Weak functional response to agricultural landscape homogenisation among plants, butterflies and birds

Dennis Jonason, Johan Ekroos, Erik Öckinger, Juha Helenius, Mikko Kuussaari, Juha Tiainen, Henrik G. Smith and Regina Lindborg

D. Jonason (dennis.jonason@natgeo.su.se) and R. Lindborg, Dept of Physical Geography, Stockholm Univ., Stockholm, Sweden. – J. Ekroos and H. G. Smith, Centre for Environmental and Climate Research, Lund Univ., Lund, Sweden. HGS also at: Dept of Biology, Lund Univ., Lund, Sweden. – E. Öckinger, Swedish Univ. of Agricultural Sciences, Dept of Ecology, Uppsala, Sweden. – J. Helenius, Dept of Agricultural Sciences, Univ. of Helsinki, Helsinki, Finland. – M. Kuussaari, Finnish Environment Inst., Natural Environment Centre, Helsinki, Finland. – J. Tiainen, Natural Resources Inst. Finland, Helsinki, Finland.

Measures of functional diversity are expected to predict community responses to land use and environmental change because, in contrast to taxonomic diversity, it is based on species traits rather than their identity. Here, we investigated the impact of landscape homogenisation on plants, butterflies and birds in terms of the proportion of arable field cover in southern Finland at local (0.25 km²) and regional (> 10 000 km²) scales using four functional diversity indices: functional richness, functional evenness, functional divergence and functional dispersion. No uniform response in functional diversity across taxa or scales was found. However, in all cases where we found a relationship between increasing arable field cover and any index of functional diversity, this relationship was negative. Butterfly functional richness decreased with increasing arable field cover, as did butterfly and bird functional evenness. For butterfly functional evenness, this was only evident in the most homogeneous regions. Butterfly and bird functional dispersion decreased in homogeneous regions regardless of the proportion of arable field cover locally. No effect of landscape heterogeneity on plant functional diversity was found at any spatial scale, but plant species richness decreased locally with increasing arable field cover. Overall, species richness responded more consistently to landscape homogenisation than did the functional diversity indices, with both positive and negative effects across species groups. Functional diversity indices are in theory valuable instruments for assessing effects of land use scenarios on ecosystem functioning. However, the applicability of empirical data requires deeper understanding of which traits reliably capture species' vulnerability to environmental factors and of the ecological interpretation of the functional diversity indices. Our study provides novel insights into how the functional diversity of communities changes in response to agriculturally derived landscape homogenisation; however, the low explanatory power of the functional diversity indices hampers the ability to reliably anticipate impacts on ecosystem functioning.

Land use change is largely held responsible for the continuing loss of global biodiversity (Sala et al. 2000). Consequences of land use change on biodiversity have mainly been assessed in terms of changes in species richness and abundance, but all species have not fared equally poorly. Whereas some species have become threatened or even extinct, others have increased in abundance and/or expanded their distribution (Hewson and Noble 2009, Fox et al. 2014). The reasons for the different responses are linked to species-specific response traits, i.e. features describing various life-history, morphological, physiological or phenological characteristics that determine how a species interacts with its surroundings (Díaz and Cabido 2001, Violle et al. 2007). Therefore, land use and environmental changes may not only result in the loss of species but more fundamentally in the loss of certain traits. Because traits associated with responses to disturbance (i.e. response traits) and ecosystem functioning (i.e. effect traits) often overlap (Lavorel and Garnier 2002, Lavorel

et al. 2011, Pakeman 2011), biotic homogenisation of communities may impair ecosystem processes and the ecosystem services they provide, e.g. nutrient retention and pollination (Tilman et al. 1996, Chapin et al. 2000, Fründ et al. 2013).

The increased recognition in ecological research of functional traits, involving both response and effects traits, has fostered the concept of functional diversity, i.e. the diversity of traits in a given community that influence organismal performance. Functional diversity is a commonly used indicator of ecosystem functioning (Cadotte et al. 2011) as well as species' responses to environmental disturbances (Mouillot et al. 2013a). Despite the advances in the use of functional diversity indices, effects of landscape homogenisation caused by agricultural rationalisation and intensification – dominating drivers of biodiversity loss – on multiple taxa largely remain elusive. Moreover, biological communities in rural landscapes are largely structured by anthropogenic disturbances acting at various spatial scales

(Tscharntke et al. 2012). Despite this, the key financial initiatives for the enhancement of agricultural landscape heterogeneity (i.e. the agri-environment schemes) are mostly being allocated opportunistically at local scales (Kleijn et al. 2006). Some of the expected biodiversity benefits will therefore not be realised due to a mismatch between the scale of management and the scales of ecological processes, e.g. biotic interactions and population dynamics (Leibold et al. 2004, Bengtsson 2010). Adding a spatial component to the analyses of functional diversity may consequently increase both our ability to understand and predict scale-dependent effects of disturbances on functional diversity and guide the design of policies such that interventions are implemented at the scale at which they are most likely to yield the desired effect.

In this study, we investigated the extent to which local (0.25 km²) and regional (> 10 000 km²) levels of landscape heterogeneity, measured by the proportion of arable field cover, currently affect the functional diversity of plants, butterflies and birds in southern Finland. We did this by the use of four functional diversity indices: functional richness, functional evenness, functional divergence, and functional dispersion, calculated on the basis of functional response traits reflecting species dispersal, competition and population persistence, which are processes known to be important in determining species distributions in human-modified landscapes (Henle et al. 2004, Ewers and Didham 2006). We hypothesised that there would be lower overall functional diversity with decreasing landscape heterogeneity, but that effects may vary depending on species group and the level of local and regional heterogeneity.

