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# Plant functional group composition and large-scale species richness in European agricultural landscapes

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## Abstract

**Question:** Which are the plant functional groups responding most clearly to agricultural disturbances? Which are the relative roles of habitat availability, landscape configuration and agricultural land use intensity in affecting the functional composition and diversity of vascular plants in agricultural landscapes?

**Location:** 25 agricultural landscape areas in seven European countries.

**Methods:** We examined the plant species richness and abundance in 4 km × 4 km landscape study sites. The plant functional group classification was derived from the BIOLFLOR database. Factorial decomposition of functional groups was applied.

**Results:** Natural habitat availability and low land use intensity supported the abundance and richness of perennials, sedges, pteridophytes and high nature quality indicator species. The abundance of clonal species, C and S strategists was also correlated with habitat area. An increasing density of field edges explained a decrease in richness of high nature quality species and an increase in richness of annual graminoids. Intensive agriculture enhanced the richness of annuals and low nature quality species.

**Conclusions:** Habitat patch availability and habitat quality are the main drivers of functional group composition and plant species richness in European agricultural landscapes. Linear elements do not compensate for the loss of habitats, as they

mostly support disturbance tolerant generalist species. In order to conserve vascular plant species diversity in agricultural landscapes, the protection and enlargement of existing patches of (semi-) natural habitats appears to be more effective than relying on the rescue effect of linear elements. This should be done in combination with appropriate agricultural management techniques to limit the effect of agrochemicals to the fields.

**Keywords:** Agricultural land use; Habitat fragmentation; Habitat loss; Landscape structure; Plant functional type; Plant growth form; Plant species richness.

**Nomenclature:** Tutin et al. (2001).

**Abbreviations:** C = Competitor; GLM = General linear modelling; pPCA = Partial principal components analysis; R = Ruderal; S = Stress tolerator.

## Introduction

During the second half of the 20th century, the intensification of agricultural land use, nitrogen and phosphorus-driven eutrophication and the increasing use of pesticides in particular, have led to a decline in biodiversity across many different taxa, with a corresponding simplification of communities and a loss of ecosystem services (Tilman et al. 2001; Swift et al. 2004; Green et al. 2005). There are many examples from Europe in which the development of high input, simplified arable systems have been associated with a decline in biodiversity (Stoate et al. 2001; Luoto et al. 2003), although the effects of land use intensity and habitat availability have not been distinguished. Lately, Murphy & Lovett-Doust (2004) and Green et al. (2005) suggested that intensive agricultural land use could be allowed, if that released large agricultural areas for nature restoration.

Contemporary landscape ecology has focused a great deal on patch-corridor-matrix landscape models, assuming that the semi-natural linear elements of agricultural landscapes (e.g. field margins, hedgerows, road verges, ditches) can compensate for the negative effects of the high intensity of agricultural land use and habitat fragmentation (Opdam 1990; Forman 1995; Le Coeur et al. 2002; Fahrig 2003). The majority of papers focusing on fragmentation deal with animal or insect species, and tend to pool the effects of habitat loss and fragmentation *sensu stricto*: isolation and habitat configuration (McCoy & Mushinsky 1994; Bender et al. 1998; Fernandez-Juricic 2000; Niemelä 2001; Fahrig 2003; Schooley & Wiens 2005). With regard to vascular plants, the current and historic use of fertilisers and pesticides in adjacent arable fields, the reduced size of natural habitat patches and increased isolation from other fragments have been shown to be the factors that affect plant species diversity and composition (de Snoo & van der Poll 1999; Kleijn & Verbeek 2000; Bruun & Fritzberger 2002; Eriksson et al. 2002; Jacquemyn et al. 2003). However, within the remaining habitat patches the surviving plant populations also have declined in size, which is attributed to the reduction in the habitat quality as a consequence of increased disturbance of these small patches by human activities (Duelli 1997; Hermy et al. 1999; Honnay et al. 1999; Bruun 2000; Dupré & Ehrlén 2002).

The other side of the coin is the actual response of a particular plant species to changes in the quality and landscape configuration of natural habitats. The plant response profile on land use change depends largely on the functional traits of that species (Hermy et al. 1999; Geertsema et al. 2002; Lavorel & Garnier 2002; Deckers et al. 2004; Kolb & Diekmann 2005; Lososová et al. 2006). The response of plant species to habitat fragmentation and deterioration depends on dispersal type and ability, but also on other

functional traits (Hodgson & Grime 1990; Dzwonko 1993; Eriksson & Jakobsson 1998; Dupré & Ehrlén 2002; Jacquemyn et al. 2003; Geertsema 2005). Several simple classifications of species into broad response groups have been proposed, such as habitat generalists or matrix species vs habitat specialists, weeds or ruderals vs species of conservation value and hemeroby classes of species (Cook et al. 2002; Brentrup et al. 2002; Dupré & Ehrlén 2002; Hill et al. 2002; Adriaens et al. 2006). Although the use of broadly identified plant functional types may conceal the detailed mechanisms that underlie the response of species to environmental or anthropogenic factors, the *ad hoc* groups are deemed to be most promising in addressing the variation of general plant communities, i.e. at landscape or global scales (Noble & Gitay 1996; Díaz & Cabido 1997; Grime et al. 1997; Díaz et al. 2004; Hunt et al. 2004; Kahmen & Poschlod 2004). However, they still have not been applied frequently in monitoring systems and environmental assessments (Hermy et al. 1999; Godefroid & Koedam 2003; Petit et al. 2004; Smart et al. 2006; Van Cauwenbergh et al. 2007).

