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Functional richness of local hoverfly communities (Diptera, Syrphidae) in response to land use across temperate Europe

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Environmental change is not likely to act on biodiversity in a random manner, but rather according to species traits that affect assembly processes, thus, having potentially serious consequences on ecological functions. We investigated the effects of anthropogenic land use on functional richness of local hoverfly communities of 24 agricultural landscapes across temperate Europe. A multivariate ordination separated seven functional groups based on resource use, niche characteristics and response type. Intensive land use reduced functional richness, but each functional group responded in a unique way. Species richness of generalist groups was nearly unaffected. Local habitat quality mainly affected specialist groups, while land use affected intermediate groups of rather common species. We infer that high species richness within functional groups alone is no guarantee for maintaining functional richness. Thus, it is not species richness per se that improves insurance of functional diversity against environmental pressures but the degree of dissimilarity within each functional group.

Global change has emerged as a serious threat to biodiversity. Among various factors of human alteration, anthropogenic land use has been suggested as the most influential one (Sala et al. 2000, Buckley and Roughgarden 2004). In many countries, land use is dominated by agriculture which has been subjected to major changes in the course of industrialisation. The intensification of agricultural land management and the loss of area, connectivity and diversity of semi-natural habitat led to significant declines in species richness (Krebs et al. 1999, Robinson and Sutherland 2002). In turn, the loss of species interferes with ecological functions and ecosystem services of species assemblages (Naeem et al. 1994, Hooper and Vitousek 1997, Loreau 1998, Tilman 2000, Diaz and Cabido 2001, Loreau et al. 2001, Petchey 2004). Yet, a better understanding of the consequences of biodiversity loss on community functioning is essential in the context of global environmental change (Chapin III et al. 2000, Hooper et al. 2005).

Several hypotheses have been proposed to explain the relationship between biodiversity and ecosystem functioning (reviewed by Naeem 1998), among which the insurance hypothesis (Lawton and Brown 1994, Yachi and Loreau 1999), as a modification of the redundancy hypothesis (Walker 1992), provides great explanatory power (Loreau et al. 2001). Simulations confirm that if species exhibit similar ecological functions (i.e. are functionally redundant) a loss of species within a particular functional group may be compensated by other members of that very group (Yachi and Loreau 1999). Consequently, a high number of species

per functional group is likely to provide insurance of community functioning against increasing land-use pressure and therewith facilitates long-term sustainability of ecosystems and their services (Tscharntke et al. 2005). Ongoing extinction of species, on the other hand, bears the risk of losing functional diversity within a community (Fonseca and Ganade 2001).

Research on the relationship between diversity and functional aspects, however, has been dominated by small-scaled experiments within a single trophic level, usually primary producers (Loreau et al. 2001, Balvanera et al. 2006). Such an experimental approach examines whether diversity per se has an effect on community functioning while other environmental variables are held constant. Thus, most of these experiments were not designed to investigate changes in ecosystem functioning that can be related to environmental change and the resulting particular patterns of species loss. In natural systems, however, environmental change is not likely to act on biodiversity per se, e.g. by random, nondirectional extinction, but rather according to species traits that affect assembly processes of local communities. Consequently, recent calls have been made to investigate the relationship between environmental change and functional groups in natural systems across local, landscape, and regional scales as well as multiple trophic levels (Wardle et al. 2000, Loreau et al. 2001, Petchey and Gaston 2002, Diaz et al. 2003, Naeem and Wright 2003, Symstad et al. 2003, Hooper et al. 2005, Tscharntke et al. 2005). Therefore, studies in agricultural systems seem to be valuable since the effects of anthropogenic land use on species richness and ecosystem functioning can be enormous and, in contrast to experiments, they can be studied in situ on a variety of functional groups. Studies in (semi-)natural systems can also bear the potential to disentangle the particular effects of different anthropogenic pressures such as agricultural management and changes in landscape structure.

Results from the recently completed EU research project 'Greenveins' demonstrate robust relationships between the diversity of plants, birds, and arthropods and both landscape structure and agricultural land-use intensity across temperate Europe. It has been shown that increasing human land use not only decreases species richness at the local (Hendrickx et al. 2007) and landscape scale (Billeter et al. unpubl.), but also affects assembly processes mediated by species traits, thus influencing local community composition (Schweiger et al. 2005). These studies suggest that the assemblage of local communities is mainly determined by two interacting processes which are both altered by land use. While habitat loss and pesticide burden particularly contribute to the extinction of specialised and rare species, habitat fragmentation per se and the disrupted exchange of individuals between local communities affect less mobile species. Reduced inter-patch dispersal adversely affects (meta-)population dynamics, so that low dispersing species are prone to extinction (Hanski and Gilpin 1997, Tscharntke and Brandl 2004, Schweiger et al. 2005). Consequently, intensively utilised landscapes will be dominated by generalist and highly mobile species.