Material and methods

Selection of study sites

Field data were collected in five regions in southern Finland (59°57′–63°42′N, 19°41′–30°53′E) in 2001 (four mainland regions) and 2002 (the Åland Islands; Fig. 1). The southern (S) and south-western (SW) regions in mainland Finland are characterised by low landscape heterogeneity due to high arable field cover, primarily cereals. In contrast, the less intensively cultivated eastern (E) and western (W) regions and the Åland islands (AI) are characterised by a heterogeneous landscape structure with lower arable field cover (Luoto 2000, Ekroos et al. 2013). Therefore, our use of the term 'landscape heterogeneity' refers to the proportion of arable field cover, which is a widely used proxy for landscape complexity and land use intensity due to its correlation with other landscape descriptors such as the proportion of forests and grassland and the Shannon–Wiener index of habitat diversity (Gabriel et al. 2006).

Using stratified random sampling (see Kuussaari et al. 2004 for details), 26 study landscapes (1 km² quadrats) were distributed within the two regions with high arable field cover (SW and S) and 27 study landscapes within the three regions with low arable field cover (W, E and AI), resulting in a total of 53 study landscapes. Each study landscape was then divided into quarters (0.25 km²). In each landscape, the quarters with highest and lowest heterogeneity as defined by the Shannon–Wiener index for habitat diversity were chosen as study units (henceforth called study squares). The Shannon–Wiener index was based on the following land use categories: 1) cultivated fields (cereal fields and sown improved grasslands for fodder production), 2) set-asides, 3) low-intensity agricultural land (mainly semi-natural grasslands or abandoned fields), 4) field margins, 5) deciduous forest, 6) coniferous forest, 7) built-up areas, and 8) waterways (see Kivinen et al. 2006 for more details). Following this site-selection procedure, fieldwork was conducted in 106 separate 0.25 km² study squares situated pair-wise within 53 study landscapes. Heterogeneous study squares had lower arable field cover compared with homogeneous study squares regardless of the regional level of agricultural land use. Moreover, heterogeneous and homogeneous study squares had on average lower arable field cover in the regions with low levels of agricultural land use compared with high levels, respectively (Table 1; Ekroos et al. 2013). Therefore, we chose to include arable field cover as an estimate of landscape heterogeneity in the analyses.
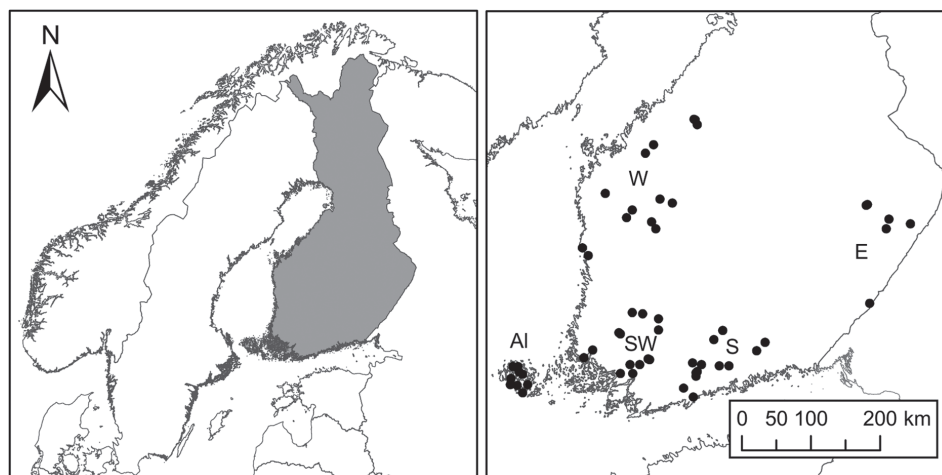

Figure 1. Location of the study landscapes in five regions in Finland characterised as homogeneous (SW, S, n = 26) and heterogeneous (W, E, AI, n = 27) in terms of the proportion of arable field cover.

Table 1. Mean and $CI_{95\%}$ of the proportion of arable field cover in heterogeneous and homogeneous study squares and in regions of high and low levels of agricultural land use. Differences are significant at $p < 0.001$.

	Regional level of agricultural land use			
	High		Low	
Heterogeneous study squares	45.18	(39.63–50.72)	29.59	(25.92–33.26)
Homogeneous study squares	81.19	(78.60–83.78)	61.14	(56.09–66.19)
All	63.18	(57.21–69.15)	45.38	(40.12–50.64)

Field data collection

Butterflies and vascular plants

For butterfly surveys, ten 50 m long transects within each of the 106 study squares ($n_{tot} = 1060$) were established primarily in three non-crop habitat types: boundaries between two arable fields, forest verges between an arable field and a forest and semi-natural grasslands. The habitat types could not be represented by an equal number of transects because of the different landscape composition of the study squares (Kuussaari et al. 2007). Field boundaries comprised 60% of all transects, forest verges 25% and semi-natural grasslands 15%. The field boundaries and the forest verges were on average 2.2 and 2.4 m wide, respectively, without any trees and bushes apart from a few scattered individuals not directly subjected to agrochemicals and generally unmanaged. If mown, this usually occurred once in the summertime. Transects in semi-natural grasslands were placed centrally to avoid edge effects. A minority of the semi-natural grasslands were regularly managed (Kuussaari et al. 2007). The distance between transects always exceeded 50 m.

Butterflies (Rhopalocera) were surveyed along the ten transects using the method of Pollard and Yates (1993), in which all individuals 5 m in front of and to the sides of the surveyor are identified to the species level. Butterfly surveys were performed during seven survey rounds between mid-May and the end of August at approximately two-week intervals.

Vascular plants (henceforth called plants), including trees and grasses, were recorded and their cover (%) estimated using an ordinal scale of nine classes (1 = <0.125%, 2 = 0.125–0.5%, 3 = 0.5–2%, 4 = 2–4%, 5 = 4–8%, 6 = 8–16%, 7 = 16–32%, 8 = 32–64%, 9 = >64%) within 1 m wide and 50 m long transects. Six of the 10 butterfly transects per study square were surveyed for plants (Kivinen et al. 2006).