In the current paper we hypothesise that in the case of plants, which are organisms with high habitat quality requirements and low mobility, the functional group composition at landscape scale and species richness within groups is primarily determined by natural and semi-natural habitat availability, secondarily by land use intensity in agricultural fields (e.g. via leaching) and least by the connectivity of habitats. Therefore, we intend to elucidate the ecological and anthropogenic drivers of functional diversity across agricultural landscapes in temperate Europe. We expect that in agricultural landscapes, the response of some functional groups to agricultural pressure is more apparent and these ones can be used as reliable indicators in the monitoring of land use changes.

## Methods

The study was a part of the EU research project 'GREENVEINS', which aimed to establish large scale relationships between the species diversity and landscape structure and agricultural land use intensity for temperate Europe (Schweiger et al. 2005; Herzog et al. 2006; Hendrickx et al. 2007; Billeter et al. in press). We used 25 agricultural landscape areas (each 16 km<sup>2</sup>), representing wide gradients of land use intensity and landscape structure in Europe. The sample sites were distributed over seven countries across temperate Europe: France, Belgium, The Netherlands, Germany, Switzerland, the Czech Republic and Estonia (three or four study areas per country) (see Herzog et al. 2006 for the geographical location and description of these sites).

The habitat composition of 4 km × 4 km landscape study sites was mapped from aerial photographs and verified in the field (cf. Bailey et al. 2007) using two types of habitats: natural or semi-natural ('greenvein') and anthropogenic ('non-greenvein') habitats (terminology by Grashof-Bokdam & van Langevelde 2005). Variables of landscape structure were calculated from these binary maps with a grid size of 1 m × 1 m using the FRAGSTATS software package (McGarigal et al. 2002) (App. 1). Indices of agricultural land use intensity (App. 1) were adopted from standardised interviews with approximately ten farmers or land managers within each study site (Herzog et al. 2006).

To avoid species-area and sampling intensity effects, a stratified randomised sampling scheme was used. Generally, 240 2 m × 2 m sampling plots were located randomly in three types of landscape elements: arable fields, linear semi-natural landscape elements (field borders or edges of habitat patches) and semi-natural and natural habitat patches (grasslands, forests etc.) with a predetermined ratio (1:5:4 respectively to arable:linear:patch elements). Large-scale plant diversity in each landscape study site was estimated by pooling species lists of these 2 m × 2 m survey plots. In total, 5926 plots were described and a total of 1364 vascular plant species were recorded.

We covered the wide range of functional traits of species, pointed out by previous studies (Körner 1994; Noble & Gitay 1996; Grime et al. 1997; Hermy et al. 1999; Brentrup et al. 2002; Hill et al. 2002; Adriaens et al. 2006; Lososová et al. 2006). We will use the term plant functional group, which covers various emergent groups, strategies, functional types or specific response groups, according to the terminology developed by Lavorel et al. (1997).

In order to make the analytical approach both more objective and more uniform, the classification of each species was made with the help of the independent database of BIOLFLOR (Klotz et al. 2002). Based on BIOLFLOR data, we included two additional functional group classifications, which have not been used in earlier papers. First, we classified species into two 'nature quality indicator' classes (App. 2), combining information about species distribution among habitats, as well as on the accumulated knowledge about species origin (native or alien) and current invading status in Europe, strategy type, tolerance to disturbance and response to land use intensity (Brentrup et al. 2002; Hill et al. 2002; Godefroid & Koedam 2003; Gamborg & Rune 2004). The class of 'low nature quality species' included species known as exotics or aliens, cultural plants and species common in anthropogenic habitat types (i.e. common in habitats of low nature quality) such as ruderals, urbanophilic or hemerobic species. The second class, 'high nature quality species', included all other species, i.e. indigenous spe-

cies occurring predominantly in undisturbed natural and semi-natural habitats. In the second new classification, we created two versions of variables about the 'ecological flexibility' of species, based on the information either (1) about the number of floristic zones where the species occurs (App. 2) or (2) about the number of hemeroby levels listed for species in the BIOLFLOR database.

### Data processing

The data analysis consisted of two stages. First, to analyse the functional composition of the vegetation in the agricultural landscapes, we used the relative abundance of functional groups at landscape level. For categorical functional groups the abundance of functional group at landscape level ( $Abund_{Fun,group}$ ) was calculated as a sum of landscape abundance indices of individual species within a functional group. The abundance of individual species is a sum of species abundance scores over habitat types. The abundance score of a species is a product of three abundance estimates:

1. Average coverage of a species (scale 0-100%) in sampling plots within each of a particular landscape element of a particular EUNIS habitat type (e.g. single forest patch, field edge or field,  $\overline{Abundance_{SpElement}}$ );
2. Presence-absence frequency (0-100%) of a species within landscape elements (patch, field-edge, corridor) of a particular EUNIS habitat type ( $Frequency_{SpEUNIS}$ );
3. Proportional area (0-100%) of a EUNIS-habitat type within the landscape ( $Area\%_{FINI}$ ).

$$Abund_{Fun,group} = \sum_{Sp} \sum_{EUNIS} (\overline{Abundance_{SpElement}} * Frequency_{SpEUNIS} * Area\%_{EUNIS}) \quad (1)$$

The abundance of the functional groups was rescaled into proportional units of total abundance ( $R.Abund_{Fun,group}$ ), to ensure the comparability of abundance estimates over landscapes and among countries.

$$R.Abund_{Fun,group} = \frac{Abund_{Fun,group}}{\sum_{Fun.type} Abund_{Fun,group}} \quad (2)$$

For functional groups presented as continuous variables (number of hemeroby levels, number of floristic zones), we calculated the abundance-weighted average. The strategy types according to Grime (1977) (C, R, S, CR, CS, RS and CRS) were fuzzy coded by a transformation into three quantitative weight variables – the weight of the C, R and S type with values being either 1, 0.5 or 0.33 (Grime et al. 1988; Hunt et al. 2004).