Intensified land use and the corresponding selection for generalists and highly mobile species are therefore very likely to affect the structure and distribution of functional groups in a characteristic way. This may lead to the following expectation: Functional groups which mainly consist of specialised, rare, or less mobile species are at higher risk of extinction when land use is intensified than groups dominated by generalist or highly mobile species. Such selective effects of land use on resource or dispersal limited species groups might lead to a decrease in functional richness (i.e. number of functional groups) and therewith to a decrease in ecosystem reliability and services.

In this study, we investigate this expectation using data on local hoverfly communities (Syrphidae) that were sampled in agricultural landscapes along a pan-European transect covering gradients in both land-use intensity and landscape structure. Hoverflies are one of the most biologically diverse families of the Diptera (Speight 2003) and inhabit most terrestrial and many aquatic ecosystems. The adults visit flowers and feed on pollen and nectar, which makes them the most important pollinators besides bees. The larvae show a broad variety of life styles covering a wide spectrum of resource use (Thompson and Rotheray 1998). Although most species are morphologically fairly uniform, they have a 400-fold range in body weight (from about 0.5 mg to more than 200 mg; Rojo et al. 2003). Thus, species can differ considerably in their mobility ranging from rather poor flyers that never move far from their larval habitats (<2 m; Schönrogge et al. 2006), to highly mobile species (Gatter and Schmid 1990) that can move more than two kilometres per day (Schneider 1958). Nonetheless, most hoverfly species (90%) are regarded as non-migrants (Speight 2003). The broad spectrum of life history strategies, especially regarding the degree of specialisation and mobility, and a corresponding broad spectrum of functional characteristics makes hoverflies ideal organisms for the analysis of the relationships between land use and community functioning across several scales.

Anthropogenic land use is assumed to affect ecosystem functioning by altering the number and composition of functional groups, but methods of classification are still discussed (Gitay and Noble 1997, Wilson 1999, Naeem and Wright 2003). Three different types of approaches to functional groups can be distinguished: 1) based on the response of organisms to perturbations (Gitay and Noble 1997); 2) based on the use of the

same resource (alpha guilds sensu Wilson 1999); and 3) based on the possession of similar traits regardless of their interrelationships with ecosystem functioning (data-defined functional groups senu Gitay and Noble 1997, or 'emergent' functional groups sensu Lavorel et al. 1997). However, there is no specific type of functional classification that is appropriate universally (Hooper et al. 2002). Some authors argue to distinguish strictly between response and effect functional groups (Naeem and Wright 2003), for the restriction of functional groups based on the response to perturbations (Gitay and Noble 1997), or for the strict use of objective criteria and multivariate methods to determine functional groups (Grime et al. 1997, Blondel 2003). However, a common criticism of studying the effects of functional group diversity on ecosystem processes is that the underlying rationale may be circular. If functional groups have been defined a priori by their influence on an ecosystem process under investigation, then, by definition, removing or adding species to that group will alter the process (Hooper et al. 2002). Thus, in order to capture 'what species do in ecosystems' (Lawton 1994), it seems adequate to characterise functional groups not only according to effect type such as trophic position, or response type to environmental factors, but using an array of traits that cover a broad spectrum of a species' ecology.

In this study, we apply such a general concept of functional groups by using a mixture of resource-use traits (e.g. food type), niche characteristics (e.g. microhabitat), and response type (e.g. inundation tolerance). This makes our approach advantageous in two ways: It avoids the circular argument and it allows to analyse the relationship between biological traits (related to resource use and dispersal) and land use. An existing database on the biological traits of European hoverflies (''syrph the net'', Speight 2003) provided the basis for classifying hoverflies into functional groups.

Specifically, we addressed the following hypotheses: 1) species richness in each functional group decreases with intensified land use, whereas functional groups with a high proportion of species characterised by resource or dispersal limitation are most susceptible; 2) increasing land use leads to the loss of functional groups.

