26.5	0.0	0.0	22.6	5.5	0.0
49.37	6	76.37	0.0	8.2	5.3	6.5	0.0	28.5	42.8	8.6	0.0
49.83	5	61.09	0.0	34.5	0.0	22.8	0.0	10.0	27.0	5.7	0.0
50.63	5	86.55	0.0	38.3	5.6	26.2	0.0	0.0	24.4	5.5	0.0
50.97	5	50.91	10.8	32.5	0.0	23.7	0.0	0.0	27.3	5.7	0.0
52.00	7	86.55	12.6	7.0	23.4	27.1	0.2	0.0	24.6	5.0	0.0
55.21	6	71.27	0.0	15.7	7.7	30.9	0.0	15.9	24.3	5.5	0.0
55.90	4	56.00	0.0	34.4	0.0	17.3	0.0	0.0	38.6	9.7	0.0
56.01	5	86.55	0.0	38.3	0.0	24.6	1.5	0.0	29.9	5.7	0.0
56.47	4	81.46	0.0	25.3	0.0	28.6	0.0	0.0	27.8	18.2	0.0
58.42	5	61.09	0.0	14.2	0.0	7.0	0.0	22.6	51.4	4.8	0.0
58.42	7	112.00	5.2	22.3	7.0	28.6	1.0	0.0	28.8	7.1	0.0
58.65	8	112.00	0.0	8.4	13.6	24.7	0.0	5.5	33.9	5.6	8.2
59.22	6	112.00	3.9	9.9	16.6	37.7	0.0	0.0	21.5	10.4	0.0
61.63	6	81.46	0.0	15.0	7.9	15.1	0.0	9.5	46.5	6.0	0.0
63.92	5	81.46	8.0	20.5	0.0	39.5	0.0	0.0	24.4	7.6	0.0
67.93	6	91.64	0.2	18.8	4.6	33.1	0.0	0.0	34.8	8.5	0.0
68.16	4	50.91	0.0	26.1	0.0	40.9	0.0	0.0	27.3	5.7	0.0
72.74	5	122.18	0.0	18.8	0.0	57.7	0.8	0.0	14.2	8.5	0.0

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Appendix A.

See Table A1.

Appendix B.

See Table B1.

Appendix C.

See Table C1.

References

Benton, T., Vickery, J., Wilson, J., 2003. Farmland biodiversity: is habitat heterogeneity the key? Trends Ecol. Evol. 18 (4), 182–188.

Berg, A., Ahrne, K., Ockinger, E., Svensson, R., Soderstrom, B., 2011. Habitat-specific butterfly communities in Swedish forest farmland mosaics – implications for conservation. Biol. Conserv. 144, 2819–2831.

Bergman, K., Ask, L., Askling, J., Ignell, H., Wahlman, H., Milberg, P., 2008. Importance of boral grasslands in Sweden for butterfly diversity and effects of local and landscape factors. Biodivers. Conserv. 17, 139–153.

Bergman, K., Ask, L., Ekberg, O., Ignell, H., Wahlman, H., Milberg, P., 2004. Landscape effects on butterfly assemblages in an agricultural region. Ecography 27, 619–628.

Brennan, J., Bender, D., Contreras, T., Fahrig, L., 2002. Focal patch landscape studies for wildlife management: optimizing sampling effort across scales. In: Liu, J., Taylor, W. (Eds.), Integrating Landscape Ecology into Natural Resource Management. Cambridge University Press, Cambridge, MA, pp. 68–91.

Burel, F., Baudry, J., 2005. Habitat quality and connectivity in agricultural landscapes: the role of land use systems at various scales in time. Ecol. Indicat. 5, 305–313.

Burnham, K., Anderson, D., 2002. Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach, 2nd ed. Springer-Verlag.

Concepcion, E., Diaz, M., Baquero, R., 2008. Effects of landscape complexity on the ecological effectiveness of agri-environment schemes. Landscape Ecol. 23, 135–148.

