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Homogenization of lepidopteran communities in intensively cultivated agricultural landscapes

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Summary

1. Landscape simplification and habitat fragmentation may cause severe declines of less mobile and habitat specialist species and lead to biotic homogenization of species communities, but large-scale empirical evidence on biotic homogenization remains sparse.

2. We sampled butterfly and day-active geometrid moth communities within 134 differently fragmented landscapes in Finland situated in five geographical regions. Overall species richness was partitioned into alpha and beta diversity and butterflies were assigned a species-specific mobility rank and habitat specificity score based on published ecological trait classifications.

3. Alpha and beta diversity of butterflies and geometrid moths decreased with increasing agricultural intensity, independently of geographical position. The responses were either linear or nonlinear with accelerating decrease of diversity when arable field cover exceeded 60%.

4. Mobility rank and percentage generalists of butterfly communities increased linearly with increasing field cover.

5. In landscapes with high agricultural intensity (> 60% field coverage), the decrease in beta diversity of butterflies was strongly associated with an increasing proportion of habitat generalists and increasing average mobility in the butterfly communities. However, there was no such relationship in landscapes with low or moderate agricultural intensity.

6. *Synthesis and applications.* We demonstrate that biotic homogenization caused by land-use change arises as a consequence of the loss of habitat specialists and poor dispersers in intensively cultivated landscapes with simplified landscape structure. Agri-environment schemes will therefore be inefficient in protecting high beta diversity unless they explicitly increase habitat availability and connectivity for habitat specialists and poor dispersers.

Key-words: agricultural intensity, agri-environment schemes, alpha and beta diversity, biodiversity loss threshold, butterflies, community similarity, day-active moths, habitat generalist, habitat specialist, mobility

Introduction

Intensification of agriculture is one of the main drivers of biodiversity declines worldwide (Tilman *et al.* 2002; Benton, Vickery & Wilson 2003; Tscharntke *et al.* 2007). An important way in which biodiversity is lost is through biotic homogenization, which refers to the dominance of generalist species resulting from local extinctions of species susceptible to external perturbations (McKinney & Lockwood 1999; Olden *et al.* 2004; Dormann *et al.* 2007). Generalists are able to utilize a wide spectrum of vegetation types whereas sensitive species tend to be habitat specialists, with strict demands on habitat quality and landscape properties (Hanski 1999; McKinney & Lockwood 1999; Olden *et al.* 2004). Simplified landscapes created by intensive land-use can be particularly detrimental to habitat specialists and species with poor dispersal abilities (Hanski 1999; Steffan-Dewenter & Tscharntke 2002). Intensified agriculture can therefore lead to biotic homogenization through loss of habitat specialists and poor dispersers, either as a response to increased use of fertilizers and pesticides, or by increased cover of arable land (Dormann *et al.* 2007; Kleijn *et al.* 2008). Thus, when increasing land-use intensity results in homogeneous landscapes, it can be assumed to select for high species mobility and low habitat specificity with a subsequent decrease in beta diversity (Dormann *et al.* 2007). Therefore, one would expect to find more species with poor dispersal

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abilities and a lower fraction of habitat generalists in communities characterized by high beta diversity.

Recent studies on farmland biodiversity have addressed the effects of habitat connectivity, landscape heterogeneity and farming systems on species richness, functional diversity and community similarity (Schweiger *et al.* 2005; Clough *et al.* 2007; Diekötter, Billeter & Crist 2008; Flynn *et al.* 2009). The occurrence and spatial arrangement of semi-natural habitats have been shown to play a key role in determining patterns of diversity in agricultural landscapes (Hendrickx *et al.* 2007; Öckinger & Smith 2007; Diekötter *et al.* 2008; Holzschuh, Steffan-Dewenter & Tscharntke 2009). However, in contrast to the predictions outlined above, an association between increasing landscape homogeneity and decreased numbers of habitat specialists and poor dispersers in natural communities has hitherto not been demonstrated.

We present empirical evidence on biotic homogenization of butterfly communities through the loss of habitat specialists (i.e. species preferring a given vegetation type) and poor dispersers associated with simplified landscape structure in intensively cultivated agricultural landscapes. We first compare the responses of butterfly and day-active geometrid moth alpha and beta diversity to increased agricultural intensity, measured as the percentage cover of arable fields. We expect both alpha and beta diversity to decrease with increasing cover of arable fields. We then relate mean species' mobility and percentage of generalists in butterfly communities with arable field cover percentage, expecting an increasing proportion of habitat generalists and higher average mobility with increasing agricultural intensity. Finally, we compare geographical regions with contrasting average agricultural intensity and expect to find the strongest relationship between butterfly diversity partitions and the proportion of habitat generalists and average mobility in the regions with high agricultural intensity.