Material and methods

Sample sites

Our study is based on data generated and compiled in the EU research project 'Greenveins'. The methods are described in detail in Schweiger et al. (2005). Hoverflies were sampled according to a common protocol in 24 sample sites of 16 km^2 in agricultural landscapes distributed over seven European countries: France (3 sample sites), Belgium (4), the Netherlands (4), Switzerland (3), Germany (4), Czech Republic (2), and Estonia (4; Fig. 1). The sample sites were predominantly agricultural (between 40% and 98% agricultural area), flat (thus potentially suitable for intensive arable agriculture), located below 400 m a.s.l., and representative of a larger area. Together, they covered a wide range of both agricultural land-use intensity and landscape structure (Herzog et al. 2006 and Table 1).

Environmental variables

Land-use intensity was assessed at sample site level by interviewing farmers in a standardised way about management practices on arable fields (Herzog et al. 2006). The number of crops in rotation, pesticide applications (insecticides, herbicides, fungicides), and the amount of nitrogen fertiliser applied per hectare and year were recorded.

Landscape structure was evaluated from digitized habitat maps based on ortho-rectified aerial photographs with a spatial resolution smaller than 1×1 m using ArcGIS software (ESRI 2003). Habitats were classified according to the European Nature Information System (EUNIS) habitat classification (available at http://eunis.eea.eu.int/habitats.jsp) and were then aggregated into woody or herbaceous elements. Three aspects of landscape structure were considered at sample site level: amount of habitat per sample site (percentage woody and herbaceous elements); spatial configuration of woody and herbaceous elements measured with landscape metrics using FRAGSTATS (McGarigal et al. 2002); and habitat diversity (number of EUNIS habitat types per sample site). Since many landscape indices are often correlated, we subjected the following metrics to a principal component analysis (PCA): number of patches, patch density, edge density, proximity index, Euclidean nearest neighbour distance, patch cohesion index, splitting index, and clumpiness index. In order to minimise collinearity, indices were selected according to the highest loadings ($|r| > 0.74$) on the first two PCA-axes which explained together more than 65% of the variance. The selected indices were mean Euclidean nearest neighbour distance and mean proximity index for woody and herbaceous elements. The mean Euclidean nearest neighbour distance denotes the distance from one habitat patch to its nearest neighbour of the same type averaged over the sample site. The proximity index describes the size-weighted distance between habitat patches. Large proximity values indicate landscapes with large patches situated close to each other.