Birds

Farmland birds (sensu Tiainen and Pakkala 2001; see also Ekroos et al. 2013) were surveyed twice in 2001 and three times in 2002 using territory mapping. Because two out of the 106 study squares, both situated in the same highly cultivated region (S), were surveyed on fewer occasions, they were excluded from all analyses involving birds. Surveys were made from early May to mid-June during sunrise and comprised the entire open area of the 0.25 km² study square including farmyards, arable fields, set-asides, semi-natural grasslands,

islets of other habitats and various types of verges (essentially all habitats maintained and managed by farming). All farmland birds displaying territorial behaviour (e.g. contact calls, territorial contests) or other behaviour that could be signs of breeding (e.g. nest building, alarming because of vicinity of nest) were recorded on large-scale visit maps. All records were afterwards transferred to species-specific maps for territory interpretation. The separation between territories was made easy by simultaneous observations which had systematically been registered in the field between conspecifics of the same sex (for details, see Tiainen et al. 2004). Finally, the estimated centroid of each territory was stored in a GIS database.

Functional trait selection

For each species group a number of functional response traits (Lavorel and Garnier 2002) were selected (see Table 2 for trait description, data completeness and references). Although the same functional response traits could not be applied to all species groups, they were selected to be common predictors of species responses to land use and environmental changes in terms of dispersal, competition and population persistence (Henle et al. 2004).

For butterflies, average wing span, degree of larval host plant specialisation and potential egg production were selected as functional response traits. Average wingspan is an easily accessible proxy for dispersal ability (Sekar 2012, Kuussaari et al. 2014), which is a main determinant for species persistence in fragmented landscapes (Ewers and Didham 2006). Specialist species, i.e. those dependent on a limited number of host plants, require (typically) large habitat patches and mosaic landscapes with a high probability of host plant occurrence. Consequently, specialists are more vulnerable to habitat loss and fragmentation than generalists (Steffan-Dewenter and Tscharntke 2000, Öckinger et al. 2010). Specialisation was categorised from 1 (most specialised) to 5 (least specialised) based on the number of host plants in combination with the number of plant families and genera (Table 2). Potential egg production was used as a measure of reproductive potential. Low reproductive rate has been suggested to lead to decreased metapopulation persistence and to increased risk of stochastic extinctions due to lower emigration rates and probability of successful colonisations (Keeling 2000, Henle et al. 2004); the risk of stochastic extinctions is in turn affected by landscape composition (Hanski 1999).

The plant functional response traits selected were leaf dry matter content (LDMC), life-span, seed mass and terminal velocity. LDMC predicts species responses to changes in land use (Garnier et al. 2004) and is positively related to greater population temporal stability (Majeková et al. 2014). Life span explains species' responses to habitat area and connectivity (Lindborg 2007), and seed mass is a key trait for resistance against habitat degradation and seedling competitive ability (Jakobsson and Eriksson 2000, Jonason et al. 2014). Terminal velocity measures the speed by which a diaspore travels through still air. This measure was moderately correlated with seed mass ($R^2 = 0.34$, $n = 288$, $p = <0.001$). However, both traits were kept for analyses

Table 2. Description of the functional response traits used in the study.

Species group	Functional trait	Description	Data coverage	Reference
Butterflies	Wing span	Average wingspan (cm)	100%	Bink 1992
	Egg production	The estimated number of eggs laid in a life-time	100%	Bink 1992
	Host plant specialisation	Five categories: 1) 1–2 host plant from the same genus 2) 2 host plants from different genera 3) > 3 host plants from the same genus 4) > 3 host plants from different genera but within the same family 5) > 3 host plants from > 2 families	100%	Eliasson et al. 2005
Plants	LDMC	Leaf dry matter content, i.e. leaf dry mass/fresh mass (mg g^{-1})	87%	Kleyer et al. 2008
	Life span	Categorised as long-lived (perennial species) or short lived (annuals and biennials)	100%	Kleyer et al. 2008
	Seed mass	Average seed mass without appendages (mg)	90%	Kleyer et al. 2008
	Terminal velocity	The maximum velocity of a falling diaspore in still air (m s^{-2})	74%	Kleyer et al. 2008
Birds	Nest site	Five categories: trees, ground, herbs/bushes, cavities, houses	100%	Cramp 1977
	Summer diet	Four categories: invertebrates, invertebrates and seeds, carnivorous and polyphagous	100%	Cramp 1977
	Clutch size	Average clutch size	100%	Jetz et al. 2008
	Territory size	Three categories: ≤ 0.5, 1–2 and > 2 ha	100%	Tiainen et al. unpubl.
	Migration strategy	Two categories: wintering areas in Africa or southern Asia (long-distance migrants) or in Europe (short-distance and partial migrants and sedentary species).	100%	Saurola et al. 2013, Valkama et al. 2014

because they represent partly separate survival strategies: competition and resistance (seed mass) and wind dispersal (terminal velocity) (sensu Jonason et al. 2014). Moreover, the terminal velocity accounts for seed morphology (e.g. appendages), which is not always included in calculations of seed mass (Kleyer et al. 2008).

For birds, five functional response traits were used: nest site, summer diet, average clutch size, territory size and migration strategy. Nest site availability may be related to landscape heterogeneity and land use intensity. Summer diet was used to capture the effects of the loss of invertebrate food resources caused by agricultural intensification (Vickery et al. 2001, Hallmann et al. 2014). Clutch size is a measure of reproductive potential and territory size was used as a measure of the spatial scale of landscape utilisation. Migration strategy was incorporated to account for the fact that species may be differentially affected by the land use in their overwintering grounds or along their migratory route compared with their breeding grounds in Finland (Laaksonen and Lehikoinen 2013), i.e. residents can be expected to respond more strongly to local habitat factors in the study landscapes compared with migrants.

Estimates of functional diversity

Based on the work of Mason et al. (2005), Villéger et al. (2008) proposed three independent indices of functional diversity describing the distribution of species and their abundances in a multidimensional trait space: functional richness, functional evenness and functional divergence. Functional richness measures the total volume of multidimensional trait space, i.e. functional space, encompassing a community of species. The index is incidence based, thus treating abundant and rare species equally. Consequently, functional richness is determined by the presence of species situated along the margin of functional space. Functional evenness complements functional richness by measuring the evenness of the abundance distribution among all species in functional space, whereas functional divergence describes the proportion of species with the most extreme trait values (Mouillot et al. 2013a). High functional evenness means effective use of functional space whereas low functional evenness indicates that some parts of the functional space are underused (assuming an even allocation of resources) (Mason et al. 2005). Similarly, high functional divergence indicates a lower overlap in functional space between the dominant species and thus lower competition because of higher trait divergence and niche differentiation. In addition, Laliberté and Legendre (2010) introduced the functional dispersion index, which quantifies the abundance weighted mean distance to the centroid of functional space defined by a community as a measure of community specialisation.