Cormont, A., Malinowska, A., Kostenko, O., Radchuk, V., Hemerik, L., WallisDeVries, M., Verboom, J., 2011. Effect of local weather on butterfly flight behaviour, movement, and colonization: significance for dispersal under climate change. Biodivers. Conserv. 20, 483–503.

Croxton, P., Hann, J., Greatorex-Davies, J., Sparks, T., 2005. Linear hotspots? The floral and butterfly diversity of green lanes. Biol. Conserv. 121, 579–584.

Dallimer, M., Marini, L., Skinner, A., Hanley, N., Armsworth, P., Gaston, K., 2010. Agricultural land-use in the surrounding landscape affects moorland bird diversity. Agric. Ecosyst. Environ. 139, 578–583.

Davis, J., Debinski, D., Danielson, B., 2007. Local and landscape effects on the butterfly community in fragmented Midwest USA prairie habitats. Landscape Ecol. 22, 1341–1354.

Debinski, D., Ray, C., Saveraid, E., 2001. Species diversity and the scale of the landscape mosaic: do scales of movement and patch size affect diversity? Biol. Conserv. 98, 179–190.

Delattre, T., Vernon, P., Burel, F., 2011. An agri-environmental scheme enhances butterfly dispersal in European agricultural landscapes. Agric. Ecosyst. Environ., http://dx.doi.org/10.1016/j.agee.2011.06.018.

Dennis, R., 2010. A Resource-based Habitat View for Conservation: Butterflies in the British landscape. Wiley-Blackwell, United Kingdom.

Dennis, R., Shreeve, T., Van Dyck, H., 2003. Towards a functional resource-based concept for habitat: a butterfly biology viewpoint. Oikos 102, 417–426.

Dennis, R., Shreeve, T., Van Dyck, H., 2006. Habitats and resources: the need for a resource-based definition to conserve butterflies. Biodivers. Conserv. 15, 1943–1966.

Devictor, V., Jiguet, F., 2007. Community richness and stability in agricultural landscapes: the importance of surrounding habitats. Agric. Ecosyst. Environ. 120, 179–184.

Dormann, C., Schweiger, O., Augenstein, I., Bailey, D., Billeter, R., de Blust, G., DeFilippi, R., Frenzel, M., Hendrickx, F., Herzog, F., Klotz, S., Liira, J., Maelfait, J., Schmidt, T., Speelmans, M., van Wingerden, W., Zobel, M., 2007. Effects of landscape structure and land-use intensity on similarity of plant and animal communities. Glob. Ecol. Biogeogr. 16, 774–787.

Dover, J., 1990. Butterflies and wildlife corridors. In: Annual Review of the Game Conservancy for 1989, vol. 21, pp. 62–64.

Dover, J., 1996. Factors affecting the distribution of satyrid butterflies on arable farmland. J. Appl. Ecol. 33, 723–734.

Dover, J., Rescia, A., Fungarino, S., Fairburn, J., Carey, P., Lunt, R., Dover, C., 2010. Can hay harvesting detrimentally affect adult butterfly abundance? J. Insect Conserv. 14, 413–418.

Dover, J., Settele, J., 2009. The influences of landscape structure on butterfly distribution and movement: a review. J. Insect Conserv. 13, 3–27.

Dover, J., Sparks, T., 2000. A review of the ecology of butterflies in British hedgerows. J. Environ. Manage. 60, 51–63.

Dover, J., Sparks, T., Clarke, S., Gobbett, K., Glossop, S., 2000. Linear features and butterflies: the importance of green lanes. Agric. Ecosyst. Environ. 80, 227–242.

Dowdeswell, W., Fisher, R., Ford, E., 1940. The quantitative study of populations in the Lepidoptera. I. *Polygommatus icarus* Rott. Ann. Hum. Genet. 10, 123–136.

Dunning, J., Danielson, B., Pulliam, H., 1992. Ecological processes that affect populations in complex landscapes. Oikos 65, 169–175.

Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. Annu. Rev. Ecol. Evol. Syst. 34, 487–515.