Materials and methods

STUDY AREA AND DESIGN

Data were collected from 134 agricultural landscapes of 0·25 km^2 placed in a pair-wise fashion in five geographical regions in Finland (59°57′–63°42′N; 19°41′–30°53′E; see Kuussaari *et al.* 2007b for a map of the study landscapes): the main Åland island ('Al', $n = 20$), southern Finland ('S', $n = 30$), south-western Finland ('SW', $n = 34$), eastern Finland ('E', $n = 20$) and western Finland ('W', $n = 30$). Regions Al, SW and S are situated in the hemiboreal and southern boreal zones, and W and E in the middle boreal zone. Although Åland is not a part of mainland Finland, it is a sufficiently large island (970 km^2) to be compared with continental areas.

The extent of arable land in the studied landscapes differed markedly between the five geographic regions (regional average ranging from 39·1% to 62·8%) and varied between landscapes covered mainly by forests to landscapes dominated by agriculture. The most intensively cultivated regions (S and SW; referred to as regions with 'high agricultural intensity') were located in the south, whereas the less intensively cultivated regions (referred to as regions with 'moderate-low agricultural intensity') were located both in the south (Al) and in the north (E, W). Climatic and edaphic factors in the southern regions S and SW were most suitable for agriculture and hence study sites in these regions had the highest percentage of cultivated fields. In Al, landscapes consisted of a highly heterogeneous mosaic of forests, rocky outcrops and arable land, with a relatively high percentage of open semi-natural habitats, such as meadows and pastures. The northern regions, W and E, were mainly dominated by forests and mires with agricultural land concentrated in the most productive areas along water bodies. The 134 studied landscapes formed a representative cross-section of agricultural landscape types occurring in Finland. The mean, minimum and maximum percentages of cultivated fields in them were 53%, 0·1% and 92%, respectively.

Study landscapes were selected using a stratified random sampling protocol based on 67 1 km^2 grid cells from the five study regions (Table 1, see Kuussaari, Heliölä & Luoto 2004 for details). Each 1 km^2 grid cell was subdivided into four 0·25 km^2 squares. Among these four squares, the ones with the highest and lowest landscape

Table 1. Study site landscape characteristics, diversity partitions of butterflies and geometrid moths and mean mobility rank and generalist percentage of local butterfly communities separately for five geographical regions. Numbers refer to regional averages and standard deviations

	South-western Finland ($n = 34$)	Southern Finland ($n = 30$)	Western Finland ($n = 30$)	Eastern Finland ($n = 20$)	Åland ($n = 20$)
Study site landscape characteristics					
Field cover (%)	62·9 ± 20·9	62·8 ± 23·1	49·0 ± 21·9	41·1 ± 16·0	39·0 ± 18·3
Open semi-nat· (%)	2·4 ± 4·1	2·8 ± 5·7	0·6 ± 1·3	0·8 ± 1·8	10·4 ± 5·5
Forest cover (%)	24·8 ± 22·2	22·0 ± 20·4	34·5 ± 19·3	44·9 ± 16·7	38·7 ± 19·0
Shannon-Wiener diversity index[1]	0·9 ± 0·2	0·9 ± 0·3	1·1 ± 0·2	1·2 ± 0·2	1·3 ± 0·2
Butterfly diversity					
Alpha	5·4 ± 0·9	7·3 ± 1·5	3·9 ± 1·6	4·3 ± 1·7	7·5 ± 1·8
Beta	10·6 ± 2·8	12·5 ± 3·3	8·2 ± 3·1	13·1 ± 3·4	16·4 ± 3·2
Generalists (%)	63·8 ± 10·4	59·9 ± 9·6	59·5 ± 13·2	54·0 ± 8·9	54·6 ± 7·5
Mobility rank	6·9 ± 0·3	6·9 ± 0·2	6·8 ± 0·2	6·2 ± 0·2	6·7 ± 0·2
Geometrid diversity					
Alpha	3·6 ± 1·1	3·3 ± 0·3	2·6 ± 1·7	2·9 ± 0·6	2·8 ± 0·7
Beta	8·6 ± 2·1	7·8 ± 2·0	6·0 ± 2·2	6·0 ± 1·4	8·1 ± 1·4