We performed a partial principal component analysis (pPCA; ter Braak & Šmilauer 2002) on the relative abundance scores of functional groups ( $R.Abund_{Fun,group}$ ). First, we removed the effect of the geographical location (latitude and longitude co-ordinates of the centroids of landscape study sites) characterising climatic conditions, and the factor effect of a particular country characterising

specific land use history and spatial grouping of landscapes within a country, through general linear modelling (GLM, Statistica ver 6.5). Then we applied the pPCA on the GLM residuals of the relative abundance scores of functional groups.

In the second step of analyses we investigated the response of landscape scale (4 km × 4 km) plant species richness within plant functional groups to gradients of landscape structure and land use intensity, using general linear mixed modelling (PROC MIXED in SAS ver. 8.2; Littell et al. 1996). The first general linear mixed model focused on the determinants of species richness within five growth forms: pteridophytes (horse tails and ferns), legumes, other forbs (*sensu stricto*), grasses and sedges. Note that within the growth form group system, used in mixed models of species richness, the classification level 'woody plant' was skipped in the analyses because their richness is constantly low and the occurrence of trees and shrubs depends directly on management activities, mostly on planting (Billetter et al. in press).

In the other two following models we focused on the most revealing and widely applicable functional groups – nature quality indicator classification (high vs. low) and life-span types (annual vs perennial). In these models we applied the methodology of the factorial decomposition of functional groups (Liira & Zobel 2000; Liira et al. 2002). The hierarchical structure of functional groups was implemented to reduce the possible effect of relatedness of species within functional groups (Harvey & Pagel 1991; Kelly 1996). Therefore, the effect of growth form was considered first in the model, followed by the inclusion of the effect of the functional group of interest. In those two models, we restricted to the growth form classification of two classes: graminoids and forbs (*sensu lato*) (App. 2), as the finer classification of growth forms with five growth form types (used previously) resulted in unbalanced factor design due to missing data in several combination between growth form and functional group of interest.

In order to correct for the variation between regions due to differences in biogeography and species pools (Zobel 1997), we included the factor variable 'plant growth form' nested in the factor variable 'country' in the model as a complex random factor. A repeated factor model design with an unstructured correlation-matrix (Littell et al. 1996) between levels of functional groups was included to correct for possible correlations in measurements of the richness in the same vegetation plots of landscape study sites. We corrected analyses for variations in sample size by including in the model the log-transformed number of sample plots as a continuous factor, according to the principles of species-area relationship (Arrhenius 1921). Random factors and unstructured covariance settings were always held in the model.

Species richness was log-transformed to normalise residual distribution and avoid multiplicative effects. We used a stepwise variable exclusion procedure to find the optimal set of statistically significant metrics of landscape structure and land use intensity predicting plant diversity within functional groups (see App. 1. The final model consisted only of those metrics that showed significant main effects and/or had a significant interaction with the factor variable of the functional group in effects on plant species richness. If the interaction term was significant, the main effects of both factors were kept in the model, as stipulated in statistical methodology. We will only present the results of the fixed effects part of the model, as these are the most important ones for ecological interpretation.

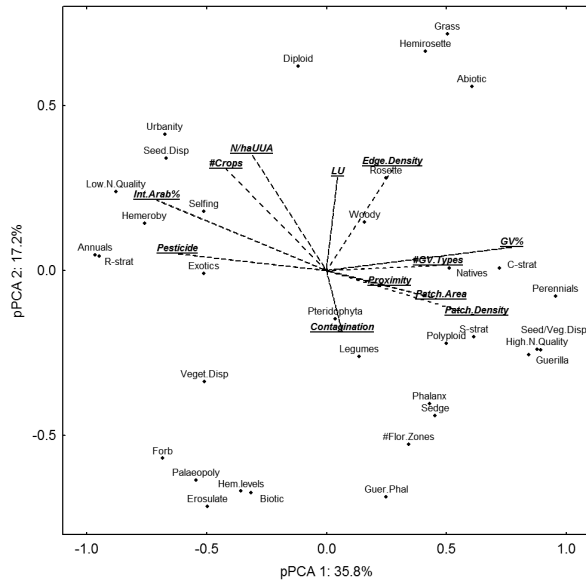
## Results

### 1. Plant functional group composition in agricultural landscapes

We used pPCA to determine the major compositional gradients of functional groups in agricultural landscapes. After considering the effects of geographical location and country, the first two axes of the pPCA describe 53% of the total variation of functional group composition in 4 km × 4 km landscape study sites. The first pPCA axis, describing 35.8% of variation (Fig. 1), is associated with a gradual transition between two clusters of traits with contrasting functional groups: from the dominance of low nature quality plant species, neophytes, urbanophilic and R strategy plants to the dominance of high nature quality species, C and S strategy plants and species with a wide environmental distribution range. This major transition in the functional composition of vegetation is also presented by shifts from the dominance of annuals and selfing species to dominance of perennials, and from seed dispersed to clonal (phalanx or guerrilla) type vegetative dispersal.