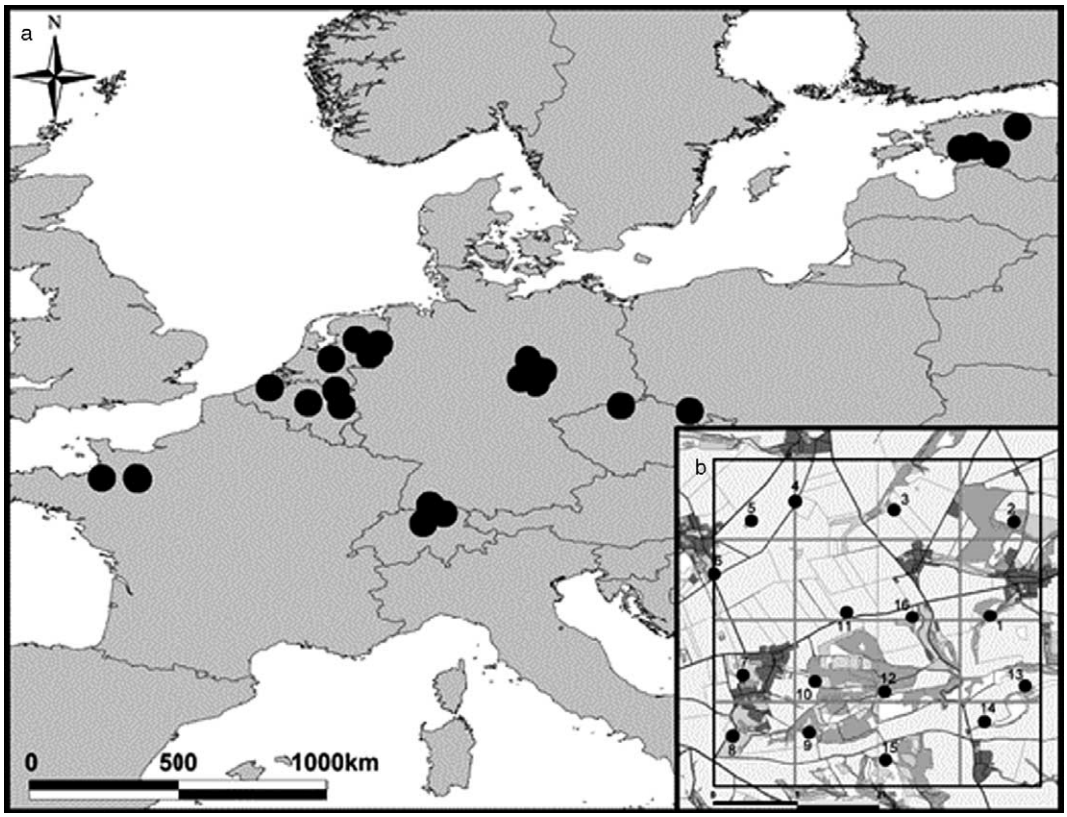

Fig. 1. distribution of sample sites across Europe (a), and the stratified random hoverfly sampling design in one of the sample sites (b). A duplicated trap set was placed at a randomly chosen ecotone between semi-natural habitat and arable field within each of 16 grid cells of 1 km^2.

Since landscape structure affects local communities not only at the landscape scale but also at the local scale, we considered the very same metrics (except for spatial configuration) at the local scale, too. These were calculated for circular areas with a radius of 50 m around hoverfly sample points and comprised the amount of woody and herbaceous elements (percentage cover) and local habitat diversity (number of EUNIS habitat types). A radius of 50 m seems appropriate because most European hoverfly species are considered as non-migrants (Gatter and Schmid 1990, Speight 2003) which rarely disperse more than 50 m (Lövei et al. 1998, Wratten et al. 2003).

Besides local and landscape factors, regional variation is very likely to affect local species or functional richness. In order to correct for such large scale

Table 1. Mean values of environmental variables across seven European countries (±one standard deviation).

Country	Crop	Pesticide	Nitrogen	%SNH	Proximity	Diversity	Loc.%SNH	Loc. diversity
Be (4)	4.0 (±2.4)	3.1 (±2.3)	238 (±51)	28 (±14)	37 (±27)	31 (±4)	48 (±21)	3.6 (±0.4)
Cz (2)	3.6 (±0.3)	0.8 (±1.2)	55 (±23)	40 (±19)	235 (±207)	29 (±1)	72 (±7)	3.3 (±0.3)
Est (4)	3.7 (±1.5)	0.7 (±0.5)	140 (±135)	31 (±5)	76 (±44)	29 (±2)	54 (±29)	3.6 (±0.8)
F (3)	5.4 (±0.3)	2.3 (±0.3)	206 (±37)	34 (±10)	25 (±17)	22 (±2)	50 (±10)	3.2 (±1.0)
D (4)	7.0 (±1.1)	3.2 (±0.8)	190 (±44)	18 (±11)	52 (±40)	25 (±5)	43 (±23)	3.2 (±0.7)
CH (3)	5.9 (±1.0)	1.4 (±0.3)	159 (±26)	34 (±15)	24 (±16)	31 (±3)	51 (±17)	4.3 (±0.5)
Nl (4)	2.5 (±0.2)	0.5 (±0.3)	317 (±37)	16 (±6)	23 (±22)	28 (±3)	35 (±19)	3.5 (±0.8)

Crop, number of crops in rotation; pesticide, number of pesticide applications to major crops per year; nitrogen, nitrogen application ($kgha^{-1}y^{-1}$); %SNH, proportion of semi-natural habitats (woody and herbaceous elements aggregated); proximity, proximity index of semi-natural habitats; diversity, number of habitat types per sample site; loc. %SNH., local proportion of semi-natural habitats; loc. diversity, local number of habitat types. Be, Belgium; Cz, Czech Republic; Est, Estonia; F, France; D, Germany; CH, Switzerland; Nl, The Netherlands.

Table 2. Life history traits of hoverflies used in the analysis. 1–7: taken from Speight et al. (2001), 8 and 9 taken from Dziock (2006).