Fahrig, L., 2007. Non-optimal animal movement in human-altered landscapes. Funct. Ecol. 21, 1003–1015.

Fahrig, L., Nuttle, W., 2005. Population Ecology in Spatially Heterogeneous Environments. Issues and Perspectives in Landscape Ecology. Springer-Verlag, New York, pp. 95–118.

Fahrig, L., Baudry, J., Brotons, L., Burel, F., Crist, T., Fuller, R., Sirami, C., Siriwardena, G., Martin, J., 2011. Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. Ecol. Lett. 14, 101–112.

Fry, G., Main, A., 1993. Restoring seemingly natural communities on agricultural land. In: Saunders, D., Hobbs, R., Ehrlich, P. (Eds.), Nature Conservation. Surrey Beatty and Sons, Australia, pp. 225–241.

Gaba, S., Chauvel, B., Dessaint, F., Bretagnolle, V., Petit, S., 2010. Weed species richness in winter wheat increases with landscape heterogeneity. Agric. Ecosyst. Environ. 138, 318–323.

Goodwin, B., Fahrig, L., 2002. How does landscape structure influence landscape connectivity? Oikos 99, 552–570.

Heal, H., 1965. The wood white, *Leptidea sinapis* L., and the railways. Irish Naturalists' J. 15, 8–13.

Hendrickx, F., Maelfait, J., van Wingerden, W., Schweiger, O., Speelmans, M., Aviron, S., Augenstein, I., Billeter, R., Bailey, D., Bukacek, R., Burel, F., Diekotter, T., Dirksen, J., Herzog, F., Liira, J., Roubalova, M., Vandomme, V., Bugter, R., 2007. How landscape structure, land-use intensity and habitat diversity affect components of total arthrod diversity in agricultural landscapes. J. Appl. Ecol. 44, 340–351.

Holzschuh, A., Steffan-Dewenter, I., Kleijn, D., Tscharntke, T., 2007. Diversity of flower-visiting bees in vereal fields: effects of farming system landscape composition and regional context. J. Appl. Ecol. 44, 41–49.

Holzschuh, A., Steffan-Dewenter, I., Tscharntke, T., 2010. How do landscape composition and configuration, organic farming and fallow strips affect the diversity of bees, wasps and their parasitoids? J. Anim. Ecol. 79, 491–500.

Krauss, J., Steffan-Dewenter, I., Tscharntke, T., 2003. How does landscape context contribute to effects of habitat fragmentation on diversity and population density in butterflies? J. Biogeogr. 30, 889–900.

Marini, L., Fontana, P., Battisti, A., Gaston, K., 2009. Agricultural management, vegetation traits and landscape drive orthopteran and butterfly diversity in a grassland-forest mosaic: a multi-scale approach. Insect Conserv. Divers. 2, 213–220.

McKenna, D., McKenna, K., Malcom, S., Berenbaum, M., 2001. Mortality of Lepidoptera along roadways in central Illinois. J. Lepidopterists' Soc. 55, 63–68.

McLaughlin, A., Mineau, P., 1995. The impact of agricultural practices on biodiversity. Agric. Ecosyst. Environ. 55, 201–212.

Munguira, M., Thomas, J., 1992. Use of road verges by butterfly and burnet populations, and the effect of roads on adult dispersal and mortality. J. Appl. Ecol. 29, 316–329.

Newcomb, L., 1977. Newcomb's Wildflower Guide. Little Brown and Company.

Noordijk, J., Delille, K., Schsffers, A., Sykora, K., 2009. Optimizing grassland management for flower-visiting insects in roadside verges. Biol. Conserv. 142, 2097–2103.

Ockinger, E., Smith, H., 2006. Landscape composition and habitat area effects butterfly species richness in semi-natural grasslands. Oecologia 149, 526–534.

Ohl, C., Drechsler, M., Johst, K., Watzold, F., 2008. Compensation payments for habitat heterogeneity: existence, efficiency, and fairness considerations. Ecol. Econ. 67, 162–174.