The four multidimensional functional diversity indices were independently calculated for each species group using the dbFD function in the FD package (Laliberté et al. 2014) as implemented in the statistical computing language R (R Development Core Team). We included all four indices to cover different aspects of functional diversity (Villéger et al. 2008, Laliberté and Legendre 2010) and thus to provide complementary information to our research question. Prior

to the analysis, the total species richness and abundance of butterflies, the species richness and cover of plants and the species richness and number of farmland bird territories in each study square were pooled over transects and survey rounds.

Initially, the FD package computes a Gower (1971) dissimilarity matrix using trait data, which allows for both continuous and categorical variables. Second, a principal coordinates analysis (PCoA) returns axes which, together with species abundance data (not for functional richness), are used as 'new traits' to compute the functional diversity indices for each study square. The two first axes of the PCoA analyses are shown in Fig. 2. To correct for negative eigenvalues of the PCoA axes, i.e. axes which cannot be represented in a Euclidean space, a square root (default in the package) or Cailliez correction (Cailliez 1983) was applied. For farmland birds and butterflies the number of axes in the PCoA were specified as the maximum number of axes that allows the $s > t$ condition to be met, and for plants maximum number of traits that allows the $s \geq 2t$ condition to be met, where s is the number of species and t the number of traits (Laliberté et al. 2014). The quality, an approximate value for R^2, of the reduced-space representation needed to calculate functional richness and functional divergence was 0.36 for birds (two axes used), 0.49 for butterflies (five axes used) and 0.19 for plants (five axes used).

Because the indices of functional diversity are sensitive to trait data incompleteness (Pakeman 2014), trait values missing from the trait databases were filled prior to analyses by use of the method of multivariate imputation by chained equations (mice package, van Buuren et al. 2014).

Statistical analyses

Due to the hierarchical structure of the study design, linear mixed models (LMM) fit by maximum likelihood (lmerTest package, Kuznetsova et al. 2015) were used to calculate the relationship between the functional indices and the local and regional level of agricultural land use. The local level of agricultural land use was defined by use of the continuous measure of the proportion of arable field cover (i.e. annually tilled crops) within each 0.25 km^2 study square, where high and low proportions were indicative of high and low levels of agricultural land use at this scale, respectively. The regional level of agricultural land use was categorised as high or low as determined by the regional differences in the proportion of arable field cover (see Selection of study sites). In separate LMMs, the functional indices for each species group were used as response variables, and the proportion of arable field cover in the study squares and the regional level of agricultural land use (two categories, high/low) were fixed factors. Because the 0.25 km^2 heterogeneous and homogeneous study squares were situated pairwise within a 1 km^2 landscape square, landscape pair identity was added as a random factor. In addition, we performed LMMs as described above but with the interaction between the proportion of arable field cover and the regional level of agricultural land use as a fixed factor. We did this to test if the response of the functional diversity indices to the proportion of arable field cover varied depending on the regional
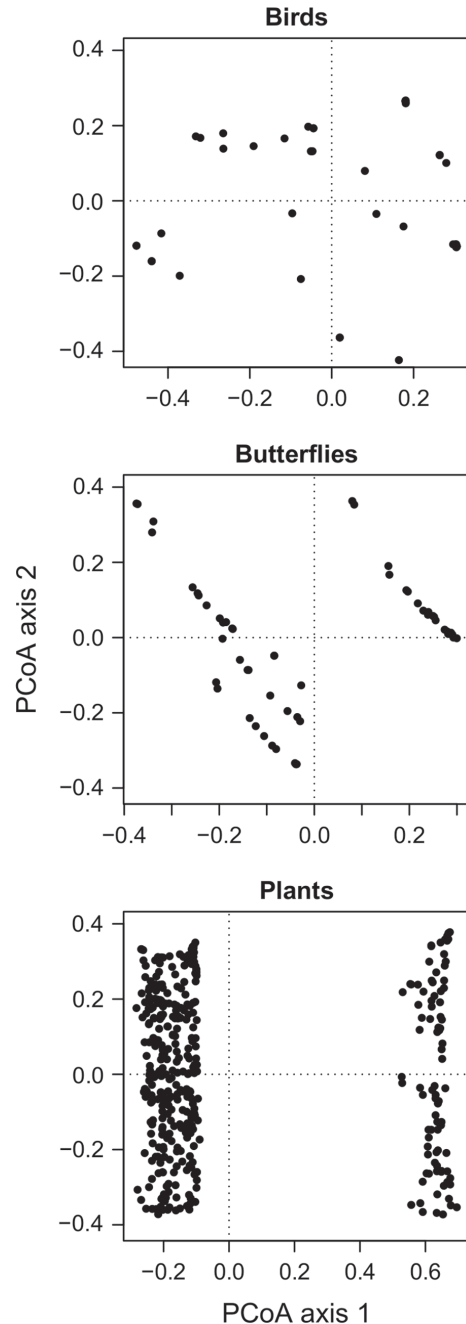

Figure 2. Graphical representation of the trait space amongst species of farmland birds, butterflies and plants based on the two first axes derived from principal coordinate analyses (PCoA), which was in turn used to calculate the functional diversity indices.

level of agricultural land use. All model residuals were plotted and visually inspected for normality using the qqPlot function in the CAR package (Fox et al. 2015). P-values were obtained from maximum likelihood t-tests by use of the Satterthwaite approximation to estimate denominator degrees of freedom (lmerTest package, Kuznetsova et al. 2015). To assess the goodness-of-fit of the LMMs, marginal and conditional R^2 values were calculated by the MuMIn package (Bartoń 2015). Marginal R^2 is the proportional variance explained by the fixed factors, whereas the conditional R^2 explains the proportional variance of the entire

model including both fixed and random factors (Nakagawa and Schielzeth 2013).