[1] $-\Sigma_i (P_i \times \ln P_i)$.

heterogeneity were picked out as study landscapes. We therefore had 134 separate study landscapes, with two adjacent landscapes placed pair-wise within the 1 km^2 squares exhibiting different structural diversity. In each 0·25 km^2 study landscape we placed ten 50 m long transects, where lepidopteran diversity was sampled (see Kuussaari *et al.* 2007b for an illustration of a sampled landscape). All transects were placed in non-crop habitats representing one of three distinct habitat types: field boundaries situated between two adjacent fields, forest verges situated between a field and a forest area, and patches of semi-natural grasslands. These semi-natural grasslands were usually small patches (min = 0·01, max = 11·7 and average = 0·8 ha) of non-cropped habitats, and situated either between fields or fields and forests. Within each landscape, transects were placed in one of the three habitat types approximately according to the proportions in which these were available.

Butterflies (Lepidoptera, Papilionoidea and Hesperioidea) and day-active geometrid moths (Lepidoptera, Geometroidea) were censused along transect lines applying the method described by Pollard (1977). Censuses were carried out only when weather conditions allowed butterfly activity (see Kuussaari *et al.* 2007b). If necessary, lepidopterans were caught with a net and caught individuals were released immediately after identification. The field work was done during 2001 in continental Finland (regions S, SW, W and E) and during 2002 in the main island of Åland. Transect counts were repeated seven times per season during May–August, with *c.* 2 week intervals. In areas where sampling was conducted during both 2001 and 2002 (20 study landscapes in S), no between-year differences in species richness were found and hence study year was not considered an important variable in this study (Kivinen *et al.* 2006).

LANDSCAPE VARIABLES

As a surrogate measure for agricultural land-use intensity, we calculated the percentage of arable fields (consisting of cereal and fodder fields) in the 0·25 km^2 study landscapes, derived from aerial photographs as described by Kivinen *et al.* (2006). Arable field cover correlated negatively with the amount of open semi-natural habitats in the landscapes ($r = -0{\cdot}21$, $P = 0{\cdot}013$) as well as with landscape diversity (Shannon diversity; $r = -0{\cdot}66$, $P < 0{\cdot}0001$) and can be viewed as the major component in shaping landscape structure in agricultural landscapes. The percentage of arable field cover in the study landscapes also correlated with field cover within a 2-km buffer surrounding the study landscapes ($r = 0{\cdot}49$, $P < 0{\cdot}0001$) and thus serves as a rough estimate of land-use also in the wider surroundings.

DIVERSITY PARTITIONING

Overall species diversity was partitioned into alpha and beta components by applying the additive partitioning approach $\alpha + \beta = \gamma$ (Allan 1975; Wagner, Wildi & Ewald 2000; Veech *et al.* 2002) for each study landscape separately. Gamma diversity was defined as the total number of species observed within a study landscape. For each study landscape, alpha diversity was defined as the mean species richness observed in the ten transects. Beta diversity was then calculated by subtracting alpha diversity from gamma diversity ($\beta = \gamma - \alpha$).

DETERMINATION OF ECOLOGICAL TRAITS

We classified butterfly habitat specificity and mobility according to species-specific habitat breadth and mobility rank provided by Komonen *et al.* (2004), which were based on a literature review and an expert survey, respectively. Our measurement of habitat specificity categorized species according to their ability to utilize different habitats. The variable consisted of four categories, ranging from one (the species uses only one of four major habitat types) to four (the species uses all four major habitat types). The four major habitat types were open habitats heavily exposed to anthropogenic influence, semi-natural grasslands, forest edges and bogs (see Komonen *et al.* 2004). We then quantified the degree of habitat specificity of butterfly communities within the study landscapes as the percentage of habitat generalists by dividing the number of generalist species (habitat breadth classes three or four) by the total number of species observed in the study landscape and multiplying the outcome with 100. Mobility rank values were assigned for each species. These varied between 1·7 (the most sedentary) and 8·8 (the most mobile species in our data set) and followed a normal distribution. This allowed us to quantify the mean mobility of a butterfly community within a study landscape by calculating the arithmetic mean of the species-specific mobility ranks over all observed species in each study landscape.