Trait variable	Categories (number)
Larval microhabitat	Trees, upward climbing lianas, herb layer, timber, dung, litter, stones, nests of social insects, root zone, on/in water plants, submerged sediment/debris, water-saturated ground (12)
Larval food	saprophagous, saproxylic, phytophagous, zoophagous (4)
Development length (egg/larva/puparium)	Less than 2 months, 2– 6 months, 7–12 months, more than one year (4)
Inundation tolerance	No inundation tolerance, tolerant and short breathing tube, tolerant and medium sized breathing tube, tolerant and long breathing tube (4)
No. of generations per year	Less than one, one generation, two generations, more than two (4)
Migratory status	Non-migrating, recorded migrant, strongly migratory (3)
Flight period in Europe	Feb, Mar, Apr, May, Jun, Jul, Aug, Sep, Okt, Nov (10)
Body size	Less than 5, 5–5.9, 6–6.9, 7–7.9, 8–8.9, 9–9.9, 10–11.9, 12–14.9, more than 15mm (9)
Distribution in Europe	Ubiquitous, very common, common, local, scarce, rare, very rare (7)

gradients, we also considered the geographical position (i.e. latitude and longitude) of each sample site as a covariate in the analysis.

Our list of pre-selected explanatory variables finally comprised 15 variables. At the local scale we considered habitat diversity and amount of woody and herbaceous elements. At the landscape scale we measured habitat diversity, amount of woody and herbaceous elements, Euclidean distance and proximity for woody and herbaceous elements, crops in rotation, and pesticide and nitrogen application. At the regional scale we corrected for latitude and longitude.

Hoverfly sampling

We sampled local hoverfly communities in a stratified random way with 16 duplicated sets of combined flight traps (a combination of flight and yellow pan trap; Duelli et al. 1999) per sample site (sampling scheme in Fig. 1). Sampling was carried out following a 'minimum effort while maximising efficiency' approach (Duelli 1997). We sampled during two periods of maximum activity and density of the species (7 weeks in autumn 2001 and 5 weeks in early summer 2002). The samples of each trap set were pooled and the specimens were identified to species level, resulting in information about 16 local communities per sample site.

Statistical analysis

In total 133 hoverfly species were trapped. Trait data were not available for five species which were omitted from the data table, leaving 128 species in the analysis. Species were classified into functional groups according to nine trait variables (larval microsite, larval food, development length, inundation tolerance, number of generations per year, migratory status, flight period, body size and distribution in Europe) comprising a total of 57 categories (provided by Speight et al. 2001 and Dziock 2006; Table 2). The species traits were fuzzy coded on a 0 to 3 scale following the approach of Chevenet et al. (1994). Since the fuzzy coded trait data consisted of discrete character states rather than continuous ones, we used fuzzy coded multiple correspondence analysis (MCA; Castella and Speight 1996). The number of relevant factorial axes we retained in the analysis was determined by the scree test (Cattell 1966). Following the MCA, we used the factorial loads at the reduced number of axes to carry out a cluster analysis of the species (using Euclidean distance and Ward-algorithm; Chevenet et al. 1994). Functional groups were then identified based on visual inspections of the resulting dendrograms and ecological sense.

Species richness within each functional group was analysed separately, because previous multivariate analyses of variance (MANOVA; not shown) indicated highly differentiated response patterns. Local species richness per functional group was related to explanatory variables using generalised linear mixed effects models (GLMM) via penalised quasi-likelihood estimation (PQL; Breslow and Clayton 1993). This allowed the sample site effect to be accounted for as a random variable. Thus, local communities (sample point data) were considered to be nested within landscapes (sample sites). Other variables were treated as fixed effects. As species richness data were counts, a Poisson error distribution with a log link function was used in all statistical analyses (Quinn and Keough 2002). We allowed for curvilinear effects of the explanatory variables by incorporating their logarithmic and quadratic terms. In order not to over-parameterise the models, we reduced the set of linear, logarithmic and quadratic terms first. Therefore, we performed single variable regressions of linear, linear and quadratic, and logarithmic terms on species richness per functional group, and included only the most significant term(s) of each variable in the initial models. In case of second order terms, both linear and quadratic terms were used initially. The explanatory variables were standardised to

mean zero and unit standard deviation to make the coefficient estimates comparable in terms of importance (Quinn and Keough 2002). The initial models were simplified by stepwise regression, wherein we manually removed variables according to their p-values. Since the penalised quasi-likelihood approach does not calculate true likelihood, likelihood ratio tests and likelihood-based t statistics are not available. Therefore, we did not use measures of model fit for model simplification but relied on p-values and we retained only effects significant at the 0.05 level in the final minimal adequate models. Nevertheless, all final models happened to have also lowest values of Akaike's information criterion (AIC; Sakamoto et al. 1986). To give an impression about the relative importance of each predictor, we provide their standardised partial regression coefficients.