Results

In total, 396, 57 and 40 species of plants, butterflies and birds were found, respectively (Supplementary material Appendix 1). The species richness of plants and butterflies decreased as the study squares progressively became dominated by agriculture whereas the bird species richness increased both at the local and region scale. The number of species in the study squares strongly influenced the functional richness, particularly for butterflies and plants, whereas the correlation between species richness and the three other functional diversity indices were relatively weak. The functional richness of plants and butterflies correlated significantly, but none of the additional functional diversity indices correlated between taxa (Supplementary material Appendix 2).

The functional richness of butterflies, but not plants, decreased with increasing proportion of arable field cover in the study squares, but there were no differences in functional richness between regions of high and low levels of agricultural land use for any of the species groups (Table 3). The fixed factor of the significant model explained little of the total variation ($R^2_{marginal} = 0.11$), whereas the goodness-of-fit for fixed and random factors together was higher ($R^2_{conditional} = 0.46$; Table 3).

Butterfly functional evenness was related to the interaction between the proportion of arable field cover and region caused by a negative relationship to the proportion of arable field cover in regions of high levels of agricultural land use (Fig. 3). However, the explanatory power of the interaction was low ($R^2_{marginal} < 0.012$; Table 3). For birds, the functional evenness decreased with increasing proportions of arable field cover but was not affected at the regional level of agricultural land use. There were no effects of the levels of agricultural land use locally or regionally on plant functional evenness (Table 3).

The functional divergence of butterflies was lower in the two regions with high levels of agricultural land use compared with the three less cultivated regions, whereas no such effects were found for plants or birds. Butterfly and bird functional dispersion also decreased with increasing arable field cover. For butterflies, the fixed factors of the significant models explained 27% (functional divergence) and 29% (functional dispersion) of the total variation, and the whole models explained 70% and 77% of the variation in functional divergence and dispersion, respectively (Table 3). The variation explained by bird functional divergence was approximately half that of the butterflies.

Table 3. Results of LMMs analysing effects of the proportion of arable field cover (PA) within each 0.25 km² study square and regional level of agricultural land use (Region), as well as the interaction between PA and Region, on functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), functional dispersion (FDis), and species richness. Landscape pair, i.e. the pair of adjoining heterogeneous and homogeneous study units, was used as a random factor. Effects significant at p < 0.05 are shown in bold.

|	Butterflies			Plants			Birds		
	PA	Region	PA × Region	PA	Region	PA × Region	PA	Region	PA × Region
FRic									
Est	−5.22E-05	1.48E-04	−9.43E-06	−9.34E-07	7.24E-06	2.22E-06	2.037e-04	−1.613e-02	−7.421e-04
SE	1.50E-05	8.09E-04	3.05E-05	5.78E-07	3.32E-05	1.17E-06	3.441e-04	1.524e-02	6.860e-04
P	**<0.001**	0.86	0.76	0.11	0.83	0.063	0.55	0.29	0.282
$R^2_{marginal}$	0.11		0.12	0.022		0.053	0.035		0.024
$R^2_{conditional}$	0.46		0.45	0.46		0.48	0.035		0.024
FEve									
Est	−3.28E-04	0.032	1.50E-03	1.91E-04	2.24E-02	−8.63E-05	−9.416e-04	1.198e-02	4.842e-04
SE	3.20E-04	0.017	6.34E-04	2.03E-04	1.17E-02	4.14E-04	3.167e-04	1.485e-02	6.351e-04
P	0.31	0.059	**0.02**	0.35	0.06	0.84	**0.004**	0.42	0.45
$R^2_{marginal}$	0.077		0.12	0.056		0.046	0.12		0.13
$R^2_{conditional}$	0.37		0.41	0.49		0.49	0.24		0.24
FDiv									
Est	3.70E-04	−0.087	−7.05E-04	1.07E-05	−0.013	1.01E-04	2.037e-04	−1.613e-02	−7.421e-04
SE	3.12E-04	0.02	6.37E-04	1.34E-04	7.20E-03	2.73E-04	3.441e-04	1.524e-02	6.860e-04
P	0.24	**<0.001**	0.27	0.94	0.085	0.71	0.56	0.29	0.28
$R^2_{marginal}$	0.27		0.27	0.045		0.046	0.024		0.035
$R^2_{conditional}$	0.7		0.7	0.4		0.39	0.024		0.035
FDis									
Est	1.91E-04	−0.062	−5.01E-04	1.34E-03	−4.98E-03	−5.69E-05	−9.015e-04	9.398e-03	2.805e-04
SE	1.89E-04	0.014	3.88E-04	6.95E-04	0.039	1.39E-04	2.402e-04	1.225e-02	4.842e-04
p	0.31	**<0.001**	0.2	0.058	0.9	0.68	**<0.001**	0.446	0.56
$R^2_{marginal}$	0.29		0.3	0.036		0.041	0.16		0.16
$R^2_{conditional}$	0.77		0.76	0.45		0.40	0.41		0.41
Sp. richness									
Est	−0.11	−1.79	−0.025	−0.16	−2.77	−0.091	0.043	3.031	5.62E-03
SE	0.019	1.22	0.040	0.068	5.69	0.14	0.016	0.79	0.033
P	**<0.001**	0.15	0.54	**0.019**	0.069	0.52	**0.010**	**<0.001**	0.87
$R^2_{marginal}$	0.18		0.19	0.023		0.027	0.15		0.15
$R^2_{conditional}$	0.65		0.64	0.77		0.77	0.31		0.32
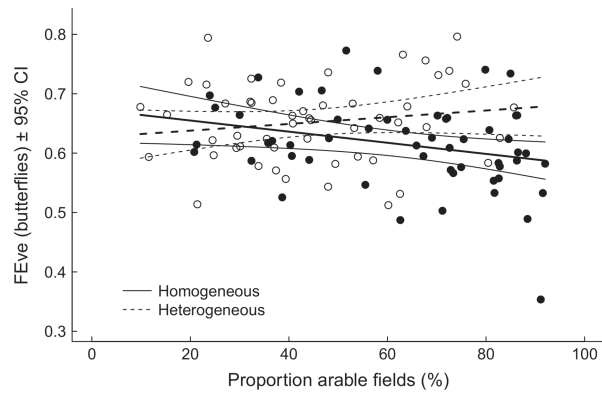
Figure 3. Butterfly functional evenness with CI$_{95\%}$ in relation to the proportion of arable land in heterogeneous and homogeneous regions.