The response trend of plant functional groups along the first pPCA axis is consistent with a complex gradient of increasing habitat availability and decreasing land use intensity. The ordination scores of the first axis are negatively correlated with: the proportion of the intensively managed arable land ( $> 150 \text{ kg-N.ha}^{-1}.\text{a}^{-1}$ ;  $r_{\text{Spearman}} = -0.71$ ;  $P = 0.001$ ); number of pesticide applications per year ( $r_{\text{Spearman}} = -0.62$ ;  $P = 0.001$ ); number of crops in rotation ( $r_{\text{Spearman}} = -0.42$ ;  $P = 0.036$ ); there were also some positive correlations: proportion of the natural/semi-natural areas ( $r_{\text{Spearman}} = 0.77$ ;  $P = 0.001$ ); patch density ( $r_{\text{Spearman}} = 0.63$ ;  $P = 0.001$ ); patch area ( $r_{\text{Spearman}} = 0.48$ ;  $P = 0.016$ ); number of habitat types ( $r_{\text{Spearman}} = 0.47$ ;  $P = 0.019$ ) (Fig. 1).





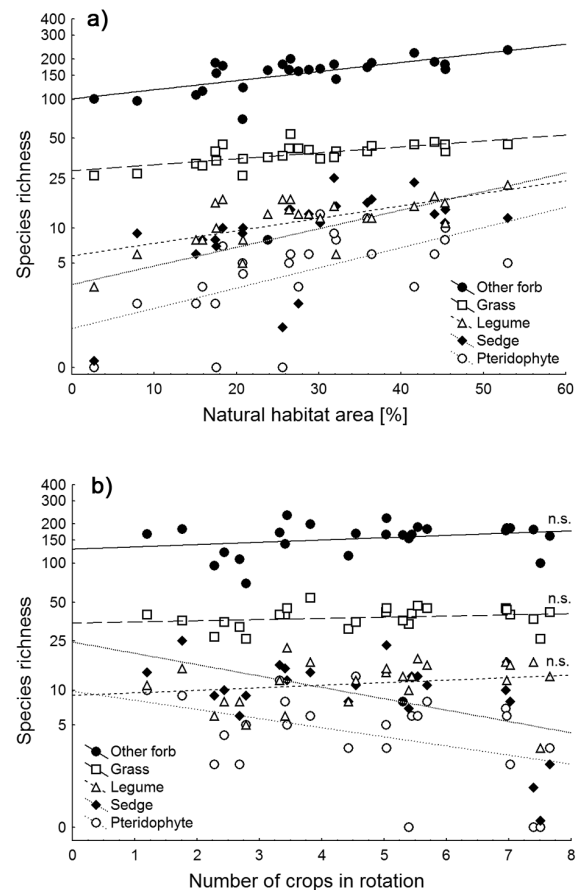
**Fig. 1.** Partial PCA ordination of plant functional group composition in the agricultural landscapes after removal of the geographical effects of longitude-latitude and general country level. Qualitative traits were transformed into dummy variables or fuzzy coded variables (see Text). Dots represent plant trait ordination. Vectors illustrate the correlation of landscape and land use parameters with the first and second axes. For abbreviations see App. 1.

The second pPCA axis, which accounted for 17.2% of variation, reflects the transition from the dominance of forbs and sedges to the dominance of grasses, from erosulate (non-rosette) species to hemirosette or rosette species, and from the prevalence of insect pollinated species to species with abiotic pollen vectors (mostly wind pollinated). It is noteworthy that agricultural landscapes located in the lower half of the ordination diagram (Fig. 1) are also dominated by generalists species characterised by a greater number of hemeroby levels. However, correlations between scores of the second axis and indicators of landscape structure or land use intensity remain statistically non-significant, even if the landscape index of edge density seems to be most correlated to that compositional transition (Fig. 1).

## 2. Species richness within functional groups

### Growth form

Forbs (*sensu stricto*) and grasses are the most species-rich growth form groups in the agricultural landscapes (Fig. 2). In a 4 km × 4 km landscape area we found 71-233 forb species and 27-55 grass species. The maximum number of sedges was 26 species, legumes 23 and pteridophytes 14 species per landscape. The mixed model with five growth forms revealed that a larger percentage of natural/semi-natural habitats in the landscape increased richness within all growth forms (Fig. 2). Pteridophytes and sedges were the most sensitive groups, as their richness was the most largely affected by the proportion of habitat area and land use intensity (estimated via crop diversity, for further explanations see Herzog et al. 2006) which significantly reduced their richness (Table 1). The impact of other potential landscape and land use drivers