Functional richness (i.e. local number of functional groups) was related to environmental variables in the same way as species richness per functional group, using generalised linear mixed effects models with Poisson error distribution and penalised quasi-likelihood estimation, and a significance level of 0.05 for model simplification.

All calculations were performed using the statistical software R 2.1.0 (R Development Core Team 2004) with the packages MASS (Ripley and Venable 2004), ade4 (Thioulouse et al. 2004) and vegan (Oksanen 2005).

Results

Functional groups

Species-trait relationships were analysed by means of multiple correspondence analysis (MCA) based on nine biological traits (Table 2). The first four factorial axes explained 33% of the total variance in species traits and were retained in further analysis according to Cattell's scree test. The trait variables with the largest contribution to species separation were microsite and food of the larvae, and inundation tolerance. This was indicated by high correlation ratios of these traits with the first four factorial axes (Table 3). The number of generations per year and body size had at least higher than average correlation ratios with some axes, while migratory status and flight period showed low correlation with all axes, thus contributing little to species separation.

Table 3. Correlation ratios (variance of the category scores to the total variance) for the nine fuzzy coded trait variables along the first four axes of the multiple correspondence analysis of the traits matrix. Figures in bold show the ratios higher than the average correlation ratio for that axis.

	F1	F2	F3	F4
Microsite	**0.49**	**0.51**	**0.46**	**0.31**
Larval food	**0.52**	**0.82**	**0.40**	0.11
Development length	0.31	0.09	**0.29**	**0.23**
Inundation tolerance	**0.55**	**0.74**	0.03	0.48
No. of generations	**0.48**	0.12	**0.29**	0.20
Migratory status	0.28	0.16	0.12	0.05
Flight period	0.10	0.02	0.01	0.00
Body size	0.19	**0.37**	**0.44**	**0.39**
EU-distribution	**0.43**	0.12	0.17	0.21
Mean correlation ratio	***0.37***	***0.33***	***0.24***	***0.22***

The cluster analysis of the species scores from the first four factorial axes of the MCA resulted in seven clearly separated and homogenous groups with very distinct ecological characteristics (Table 4). More groups would not have been biologically interpretable, while fewer groups would have led to coarse and heterogeneous groups. One of the groups consisted only of two rare species and was omitted, leaving six groups for further analysis. Species numbers in each group ranged from 11 to 35 with an average of 21 species (Table 4). Two groups consisted mainly of habitat or feeding specialists (group 1 and 2), two consisted mainly of generalists (group 5 and 6) and two were intermediate (group 3 and 4). Group 1 contained rare specialist saprophages with an affinity

Table 4. Functional grouping of hoverfly species by means of cluster analysis on the basis of factorial loads resulting from multiple correspondence analysis of the species-trait matrix. Number of species per group in brackets. Inun. Tol, Inundation tolerance; Gen. yr^{-1}, number of generations per year. A detailed species list and assignment to functional groups will be provided by the authors on request.

Group	Specialization	Distribution	Body size	Feeding style	Microsite	Inun. tol.	Gen.yr^{-1}
1 (11)	specialists	rare-uncommon	small-medium(large)	saprophagous	water plants	medium	1–2
2 (15)	specialists	uncommon-rare	medium/large	saproxylic	trees/root zone	medium	<1
3 (35)	intermediate	very common-rare	medium	phytophagous or zoophagous	herb layer/litter	none	1–2(3)
4 (25)	intermediate	common-rare	medium-(large)	zoophagous	trees/root zone	none	1–(2)
5 (22)	generalists	common-everywhere	large	saprophagous	wet microsites	high	≥1
6 (18)	generalists	everywhere-very common	medium	zoophagous	litter/herb layer	none	>2

to water plants. Group 2 contained specialised species feeding in sapruns on trees, rotting roots, or under bark with a development time larger than one year. Group 3 species live in the herb or litter layer and are either phytophagous or zoophagous with an intermediate degree of specialisation. Group 4 contained medium-sized species feeding on tree aphids or root aphids with an intermediate degree of specialisation. Group 5 had a high proportion of mostly common saprophagous generalists with large body size and high dispersal power. Group 6 represented typical r-strategists: very common generalist predators with more than two generations per year and very high migratory power.