STATISTICAL METHODS

We analysed how arable field cover percentage, our measure for agricultural land-use intensity, affected diversity partitions of butterflies and geometrid moths, as well as mean mobility and generalist percentage of butterflies, by using general linear mixed models (GLMM). Due to the pair-wise design of our study, we included the variable 'landscape pair' (i.e. a pair of the neighbouring homogeneous and heterogeneous study landscapes) in all models as a random term. In addition to percentage arable field cover, we adjusted all GLMM models for the geographical position of the study landscapes by including x- and y-coordinates, their first order polynomials and interactions (x, y, x^2, y^2, xy) as explanatory variables (Legendre & Legendre 1998). Using this modelling framework, we first analysed the effects of arable field cover percentage separately on alpha and beta diversity of both butterflies and geometrid moths. We thereafter related mean mobility rank and percentage of generalists in the butterfly communities to the cover of cultivated fields in the study landscapes. We analysed the effect of arable field cover percentage by including the quadratic term in the models to detect any nonlinear responses, but removed the term if it was not statistically significant.

In addition to the above described GLMM analyses of the whole data set, we conducted separate analyses to further evaluate the relationships between ecological traits, species diversity and landscape structure. We analysed whether mobility rank and percentage of generalists explained variation in alpha and beta diversity of butterflies differently depending on regional agricultural intensity, by conducting a separate analysis for the regions with high and moderate-low agricultural intensity. We used the same modelling framework as outlined above. Analyses were performed in SAS 9·1 (SAS Institute Inc 2004).

Results

The butterfly data consisted of 21 695 individuals belonging to 60 species, whereas we recorded 10 858 diurnal geometrid moths representing 39 species. A summary of the average observed alpha and beta diversity of butterflies and moths, as well as the average mobility rank and generalist percentage of the studied butterfly communities are shown in Table 1 for each study region separately. Beta diversity contributed to the largest fraction of gamma diversity, being 67% for butterflies and 73% for geometrid moths.

EFFECT OF AGRICULTURAL INTENSITY ON DIVERSITY PARTITIONS

Alpha diversity of geometrid moths showed a significant nonlinear negative response to increasing arable field cover (Table 2, Fig. 1a), whereas beta diversity of geometrid moths decreased linearly with increasing arable field cover (Table 2, Fig. 1b). Alpha diversity of butterflies tended to decrease nonlinearly with increasing arable field cover in the study landscape (Table 2, Fig. 1c). Beta diversity of butterflies showed a highly significant nonlinear decrease with increasing arable field cover, which became stronger when arable field cover in the study landscape exceeded 60% (Table 2, Fig. 1d). Similarly, alpha diversity of both butterflies and geometrids started to decrease after a threshold value of *c.* 60% cover of arable field (Fig. 1a and c), although for butterflies this relationship was not as strong as in beta diversity (Table 2).

Geographical position explained more variation than agricultural intensity in both alpha and beta diversity and was particularly strong in determining butterfly alpha diversity (Table 2). Species richness of butterflies decreased strongly with increasing latitude, but geographic location was not as important in determining geometrid moth diversity. For geometrid moth alpha diversity, longitudinal location was more important than the latitude of the study landscape (Table 2).

RELATIONSHIP BETWEEN ECOLOGICAL TRAITS AND DIVERSITY PARTITIONS

Geographical position did not determine percentage of generalists or mean mobility rank in butterfly communities. Instead these traits showed a strong positive linear response to increasing percentage of arable fields in the study landscapes (Table 3, Fig. 1e and f). In the regions with high agricultural intensity, butterfly alpha and beta diversity were negatively affected by percentage of generalists and mean mobility rank of butterfly communities (Table 4, Fig. 2a–d). In contrast, in the regions with moderate-low agricultural intensity, only alpha diversity of butterflies showed a near significant decrease with an increasing percentage of generalists, whereas mobility rank was not related to either alpha or beta diversity (Table 4, Fig. 2a–d). The difference in these patterns between the geographic areas of high and moderate-low agricultural intensity was particularly pronounced in the relationship between beta diversity and the species traits (Fig. 2c and d). Mobility rank and generalist percentage correlated significantly with each other (r = 0·69, P < 0·0001).

Discussion

BIOTIC HOMOGENIZATION IN AGROECOSYSTEMS

In this paper, we have presented empirical evidence for two negative consequences of simplified landscape structure. First, alpha and beta diversity of butterflies and day-active geometrid moths decreased with increasing cover of arable fields in the studied 134 agricultural landscapes. These decreases accelerated when arable field cover exceeded 60% of the landscape, suggesting a threshold value above which agricultural intensification has increasingly negative effects on butterfly diversity. Secondly, the percentage of generalist species and average mobility of butterfly communities increased with increasing arable field cover. Our results indicate that butterfly alpha and beta diversity decrease as poor dispersers and habitat specialists disappear from local communities in landscapes with high arable field cover. The observed responses of butterfly communities to changes in landscape structure are in a good agreement with the prediction that increasing land-use intensity should lead to more homogeneous communities (Dormann *et al.* 2007).