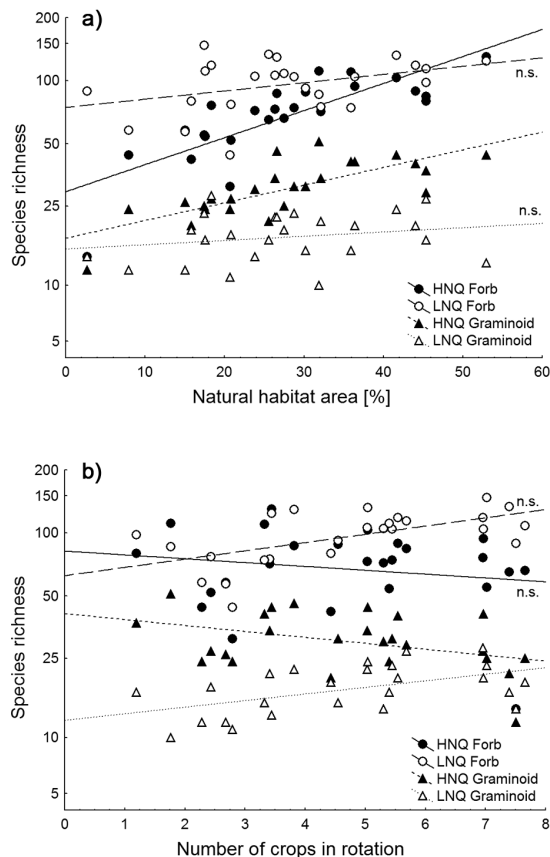
**Fig. 2. a.** The correlation between the proportion of natural and semi-natural habitat area and species richness in growth form groups (narrow groups); **b.** The correlation between the number of crops in rotation per farm and species richness in growth form groups. The significance of trend-lines is taken from the model in Table 1.

on species richness within growth form groups remained non-significant.

#### Nature quality indicator classes

The richness of natural quality groups within forbs (*sensu lato*) is relatively the same, varying from 15 to 131 species in high nature quality forbs and from 45 to 148 species in low nature quality forbs (Fig. 3). Within the graminoids the richness of high nature quality graminoids varied more between landscapes (13–52 species per landscape) than graminoids of low nature quality (11–29 species per landscape area).

The hierarchical mixed model analysis, primarily taking into account the effects of broad growth forms (forbs and graminoids) and secondly estimating the effect of nature quality groups shows that the increasing pro-



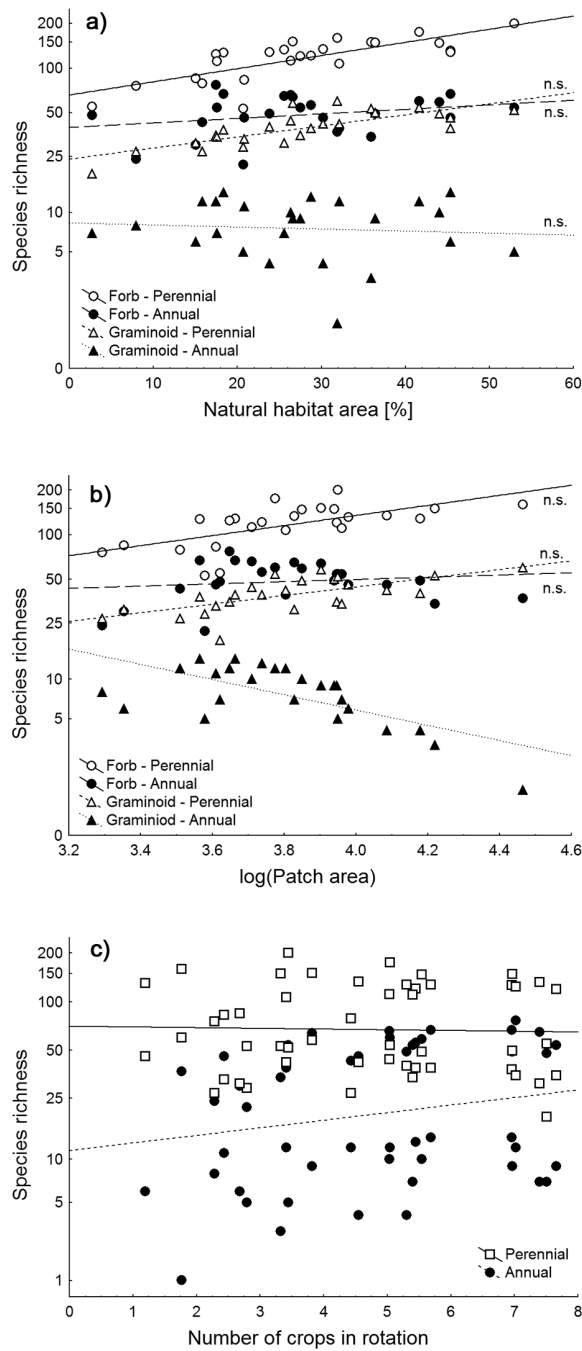
**Fig. 3. a.** The correlation between the proportion of natural and semi-natural habitat area and species richness in nature quality groups and growth form classes (*sensu lato*); **b.** The correlation between the number of crops in rotation per farm and species richness in nature quality groups and growth form classes. The significance of trend-lines is taken from the model in Table 2.

**Table 1.** Mixed model test results of fixed effects on large scale species richness within ‘growth form’ types. Random factors such as country, nested in a ‘growth form’ and the test of unstructured covariation matrix between growth forms are not presented. The betas are the standardised (scale free) estimates of the slope values. Bold variables are significant ( $\alpha < 0.05$ ).