Discussion

How biodiversity and ecosystem functioning relates to land use and landscape composition is a major challenge for conservationists and policy makers and therefore currently the focus in many scientific projects. Traditionally, efforts to understand this relationship have focused on the role of taxonomic diversity, but greater emphasis has recently been placed on the implications for functional diversity, which is considered to be a more reliable indicator in this context (Mouillot et al. 2013a, Gagic et al. 2015). Our results showed no uniform response in functional diversity across taxa or spatial scales; however, all significant effects found revealed negative impacts of increasing landscape homogeneity in terms of the proportion of arable field cover.

Functional richness, i.e. the volume of functional space, generally displays strong positive correlation with species richness (Villéger et al. 2008, Mouchet et al. 2010), as it did in this study. The fact that the functional richness of butterflies decreased with the proportion of arable field cover at the local scale was thus expected, given that the same patter was found for butterfly species richness. On the other hand, plant and bird functional richness were not affected by the proportion of arable field cover at any scale despite negative (plants) and positive (birds) effects on species richness. The lack of effect may be explained by birds and other central-place foragers with high mobility compensating for local reductions of resources by foraging at wider spatial scales (Tscharntke et al. 2005), whereas plants often experience delayed responses to landscape changes and therefore show no visible responses (Lindborg and Eriksson 2004).

What may complicate the interpretation of the functional richness index is that it does not account for species abundance but is solely determined by the presence of the species with the most extreme trait values at the margin of the functional space. These functionally exceptional species are likely to be few in number and therefore weak representatives of the whole community that contribute relatively little to ecosystem functioning (Winfree et al. 2015, but see Hooper et al. 2005, Mouillot et al. 2013b). In principle, species with exceptional traits may generate gaps in functional space by inflating the total volume, which may lead to misinterpretations of the functional

capacity. Therefore, our results confirm the suggestion that the index of functional richness needs to be complemented by abundance-based functional diversity indices to expose the extent by which the functional space is used by species (Villéger et al. 2008, Laliberté and Legendre 2010, see also Blonder et al. 2014).

The functional evenness of farmland birds decreased with increasing proportion of arable field cover in the study squares, which indicates that landscape homogenisation affects species non-randomly based on the traits they possess (McKinney and Lockwood 1999, Ekroos et al. 2010, Öckinger et al. 2010). In this case, the lower functional evenness was driven by changes among species with low to intermediate abundances because the dominating species remained equally distant in functional space, i.e. functional divergence remained constant. Moreover, the functional dispersion decreased, which indicates higher functional specialisation of the bird community with increasing arable field cover. Although the marginal R^2 of the model was low (0.16), the result contradicts earlier studies that found that bird specialists are being replaced by generalists as landscapes become dominated by agriculture (Devictor et al. 2008, Barnagaud et al. 2011, Le Viol et al. 2012).

Although butterfly functional richness responded to the local level of agricultural land use, butterfly functional divergence and dispersion were lower at the regional scale, i.e. the most abundant species within these communities were clustered in functional space. In line with our findings for birds and in congruence with earlier studies, we show that large scale landscape homogenisation caused by agricultural land use simplifies butterfly communities, which become increasingly dominated by generalist species (Ekroos et al. 2010, Börschig et al. 2013).

There was no significant effect of the proportion of arable field cover on the plant functional diversity indices at any scale. Although plant species richness, in line with our result, is known to increase with increasing landscape heterogeneity (Kivinen et al. 2006), we show that this does not necessarily translate into changes in functional diversity (see also Purschke et al. 2013). Plants generally respond less rapidly to environmental changes than butterflies and birds because of their relatively slow population dynamics (Thomas et al. 2004). Most of the plant data were compiled from field boundaries, which frequently were treated with herbicides in Finland before the practice was forbidden in 1995 (Siiskonen 2000). Plant communities in such habitats generally consist of species highly tolerant to agricultural disturbance (Kleijn and Verbeek 2000). Therefore, effects of landscape homogenisation on plant functional diversity may have been reduced because the contemporary landscape context may be a weak predictor under such circumstances (Kuussaari et al. 2009). This is supported by Purschke et al. (2014) who found that the functional divergence of grassland plants was positively associated with the percentage of grasslands in the surrounding landscape in the past (1938) but not to the landscape at the time of the study (2007).

Measures such as the agri-environment schemes (AES) to increase the heterogeneity in agricultural landscapes are today often implemented at too small a spatial scale, leading to less optimised gain for biodiversity (Kleijn et al. 2006, Jonason et al. 2012). Our result showing both local and

regional effects on functional diversity and species richness suggest that field scale AES options indeed may be effective, but that landscape-scale AES options need to be given higher priority in order to increase the overall gain.

In conclusion, we show that plants, butterflies and birds in southern Finland generally experience weak functional responses to the proportion of arable field cover; the responses vary across species groups, functional diversity indices and spatial scales. Although functional diversity indices in theory provide a great tool for understanding the impacts of land use and environmental changes on ecosystem functioning, some controversy remains regarding their usefulness in predicting community responses to disturbances and ecosystem functions (Mouchet et al. 2010). In our study, the $R^2_{marginal}$ of the significant models explained on average 18% (range 11–29%) of the total variation, which reveals a rather limited response of functional diversity. Similarly, Gagic et al. (2015) found that the power of models to predict ecosystem functions using trait-based indices was less than 50%, with the majority of models explaining considerably less variation; despite an increasing use of functional diversity indices in ecological research, their explanatory power is often low. For proper ecological interpretation, we also need to better understand which traits can predict the ecological mechanisms we intend to capture (e.g. dispersal capacity) and which traits best reflect the vulnerability of species to environmental factors. Only then can we properly evaluate their contribution to conservation and inform management and policy making.