We found a strong negative relationship between alpha and beta diversity and the percentage of generalist species and

Table 2. Responses in alpha and beta diversity of butterflies and diurnal geometrid moths in the 134 study landscapes to geographic position (x- and y-coordinates) and percentage arable field cover analysed with generalized linear mixed models (Num d.f. = 7, Den d.f. = 60, except for beta diversity of geometrid moths, where Num d.f. = 6, Den d.f. = 61)

	Alpha diversity			Beta diversity		
	Estimate	*F*	*P*	Estimate	*F*	*P*
Butterflies						
Intercept	3·85			6·49		
x	0·08	0·19	0·661	−0·01	0·00	0·984
y	−1·89	65·21	< 0·001	−2·45	30·29	< 0·001
x^2	0·38	3·35	0·072	1·41	11·98	0·001
y^2	0·58	6·51	0·013	0·39	0·82	0·369
$x \times y$	−0·64	5·03	0·029	−0·24	0·18	0·671
Arable field (%)	4·35	2·53	0·117	14·24	6·64	0·012
Arable field (%)^2	−3·34	3·96	0·051	−11·06	10·53	0·002
Geometrid moths						
Intercept	4·00			7·82		
x	0·30	4·75	0·033	0·25	1·22	0·273
y	−0·07	0·16	0·693	−0·95	9·76	0·003
x^2	−0·52	11·60	0·001	−0·53	3·74	0·058
y^2	−0·49	7·92	0·007	−0·20	0·46	0·502
$x \times y$	0·57	7·68	0·007	0·56	2·22	0·141
Arable field (%)	−0·28	10·90	0·002	−0·44	5·87	0·018
Arable field (%)^2	−0·16	6·07	0·017			

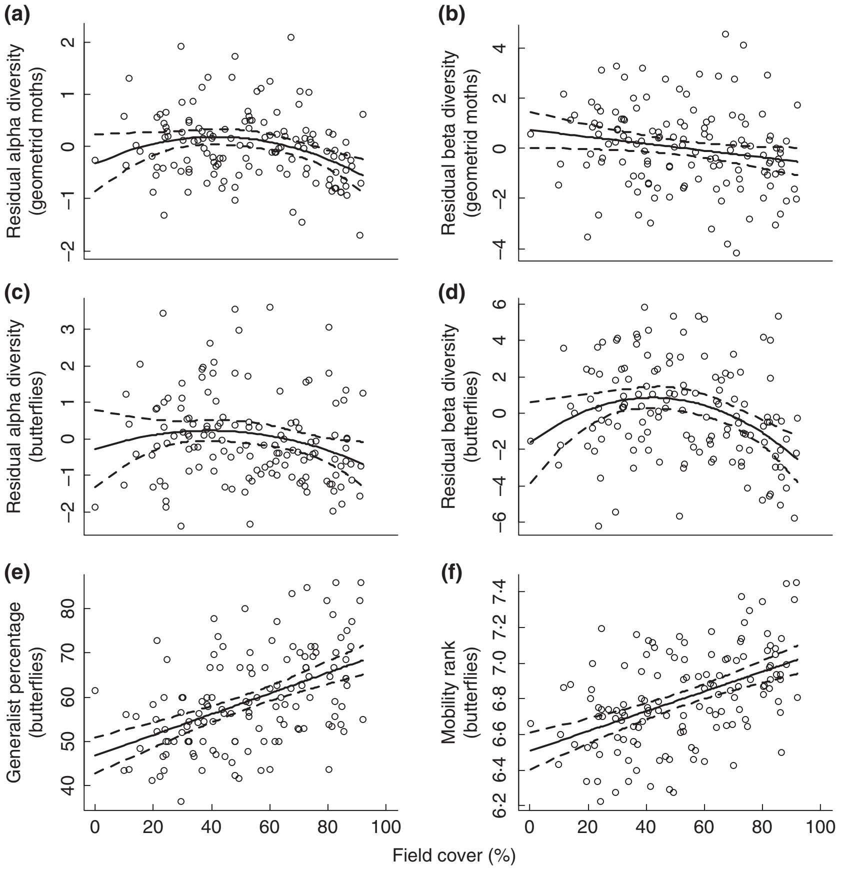

Fig. 1. Alpha and beta diversity (corrected for the effect of geographical position, see Table 2) of geometrid moths (a and b) and butterflies (c and d) as well as percentage generalists (e) and mean mobility rank (f) of butterfly communities in the 134 study landscapes, plotted against arable field cover. Dashed lines represent the 95% confidence intervals for the fitted regression lines.