Factor	P	Group	Beta	P
Log (number of plots)	<b>0.0001</b>	Pooled	<b>0.1069</b>	***
Growth form (GF)	<b>0.0001</b>			
GV%	<b>0.0002</b>			
GV%*GF	<b>0.0007</b>	Forb	<b>0.0956</b>	**
		Grass	<b>0.0581</b>	**
		Legume	<b>0.1716</b>	**
		Pteridophyte	<b>0.2526</b>	*
		Sedge	<b>0.2191</b>	*
No of crops in rotation (#CR)	0.0258			
#CR*GF	<b>0.0021</b>	Forb	0.0422	ns
		Grass	0.0001	ns
		Legume	0.0649	ns
		Pteridophyte	<b>-0.2400</b>	*
		Sedge	<b>-0.3208</b>	***

**Table 2.** Mixed model test results of fixed effects on large scale species richness in ‘nature quality indicator groups within ‘growth form’ types. Random factors such as ‘country’, nested in a ‘growth form’ and ‘nature quality indicator group’, and the test of unstructured covariation matrix between functional types are not presented. The betas are the standardised estimates of the slope values. Bold variables are significant ( $\alpha < 0.05$ ).

Factor	P	Group	Beta	P
Log(number of plots)	<b>0.0003</b>	Pooled	<b>0.1793</b>	***
Growth form (GF)	<b>0.0001</b>			
Nat.Quality (NQ)	<b>0.1853</b>	High (H), Low (L)		
GF*NQ	<b>0.0001</b>			
GV%	<b>0.0028</b>			
GV%*NQ	<b>0.0001</b>			
GV%*GF	<b>0.0171</b>			
GV%*GF*NQ	<b>0.0109</b>	HNQ Forb	<b>0.3991</b>	***
		HNQ Gram	<b>0.1612</b>	**
		LNQ Forb	0.0250	ns
		LNQ Gram	-0.0043	ns
EdgeDensity (log) (ED)	0.9790			
ED*NQ	<b>0.0124</b>	HNQ	<b>-0.0749</b>	*
		LNQ	0.0556	ns
ED*GF	0.3350			
ED*GF*NQ	0.7148			
No of crops in rotation (#CR)	0.9458			
#CR*NQ	<b>0.0003</b>			
#CR*GF	0.6006			
#CR*GF*NQ	<b>0.0287</b>	HNQ Forb	-0.0429	ns
		HNQ Gram	<b>-0.1784</b>	***
		LNQ Forb	0.0881	ns
		LNQ Gram	<b>0.1523</b>	**



**Fig. 4.** **a.** Correlation between the proportion of natural and semi-natural habitat area and species richness in life-span classes (annual vs perennial) and growth form classes (*sensu lato*); **b.** Correlation between natural patch area and species richness in life-span classes (annual vs. perennial); **c.** correlation between the number of crops in rotation per farm and species richness in life-span classes (annual vs. perennial) and growth form classes. The significance of trend-lines is taken from the model in Table 3.

portion of natural/semi-natural areas in the agricultural landscape increased the richness of high nature quality species, and forbs in particular (Table 2). The increased density of edge habitats in the landscape resulted in the remarkably decreased species richness of the high nature quality group, and in a slight increase in low nature quality species richness. Land use intensity, best characterised by crop diversity in the model, is negatively related to the landscape-scale species richness in the high nature quality group, and positively to the richness of the low nature quality group. Land use intensity effect is more evident in the case of graminoids (Table 2).

#### Life-span types (annuals and perennials)

Perennial forbs (*sensu lato*) were the most species rich functional group (54-201 species per landscape), while annual graminoids were the most species-poor group (2-15 species) (Fig. 4). The variation range of richness

**Table 3.** Mixed model test results of fixed effects on large scale species richness within 'life span' types (annuals and perennials) within the 'growth form' types (forbs and graminoids). Graminoids consist of grasses and sedges, while forbs include all the rest of species. Random factors such as 'country', nested in a 'growth form' and 'life span', and the test of unstructured covariation matrix between functional types are not presented. The betas are the standardised estimates of the slope values. Bold variables are significant ( $\alpha < 0.05$ ).

Factor	P	Group	Beta	P
<b>Log(number of plots)</b>	<b>0.0001</b>	Pooled	<b>0.1831</b>	***
<b>Growth form (GF)</b>	<b>0.1866</b>			
<b>Life span (LS)</b>	<b>0.0302</b>			
GF*LS	0.0001			
GV%	0.9824			
GV%*GF	0.5818			
GV%*LS	0.0931			
<b>GV%*GF*LS</b>	<b>0.0142</b>	Ann. Forb	0.0042	ns
		<b>Per. Forb</b>	<b>0.116</b>	*
		Ann. Gram	0.0826	ns
		Per. Gram	0.0274	ns
<b>PatchArea (PA)</b> (log-transformed)	<b>0.0223</b>			
<b>PA*GF</b>	<b>0.0008</b>			
<b>PA*LS</b>	<b>0.0005</b>			
<b>PA*GF*LS</b>	<b>0.0001</b>	Ann. Forb	-0.0672	ns
		Per. Forb	-0.0297	ns
		<b>Ann. Gram</b>	<b>-0.4595</b>	***
		Per. Gram	0.0697	ns
<b>No of Habitat Types (#HT)</b>	<b>0.0113</b>	Pooled	<b>0.0567</b>	**
#HT*LS	0.1928			
#HT*GF	0.8850			
#HT*GF*LS	0.5983			
No of crops in rotation (#CR)	0.1031			
#CR*LS	0.3986			
<b>#CR*GF</b>	<b>0.0026</b>	<b>Annual</b>	<b>0.1008</b>	**
		<b>Perennial</b>	<b>-0.0823</b>	**
#CR*GF*LS	0.0994			



of annual forbs (*sensu lato*) and perennial graminoids was similar (23-78 and 20-61 species per landscape respectively).