References

Barnagaud, J. Y. et al. 2011. When species become generalists: on-going large-scale changes in bird habitat specialization. – Global Ecol. Biogeogr. 20: 630–640.

Bartoń, K. 2015. MuMIn: multi-model inference. – R package ver. 1.15.6.

Bengtsson, J. 2010. Applied (meta) community ecology: diversity and ecosystem services at the intersection of local and regional processes. – In: Verhoef, H. A. and Morin, P. J. (eds), Community ecology: processes, models, and applications. Oxford Univ. Press, pp. 115–130.

Bink, F. A. 1992. Ecologische atlas van de dagvlinders van Noordwest-Europa. – Schuyt & Co Uitgevers en Importeurs.

Blonder, B. et al. 2014. The n-dimensional hypervolume. – Global Ecol. Biogeogr. 23: 595–609.

Börschig, C. et al. 2013. Traits of butterfly communities change from specialist to generalist characteristics with increasing land-use intensity. – Basic Appl. Ecol. 14: 547–554.

Cadotte, M. W. et al. 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. – J. Appl. Ecol. 48: 1079–1087.

Cailliez, F. 1983. The analytical solution of the additive constant problem. – Psychometrika 48: 305–308.

Chapin III, F. S. et al. 2000. Consequences of changing biodiversity. – Nature 405: 234–242.

Cramp, S. 1977. Handbook of the birds of Europe, the Middle East and North Africa: the birds of the Western Palearctic. – Oxford Univ. Press.

Devictor, V. et al. 2008. Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. – Oikos 117: 507–514.

Díaz, S. and Cabido, M. 2001. Vive la difference: plant functional diversity matters to ecosystem processes. – Trends Ecol. Evol. 16: 646–655.

Ekroos, J. et al. 2010. Homogenization of lepidopteran communities in intensively cultivated agricultural landscapes. – J. Appl. Ecol. 47: 459–467.

Ekroos, J. et al. 2013. Correlations in species richness between taxa depend on habitat, scale and landscape context. – Ecol. Indicators 34: 528–535.

Eliasson, C. U. et al. 2005. Nationalnyckeln till Sveriges flora och fauna: fjärilar. Dagfjärilar: (Hesperiidae-Nymphalidae). – ArtDatabanken, Uppsala.

Ewers, R. M. and Didham, R. K. 2006. Confounding factors in the detection of species responses to habitat fragmentation. – Biol. Rev. Camb. Phil. Soc. 81: 117–142.

Fox, J. et al. 2015. An {R} companion to applied regression, 2nd ed. – Thousand Oaks, CA.

Fox, R. et al. 2014. Long-term changes to the frequency of occurrence of British moths are consistent with opposing and synergistic effects of climate and land-use changes. – J. Appl. Ecol. 51: 949–957.

Fründ, J. et al. 2013. Bee diversity effects on pollination depend on functional complementarity and niche shifts. – Ecology 94: 2042–2054.

Gabriel, D. et al. 2006. Beta diversity at different spatial scales: plant communities in organic and conventional agriculture. – Ecol. Appl. 16: 2011–2021.

Gagic, V. et al. 2015. Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. – Proc. R. Soc. B 282: 20142620.

Garnier, E. et al. 2004. Plant functional markers capture ecosystem properties during secondary succession. – Ecology 85: 2630–2637.

Gower, J. C. 1971. A general coefficient of similarity and some of its properties. – Biometrics 27: 857–871.

Hallmann, C. A. et al. 2014. Declines in insectivorous birds are associated with high neonicotinoid concentrations. – Nature 511: 341–343.

Hanski, I. 1999. Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. – Oikos 87: 209–219.

Henle, K. et al. 2004. Predictors of species sensitivity to fragmentation. – Biodivers. Conserv. 13: 207–251.

Hewson, C. M. and Noble, D. G. 2009. Population trends of breeding birds in British woodlands over a 32-year period: relationships with food, habitat use and migratory behaviour. – Ibis 151: 464–486.

Hooper, D. U. et al. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. – Ecol. Monogr. 75: 3–35.

Jakobsson, A. and Eriksson, O. 2000. A comparative study of seed number, seed size, seedling size and recruitment in grassland plants. – Oikos 88: 494–502.

Jetz, W. et al. 2008. The worldwide variation in avian clutch size across species and space. – PLoS Biol. 6: 2650–2657.

Jonason, D. et al. 2012. Field scale organic farming does not counteract landscape effects on butterfly trait composition. – Agric. Ecosyst. Environ. 158: 66–71.

Jonason, D. et al. 2014. Vegetation in clear-cuts depends on previous land use: a century-old grassland legacy. – Ecol. Evol. 4: 4287–4295.

Keeling, M. J. 2000. Metapopulation moments: coupling, stochasticity and persistence. – J. Anim. Ecol. 69: 725–736.

Kivinen, S. et al. 2006. Multi-species richness of boreal agricultural landscapes: effects of climate, biotope, soil and geographical location. – J. Biogeogr. 33: 862–875.

Kleijn, D. and Verbeek, M. 2000. Factors affecting the species composition of arable field boundary vegetation. – J. Appl. Ecol. 37: 256–266.

Kleijn, D. et al. 2006. Mixed biodiversity benefits of agri-environment schemes in five European countries. – Ecol. Lett. 9: 243–254.

Kleyer, M. et al. 2008. The LEDA traitbase: a database of life-history traits of the northwest European flora. – J. Ecol. 96: 1266–1274.

Kuussaari, M. et al. 2004. Farmland biodiversity indicators and monitoring in Finland. – In: Groom, G. (ed.), Developments in strategic landscape monitoring for the Nordic countries. Nordic Council of Ministers, Copenhagen, pp. 29–40.

Kuussaari, M. et al. 2007. Determinants of local species richness of diurnal Lepidoptera in boreal agricultural landscapes. – Agric. Ecosyst. Environ. 122: 366–376.