Table 3. Responses in the percentage of generalists and mean mobility rank of butterfly communities in the 134 study landscapes to geographic variables and percentage arable field cover, analysed with generalized linear mixed models (Num d.f. = 6, Den d.f. = 61). Variables *x* and *y* are spatial coordinates defining the geographic locations of the study landscapes

	Generalists (%)			Mean mobility		
	Estimate	*F*	*P*	Estimate	*F*	*P*
Intercept	−1·55			1·21		
x	−0·10	0·73	0·395	−0·05	0·17	0·686
y	0·04	0·07	0·794	−0·10	0·42	0·519
x^2	0·07	0·27	0·606	−0·05	0·11	0·741
y^2	−0·00	0·00	0·977	−0·04	0·08	0·781
$x \times y$	−0·18	1·03	0·314	−0·04	0·05	0·833
Arable field (%)	1·84	30·36	< 0·001	1·87	28·01	< 0·001

Table 4. Effects of generalist percentage and mean mobility rank (corrected for geographical position, results not shown) on alpha and beta diversity in butterfly communities in the 134 study landscapes derived with general linear mixed models. Geographical regions with high and moderate-low agricultural intensity (see main text for a definition) were treated separately

		Estimate	*F*	*P*
High agricultural intensity (SW & S, *n* = 64)				
Alpha	Generalists (%)	−0·73	21·25	< 0·0001
	Mobility rank	−0·45	10·28	0·0031
Beta	Generalists (%)	−2·04	32·37	< 0·0001
	Mobility rank	−0·92	6·84	0·0137
Moderate-low agricultural intensity (Al, E & W, *n* = 70)				
Alpha	Generalists (%)	−0·38	4·13	0·051
	Mobility rank	0·002	0·00	0·99
Beta	Generalists (%)	−0·31	0·67	0·42
	Mobility rank	−0·004	0·00	0·99

mean mobility rank of butterfly communities in the regions with high agricultural intensity, where agricultural land-use predominates. However, in the regions with moderate-low agricultural intensity, no similar relationship was found. This comparison between geographic regions gives further evidence of decreasing species diversity after a threshold of *c.* 60% landscape-level field cover has been exceeded. In Finland, simplified landscape structure has led to impoverishment and homogenization of butterfly communities in the regions with high agricultural intensity, but no such homogenization has taken place in the regions with moderate-low agricultural intensity, where landscape structure is generally more heterogeneous. Our results thus provide empirical evidence for biotic homogenization driven by anthropogenic land-use changes.

Several mechanisms can lead to species loss following intensified agricultural land-use and resulting simplified landscape structure. First, agricultural land-use intensification typically leads to loss of all kinds of semi-natural landscape elements, and especially loss of species-rich, high-quality semi-natural habitats traditionally maintained by low-input agriculture