The hierarchical model, taking into account the interactive effect of life-span groups (annuals and perennials) within the broad groups of growth forms (Table 3), reveals that the number of natural/semi-natural habitat types in the landscapes has a positive effect on species richness within all life-span groups. The positive effect of habitat availability on species richness is evident only for perennial forbs. A significant negative relationship between the mean habitat patch size and large-scale species richness can be observed only in the functional group of annual graminoids. The increasing land use intensity, again described by the number of crops in rotation, causes an increase in the richness of annuals and a decrease in the richness of perennials.

## Discussion

The reviews by Vitousek et al. (1997) and Green et al. (2005) show that biodiversity conservation initiatives have mostly failed to arrest the processes of biodiversity loss – many ecosystems have rapidly declined in biodiversity, mainly because of the loss of habitats and the intensification of agricultural land use. Modelling efforts indicate that habitat loss, together with the deterioration of habitat quality, may be the main driver in biodiversity decline on a large scale (Harrison & Bruna 1999; Sala et al. 2000). Although some empirical data exists (Fahrig 2003; Wilson et al. 2003; Petit et al. 2004; Honnay et al. 1999; Yiming & Wilcove 2005), information about the impact of landscape level processes on biodiversity through large geographical range remains very scarce (Grashof-Bokdam & van Langevelde 2005).

One reason why it is difficult to consider the combined effects of land use intensity, habitat fragmentation and loss is the scale of such studies. Biodiversity studies in agricultural landscapes have typically focused either on individual landscape elements or on a single farm (Grashof-Bokdam & van Langevelde 2005). There are only a handful of studies that address the impact configuration of landscape elements on plant diversity (Burel et al. 1998; Le Coeur et al. 2002; Deutschewitz et al. 2003; Smart et al. 2006). In the current paper we focused on the landscape scale and compared 25 landscapes in Europe, in order to distinguish the effects of habitat loss, land use intensity and habitat configuration on composition of plant functional groups and plant species diversity.

The abundance and composition of plant functional groups in agricultural landscapes was mainly correlated to the combined gradient of natural habitat availability and agricultural land use intensity. Through three mixed

models, the species richness within functional groups also showed a consistent relationship to the proportion of (semi) natural habitat area. In particular, an increase in the proportional area of natural and semi-natural habitats resulted in increased abundance and richness of habitat specialists: sedges, pteridophytes, perennial forbs and the species of high nature quality. The same functional groups were negatively affected by a high intensity of agricultural land use. In contrast, intensification in agriculture enhanced the abundance and richness of annual plant species and species of low nature quality, i.e. species that are more adapted to disturbed habitats (Hodgson & Grime 1990; Bender et al. 1998; Kleijn & Verbeek 2000; Geertsema et al. 2002).

It has been suggested that mown road verges, field margins, tree lines and hedgerows may compensate the loss of natural and semi-natural habitats (Kleijn & Verbeek 2000; Moonen & Marshall 2001; Deckers et al. 2004; Cousins 2006) and constitute refugia for vulnerable species (Baudry et al. 2000; Tikka et al. 2001; Le Coeur et al. 2002; Haddad et al. 2003; Petit et al. 2004; Mix et al. 2006). We found that landscapes with high densities of edges suppressed the richness of species of high nature quality. The second pPCA gradient of functional group composition reflected the variation of plant trait composition associated with the transition from the functional groups of habitat interior species to traits of edge species. The larger patch area of natural habitats enhanced the dominance of forbs, sedges, insect pollinated or clonal plants and species with a wide environmental distribution range in the landscape. Landscapes with larger patches of habitats had lower species richness of annual grasses. Both analyses suggest that linear elements of the landscape do not function as alternative habitats or corridors for the dispersal of interior species (see also Harrison & Bruna 1999). It is well established that the life history traits of predominating species differ between the edge habitats and the interior parts of natural habitats (Grashof-Bokdam 1997; Honnay et al. 1999; Deckers et al. 2004; Kolb & Diekmann 2005), thus linear elements evidently do not provide a suitable environment for specialist species of natural and semi-natural habitats.

From our analyses it became clear that the complex gradient of high quality habitat availability in parallel to land use intensity is the main driver of plant functional group composition at the level of landscapes, while the effect of landscape structure is of less importance. To maintain plant biodiversity, ecosystem function and services at the landscape scale we suggest a focus on the importance of the habitat patch-mosaic system, consisting of large patches from various ecosystem types (Honnay et al. 1999; Cook et al. 2002; Godefroid & Koedam 2003). This conclusion is not consistent

with general knowledge as shown for animals (McCoy & Mushinsky 1994; Bender et al. 1998; Fahrig 2003; Schooley & Wiens 2005), that has already been challenged by plant ecologists (Harrison & Bruna 1999; Dauber et al. 2003; Murphy & Lovett-Doust 2004; Soons et al. 2005). Therefore, there may be a fundamental difference between animal and plant species – plants being more limited by particular habitat requirements and by sensitivity to land use intensity and generally unable to disperse along linear elements at any stage in their life cycle, while animals may at least temporarily tolerate the habitat conditions of linear elements.