Kuussaari, M. et al. 2009. Extinction debt: a challenge for biodiversity conservation. – Trends Ecol. Evol. 24: 564–571.

Kuussaari, M. et al. 2014. Higher mobility of butterflies than moths connected to habitat suitability and body size in a release experiment. – Ecol. Evol. 4: 3800–3811.

Kuznetsova, A. et al. 2015. lmerTest: tests in linear mixed effects models. – R package ver. 2.0-30.

Laaksonen, T. and Lehikoinen, A. 2013. Population trends in boreal birds: continuing declines in agricultural, northern, and long-distance migrant species. – Biol. Conserv. 168: 99–107.

Laliberté, E. and Legendre, P. 2010. A distance-based framework for measuring functional diversity from multiple traits. – Ecology 91: 299–305.

Laliberté, E. et al. 2014. FD: measuring functional diversity (FD) from multiple traits, and other tools for functional ecology. – R package ver. 1.0-12.

Lavorel, S. and Garnier, E. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. – Funct. Ecol. 16: 545–556.

Lavorel, S. et al. 2011. Using plant functional traits to understand the landscape distribution of multiple ecosystem services. – J. Ecol. 99: 135–147.

Le Viol, I. et al. 2012. More and more generalists: two decades of changes in the European avifauna. – Biol. Lett. 8: 780–782.

Leibold, M. et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. – Ecol. Lett. 7: 601–613.

Lindborg, R. 2007. Evaluating the distribution of plant life-history traits in relation to current and historical landscape configurations. – J. Ecol. 95: 555–564.

Lindborg, R. and Eriksson, O. 2004. Historical landscape connectivity affects present plant species diversity. – Ecology 85: 1840–1845.

Luoto, M. 2000. Spatial analysis of landscape ecological characteristics of five agricultural areas in Finland by GIS. – Fennia 178: 15–54.

Majeková, M. et al. 2014. Plant functional traits as determinants of population stability. – Ecology 95: 2369–2374.

Mason, N. W. H. et al. 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. – Oikos 111: 112–118.

McKinney, M. L. and Lockwood, J. L. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. – Trends Ecol. Evol. 14: 450–453.

Mouchet, M. A. et al. 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. – Funct. Ecol. 24: 867–876.

Mouillot, D. et al. 2013a. A functional approach reveals community responses to disturbances. – Trends Ecol. Evol. 28: 167–177.

Mouillot, D. et al. 2013b. Rare species support vulnerable functions in high-diversity ecosystems. – PLoS Biol. 11: e1001569.

Nakagawa, S. and Schielzeth, H. 2013. A general and simple method for obtaining R 2 from generalized linear mixed-effects models. – Methods Ecol. Evol. 4: 133–142.

Öckinger, E. et al. 2010. Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. – Ecol. Lett. 13: 969–979.

Pakeman, R. J. 2011. Multivariate identification of plant functional response and effect traits in an agricultural landscape. – Ecology 92: 1353–1365.

Pakeman, R. J. 2014. Functional trait metrics are sensitive to the completeness of the species' trait data? – Methods Ecol. Evol. 5: 9–15.

Pollard, E. and Yates, T. J. 1993. Monitoring butterflies for ecology and conservation. – Chapman and Hall.

Purschke, O. et al. 2013. Contrasting changes in taxonomic, phylogenetic and functional diversity during a long-term succession: insights into assembly processes. – J. Ecol. 101: 857–866.

Purschke, O. et al. 2014. Interactive effects of landscape history and current management on dispersal trait diversity in grassland plant communities. – J. Ecol. 102: 437–446.

Sala, O. E. et al. 2000. Global biodiversity scenarios for the year 2100. – Science 287: 1770–1774.

Saurola, P. et al. 2013. Suomen rengastusatlas: the Finnish bird ringing atlas volym 1. – Finnish Museum of Natural History.

Sekar, S. 2012. A meta-analysis of the traits affecting dispersal ability in butterflies: can wingspan be used as a proxy? – J. Anim. Ecol. 81: 174–184.

Siiskonen, H. 2000. Myrkyttäkää, ruiskuttakaa, hävittäkää...: ruotsalaisten ja suomalaisten maatalouden ammattilehtien kasvinsuojeluvalistus 1940–1980. – Suomalaisen Kirjallisuuden Seura.

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

Thomas, J. A. et al. 2004. Comparative losses of British butterflies, birds, and plants and the global extinction crisis. – Science 303: 1879–1881.

Tiainen, J. and Pakkala, T. 2001. Birds. – In: Pitkänen, M. and Tiainen, J. (eds), Biodiversity of agricultural landscapes in Finland. BirdLife Finland Conservation Series no. 3, pp. 33–50.

Tiainen, J. et al. 2004. Maatalousympäristön pesimälinnuston seuranta. – The Finnish Environ. 709: 92–109 in Finnish.

Tilman, D. et al. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. – Nature 379: 718–720.

Tscharntke, T. et al. 2005. Landscape perspectives on agricultural intensification and biodiversity–ecosystem service management. – Ecol. Lett. 8: 857–874.

Tscharntke, T. et al. 2012. Landscape moderation of biodiversity patterns and processes – eight hypotheses. – Biol. Rev. Camb. Phil. Soc. 87: 661–685.

Valkama, J. et al. 2014. Suomen rengastusatlas: the Finnish bird ringing atlas volym 2. – Finnish Museum of Natural History.

van Buuren, S. et al. 2014. Mice: multivariate imputation by chained equations in R. – J. Stat. Softw. 45: 1–67.

Vickery, J. A. et al. 2001. The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. – J. Appl. Ecol. 38: 647–664.

Villéger, S. et al. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. – Ecology 89: 2290–2301.

Violle, C. et al. 2007. Let the concept of trait be functional! – Oikos 116: 882–892.

Winfree, R. et al. 2015. Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. – Ecol. Lett. 18: 626–635.

Supplementary material (Appendix ECOG-02268 at <www.ecography.org/appendix/ecog-02268>). Appendix 1–2.