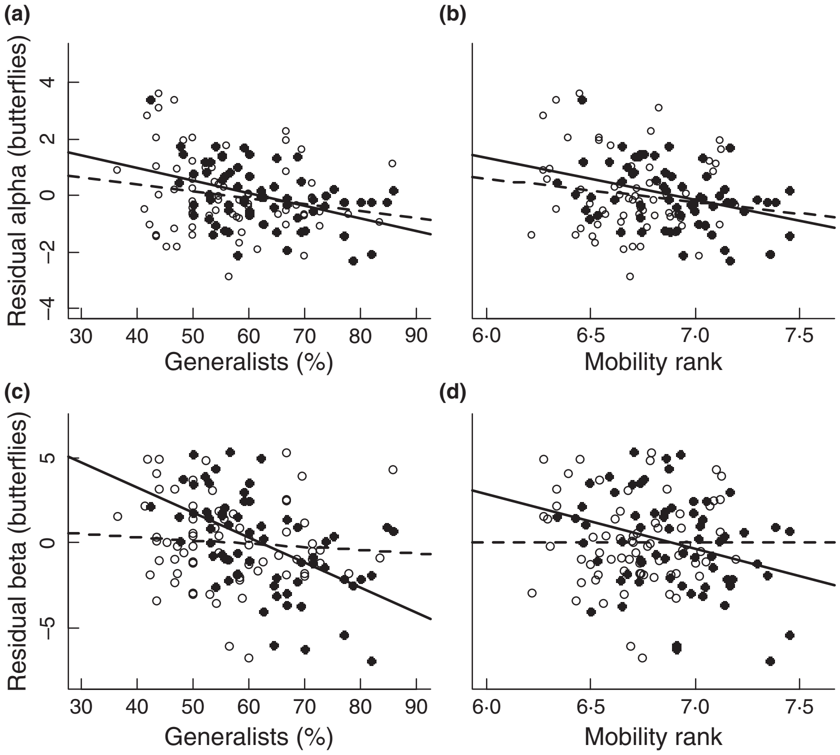

Fig. 2. Relationship between alpha and beta diversity (corrected for the effect of geographical position) and the average mobility rank and generalist percentage of butterfly communities. Solid lines and filled symbols represent regions with high agricultural intensity, whereas dashed lines and open symbols represent regions with moderate-low agricultural intensity. Upper panels show alpha diversity against generalist percentage (a) and average mobility rank (b). Lower panels depict beta diversity against generalist percentage (c) and average mobility rank (d).

(WallisDeVries, Poschlod & Willems 2002; Benton *et al.* 2003) which in turn affects primarily habitat specialists (Steffan-Dewenter & Tscharntke 2002). In this study, 10 out of 21 strict habitat specialists were associated to semi-natural grasslands, and nine to forest verges and clearings (Kuussaari *et al.* 2007a). Secondly, habitat specialists often have rather small local population sizes making them particularly prone to local extinctions due to habitat loss (e.g. Hanski *et al.* 1995). Thirdly, intensifying land-use results in decreasing connectivity of semi-natural habitats, which in turn weakens the rescue effect provided by immigrants from surrounding populations in habitat patches with small populations close to local extinction (Brown & Kodric-Brown 1977; Steffan-Dewenter & Tscharntke 2002). Loss of habitat specialists and poor dispersers may not affect alpha diversity as dramatically as it affects beta diversity, since alpha diversity measures only the number of species observed in a given locality and often largely consists of common generalist species. Beta diversity measures diversity responses at a landscape scale and is more affected by rare species than alpha diversity. Our results suggest that the decrease in beta diversity reflects the loss of specialists and poor dispersers, which in turn disappear due to landscape simplification.

Most previous studies on biotic homogenization have studied either community similarity or percentage native⁄endemic species in relation to either exotic or cosmopolitan species (Olden & Rooney 2006). Dormann *et al.* (2007) showed conceptually how increasing land-use intensity could result in biotic homogenization by affecting mobility and habitat specificity of species assemblages. They also found indications of dispersal limitation in field data of different taxa. We found not only that mobility and generalist percentage of butterfly communities were related particularly to beta diversity, but also that generalist percentage and mobility rank of butterfly communities were positively correlated (see also Komonen *et al.* 2004). This means that specialist species are facing a higher probability of local extinction due to both strict habitat requirements and poor dispersal ability. The same species that are poor in colonizing empty habitat patches also have less suitable habitat available in intensively cultivated landscapes than species with less specialized habitat requirements, and this double effect makes them even more likely to disappear due to landscape simplification. However, species with intermediate dispersal abilities have been found to be those that have declined most (Thomas 2000), highlighting the fact that a relationship between mobility, degree of habitat specificity and local extinction is likely to be conditional on the degree of landscape simplification, habitat fragmentation and spatial scale.

TAXONOMIC DIFFERENCES IN BIOTIC HOMOGENIZATION

Butterfly beta diversity showed a strong negative relationship with increasing arable field cover whereas the relationship between alpha diversity and increasing arable field cover was only marginally significant. By contrast, increasing arable field cover affected both beta and alpha diversity of geometrid moths significantly and this relationship was particularly strong in the case of alpha diversity. These results suggest that, overall, geometrid moths are more sensitive to simplified landscape structure than butterflies. This might be a consequence of geometrid moths exhibiting a lower average mobility than butterflies, which is suggested by the generally more robust wing and thorax morphology of butterflies than geometrids, but which, however, is an empirically poorly documented issue (but see Nieminen 1996; Nieminen, Rita & Uuvana 1999). Although alpha and beta diversity of geometrid moths exhibited qualitatively similar responses as those of butterflies, we were unable to link these with changes to the degree of habitat specificity or mobility, as a rigorous classification of these traits was not available for geometrid moths.