Ouin, A., Aviron, S., Dover, J., Burel, F., 2004. Complementation/supplementation of resources for butterflies in agricultural landscapes. Agric. Ecosyst. Environ. 103, 473–479.

Ouin, A., Burel, F., 2002. Influence of herbaceous elements on butterfly diversity in hedgerow agricultural landscapes. Agric. Ecosyst. Environ. 93, 45–53.

Pasher, J., Mitchell, S.W., King, D.J., Fahrig, L., Smith, A.C., Lindsay, K.E. Optimizing landscape selection design to avoid common statistical pitfalls. Landscape Ecol., submitted for publication.

Persson, A., Olsson, O., Rundlof, M., Smith, H., 2010. Land use intensity and landscape complexity – analysis of landscape characteristics in an agricultural region in Southern Sweden. Agric. Ecosyst. Environ. 136, 169–176.

Pope, S., Fahrig, L., Merriam, G., 2000. Landscape complementation and metapopulation effects on leopard frog populations. Ecology 81 (9), 2498–2508.

Ricketts, T., 2001. The matrix matters: effective isolation in fragmented landscapes. Am. Naturalist 158 (1), 87–99.

Ries, L., Sisk, T., 2008. Butterfly edge effects are predicted by a simple model in a complex landscape. Oecologia 156, 75–86.

Rossi, J., Van Halder, I., 2010. Towards indicators of butterfly biodiversity based on a multiscale landscape description. Ecol. Indicat. 10, 452–458.

Rundlof, M., Bengtsson, J., Smith, H., 2008. Local and landscape effects of organic farming on butterfly species richness and abundance. J. Appl. Ecol. 45, 813–820.

Rundlof, M., Smith, H., 2006. The effect of organic farming on butterfly diversity depends on landscape context. J. Appl. Ecol. 43, 1121–1127.

Saarinen, K., Valtonen, A., Jantunen, J., Saarnio, S., 2005. Butterflies and diurnal moths along road verges: does road type affect diversity and abundance? Biol. Conserv. 123, 403–412.

Schneider, C., Dover, J., Fry, G., 2003. Movement of two grassland butterflies in the same habitat network: the role of adult resources and size of the study area. Ecol. Entomol. 28, 219–227.

Schtickzelle, N., Mennenchez, G., Baguette, M., 2006. Dispersal depression with habitat fragmentation in the bog fritillary butterfly. Ecology 87, 1057–1065.

Steffan-Dewenter, I., Tscharntke, T., 2000. Butterfly community structure in fragmented habitats. Ecol. Lett. 3, 449–456.

Teyssedre, A., Couvet, D., 2007. Expected impact of agricultural expansion on the world avifauna. C.R. Biol. 330, 247–254.

Thomas, J., Bourn, N., Clarke, R., Stewart, K., Simcox, D., Pearman, G., Curtis, R., Goodger, B., 2001. The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. Proc. R. Soc. B 268, 1791–1796.

Thomas, J., Snazell, R., Ward, L., 2002. Are roads harmful or potentially beneficial to butterflies and other insects? In: Sherwood, B., Cutler, D., Burton, J. (Eds.), Wildlife and Roads: the Ecological Impact. Imperial College Press, London, pp. 203–222.

Tscharntke, T., Steffan-Dewenter, I., Kruess, A., Thies, C., 2002. Characteristics of insect populations on habitat fragments: a mini review. Ecol. Res. 17, 229–239.

Weibull, A., Ostman, O., Granqvist, A., 2003. Species richness in agroecosystems: the effect of landscape, habitat and farm management. Biodivers. Conserv. 12, 1335–1355.

Woodcock, B., Redhead, J., Vanbergen, A., Hulmes, L., Hulmes, S., Peyton, J., Nowakowski, M., Pywell, R., Heard, M., 2010. Impact of habitat type and landscape structure on biomass, species richness and functional diversity of ground beetles. Agric. Ecosyst. Environ. 139, 181–186.