## Conclusions

Observing plant functional groups in agricultural landscapes with different disturbance regimes, we detected two basic trends in responses of functional groups to multiple agri-environmental factors: response to habitat availability and habitat quality. In the analysis to assess the relationships between the abundance and richness of particular plant functional groups and landscape scale parameters, we revealed that various functional traits can be combined into an emergent group of nature quality indicator species, and that such a group has the highest prognostic power to describe the status of conditions for biodiversity in the agricultural landscape. The loss of species mostly concerns those inhabiting undisturbed natural or semi-natural ecosystems, while disturbance tolerant species predominate in highly fragmented or structured agricultural landscapes. The monitoring of biodiversity in agricultural landscapes would be more informative, if it distinguished between functional groups of plant species, concentrated more on the high nature quality species and treated exotics, invaders, ruderals, cultural plants, urbanophilic and hemerobic species separately.

Our study showed that in agricultural landscapes, the loss of natural and semi-natural habitat patches is the most important driver of the decline in plant diversity, while the impact of land use intensity is important only in particular cases. Contrary to our expectations, edges and linear elements mostly supported disturbance tolerant generalist species and not the species with requirements to high nature quality. These findings challenge the idea that corridors and edge communities may compensate the loss of natural and semi-natural habitats for plant species of high nature value. One conclusion of our results is that for plant biodiversity conservation, the protection of patch-mosaic systems consisting of historically continuous, natural and semi-natural habitats in agricultural landscapes is far more important than the creation of narrow linear elements or fallow land.

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For App. 1-2, see JVS/AVS Electronic Archives;  
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**App. 1.** Landscape structure metrics and land-use intensity indicators used as arguments in the model of gamma diversity.

Index name	Comments
GV%	The proportional area of all natural/semi-natural habitat elements in the landscape.
No of habitat types	The number of natural/semi-natural habitat types using EUNIS classification.
Edge density	'The edge density' of all natural/semi-natural habitat elements in the landscape (log-transformed).
Patch area	The average natural/semi-natural habitat patch area (log-transformed).
Patch density	The patch density of natural/semi-natural habitat elements per km <sup>2</sup> .
Proximity	Proximity of natural/semi-natural habitat landscape elements – the landscape index, combining patch size and distance.
Contamination	Contamination index for natural/semi-natural habitat landscape elements– the landscape index combining patch size and distance.
N/HaUUA	Nitrogen input to utilized agricultural area (UAA) (kg N/ha).
Int. Arab%	The proportional area of UUA used for intensively managed crops (N load per ha is >150 kg/ha).
No of crops in rotation	Average number of crops used in the farms.
Livestock Units (LU)	Average number of livestock units per ha (LU/ha), calculated as the weighted average per farm.
Pesticides	Average number of herbicide, insecticide, fungicide and retardant applications on the two major crops of the rotation.

**App. 2.** Species traits and functional groups, derived from the BIOLFLOR database (Klotz et al. 2002, www.ufz.de/biolflor).

Trait/Group	Comments
Nature quality indicator class	The low or high nature quality species of habitats. This is a classification combining traits (floristic status in Europe, anthropophily and ruderal strategy) and species distribution in communities (the observed presence in anthropogenic or disturbed communities) to separate exotics, weeds, ruderals and cultural plants from other native species
Floristic status	Native or introduced (exotic) species in Europe
Hemeroby type	The most common hemeroby level of a species (3 main types).
Number of hemerobic levels or hemerobic plasticity	The number of hemeroby levels described for the species (maximum=7 levels).
Urbanity type	The most common urbanity type of a species: urbanophilic, urbanoneutral and urbanophobic.
Growth form (narrow groups)	Forbs ( <i>sensu stricto</i> ), legumes, grasses, sedges, pteridophytes (ferns, horse tails, club mosses) and woody plants.
Growth form (wide groups)	Forbs ( <i>sensu lato</i> , incl. legumes and pteridophytes) vs. graminoids (incl. grasses and sedges).
Strategy type	Plant strategy categories (C, R, S, CR, CS, RS, CRS; Grime 1977). For factor analyses they were quantified into fuzzy variables with weight values 1, 0.5 or 0.33 respectively.
Rosette growth form type	Plant without leaf rosettes (erosulate-plant) and with leaf rosettes, and in case of rosettes, the presence of a leafy stem (hemirosette-plant), or else all leaves are in rosette (rosette-plant)
Life-span type	Annual or perennial lifespan.
Dominant reproduction type	Only seed, only vegetative or both (Seed/Veg).
Vegetative propagation type	Short or long distance vegetative propagation if clonal growth is present (phalanx, guerilla or both types).
Ploidy type	Diploid, polyploid, paleopolyploid species.
Pollen vector	Mostly abiotic (usually wind pollinated), biotic (insect pollinated) or self-pollinating species.
Self-incompatibility type	Self-compatible or -incompatible in pollination
Floristic variance	The number of floristic zones (#Floristic zones) in which the species is present. Zones counted: e.g. arctic, boreal, temperate, submeridional, meridional, subtropical, tropical, austral and Antarctic.

**App. 1-2.** Internet supplement to: Liira, J. et al. 2008.

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