Ecological trait classifications exist only for well-studied taxa, which limits the possibilities of studying biotic homogenization with the approach presented here. Trait classifications can also suffer from inherent errors as detailed data on species-specific traits are often scarce or even lacking for many little-studied taxa. In addition to developing new ecological trait classifications for a variety of organisms, studies are needed to address how temporal changes in beta diversity or community similarity and the distribution of ecological traits in different taxa are affected by changes in landscape structure (Olden & Rooney 2006).

Other aspects of agricultural land-use intensification, such as stress and disturbance generated by fertilizer or herbicide inputs, also probably affect the relationships between community similarity and mobility or habitat specificity (Dormann *et al*. 2007; Kleijn *et al*. 2008). The significance of different components of land-use intensity can vary between groups of organisms. For example, plant diversity has been shown to benefit from moderate to high grazing pressure by cattle (Bakker 1998; Pöyry *et al*. 2006), whereas it can be dramatically decreased by increasing fertilizer use and the consequently high amount of nutrients in the soil (Kleijn *et al*. 2008). By contrast, butterflies (Pöyry *et al*. 2006) and other arthropods (Morris 2000) tend to be negatively affected by moderate and high levels of cattle grazing and can show relatively high diversity on nutrient rich soils, with a species poor but structurally diverse vegetation (see also Marini *et al*. 2009). In fact, if the percentage of arable field cover is viewed as a disturbance regime, our results on alpha and beta diversity of butterflies seem to agree with the intermediate disturbance hypothesis (Connell 1978), according to which species richness at low (low percentage of arable field cover) and high disturbance regimes (high percentage of arable field cover) are expected to be lower as compared to intermediate disturbance regimes (*c*. 50–60% arable field cover in this study).

PREVENTING BIOTIC HOMOGENIZATION – FROM ECOLOGY TO CONSERVATION

Several countries in the European Union have established agri-environment schemes in which farmers are compensated for implementing agricultural practices that benefit farmland wildlife (Kleijn & Sutherland 2003). Tscharntke *et al*. (2005) suggested that agri-environment schemes will be most effective in simple landscapes, where 80–99% of land-use consists of cropped habitats. The effectiveness of agri-environment schemes will be poor in highly structured landscapes with < 80% cropped habitat in the landscape, because high overall diversity enables constant colonization of species. In cleared landscapes, with > 99% cropped habitat, schemes are also expected to be ineffective as the vast majority of species would be absent altogether due to habitat loss (Tscharntke *et al*. 2005).

Our results on the distribution of ecological traits suggest that agri-environment schemes implemented in extremely homogeneous landscapes will only benefit generalists and mobile species, unless the schemes are designed to explicitly create new well-connected, high-quality habitat patches which can be colonized by specialist and less mobile species. Measures currently included in most agri-environment schemes are implemented at too small a spatial scale for them to be effective (Whittingham 2007; Merckx *et al*. 2009a), not only for habitat specialists, but even for mobile habitat generalists (Merckx *et al*. 2009b). The importance of the quality of surrounding landscape structure has been well-documented in the case of biodiversity effects of organic farming (Bengtsson, Ahnström & Weibull 2005; Rundlöf & Smith 2006; Holzschuh *et al*. 2007). Considering the species richness of habitat specialists and poor dispersers in agricultural landscapes, organic farming as well as several other available management options of agri-environment schemes are probably most efficient in landscapes with intermediate landscape complexity, where at least some of these species are still expected to occur. Nevertheless, most habitat specialists and poor dispersers, such as many species associated to traditional semi-natural habitats in agricultural landscapes, are unlikely to benefit from present-day agri-environment schemes, because these are not aimed at increasing the availability of high-quality semi-natural habitats and their connectivity.

Conclusions

The traditional definition of biotic homogenization involves an anthropogenically induced colonization of non-native species, which is followed by local extinctions of native species (McKinney & Lockwood 1999). We demonstrate that anthropogenically induced changes in landscape structure can result in biotic homogenization by affecting mobility and habitat specificity, two crucially important ecological traits shaping the species composition in local communities. Land-use induced biotic homogenization is likely to have equally damaging effects on local biodiversity as the effect of introductions of non-native invasive species (Schwartz, Thorne & Viers 2006). Given the current rates of habitat loss and landscape simplification around the world, biotic homogenization caused by land use change is likely to be an important factor leading to biodiversity loss across various kinds of ecosystems worldwide.

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