Species richness per functional group

Mean species richness per functional group was 0.9 at the local scale and 5.3 at the landscape level. Variation among local communities was substantial ranging from zero to 12 species per group whereas at the landscape level a minimum of one and a maximum of 15 species per group were found. The final models analysing this variation differed in their complexity with regard to the number and character of significant parameters (Table 5). Each group responded in a unique way to land use and landscape features. No factor at the local or landscape scale influenced species richness in a similar way across all functional groups. Moreover, groups responded to a different extent to particular parameters as indicated by different standardised partial regression slopes (Table 5).

Functional richness

Local communities consisted of 2.5 functional groups on average. At this scale variation ranged from zero to six groups per sample point. The mean number of functional groups at the landscape level was 5.0. Landscapes with low functional richness (three groups) opposed landscapes with high functional richness (six groups). Factors acting at both scales significantly influenced the incidence of functional groups. At the landscape scale, intensive land use expressed as low crop diversity and low amount of semi-natural habitat led to a reduction of functional richness. Low percentage cover of wood and herbs were associated with reduced functional richness whereas habitat fragmentation did not have a significant effect (Table 6). At the local scale, decreasing habitat diversity within a radius of 50 m around sampling points resulted in a lower functional richness (Table 6).

Table 5. Standardised partial regression coefficients of significant ($P<0.05$) environmental factors retained in the final models explaining species richness within six functional groups. Nonlinear relationships are denoted as: L, logarithmic; Q, quadratic (without linear terms); H, humpshaped (linear terms are included but coefficients are not shown. Enn, Euclidean nearest neighbour distance; diversity, number of habitat types; loc, local factors.

Functional group	Longitude	Latitude	Crops	Nitrogen	Pesticide	% wood	Proximity wood	Enn wood	Proximity herb	Enn herb	Diversity	Loc.% wood	Loc.% herb	Loc. diversity
1					−0.90	−0.85	0.58Q			0.82Q	1.27	−0.70Q	−0.65L	1.04
2				−1.00L								0.45		0.64L
3	−2.90H	14.3H	0.80L	0.44	−0.37L	2.09H			0.73L			0.19L		−0.17
4	1.27L	−1.29L	0.50Q				0.40				−0.50			
5	−1.04	0.73				0.46		0.46L			0.27L		0.10	
6	0.28L													

Table 6. Final generalised linear mixed effects model of functional richness. Std. coeff, partial standardised regression slopes; Std. error, standard error; Df, degrees of freedom. Loc. Diversity, local habitat diversity measured as the number of habitat types within a radius of 50 m. Model detailes will be provided by the authors on request.

Variable	Std. coeff.	Std. error	Df	t-value	P
Intercept	0.87	0.05	359	16.99	<0.001
Crops (log)	0.20	0.05	19	3.42	0.003
% wood^2	0.15	0.05	19	2.62	0.017
% herb	−0.61	0.19	19	−3.20	0.004
% herb^2	0.60	0.19	19	3.14	0.005
Loc. diversity (log)	0.05	0.02	359	2.41	0.016

Discussion

Functional groups

Our study indicates that a more objective way of classification based on an array of traits covering a broad spectrum of a species' ecology reveals more detailed information about functional relationships under natural conditions than e.g. restricting the classification to effect or response type only (as suggested by Naeem and Wright 2003). For instance, different functional relevance is obvious for two groups of zoophagous species: The environmental factors affecting large, long lived species living on trees (group 4) differed considerably from that affecting species that are medium sized, short living and living in the herb layer (group 6). Recently effort has been made to objectively establish functional groups using multivariate methods (Simberloff and Dayan 1991, Munoz and Ojeda 1998, Pillar 1999). Considering resource traits, niche characteristics, and response type in a multivariate ordination seems proper since it resulted in clearly separated functional groups that responded to changes in land use in specific ways. The functional groups well represented the degree of specialisation, dispersal ability, and resource use: Two groups comprised mainly rare and low dispersing saprophagous specialists that were separated by different larval micro habitats; two groups of intermediate degree of specialisation consisted of mainly common phytophagous and zoophagous species also separated by larval micro habitat requirements; and further two groups embraced very common, highly mobile generalists that were separated by larval feeding style and larval micro habitat.

Species richness within functional groups

Previous analyses of the same data set revealed a general decrease in overall hoverfly species richness at the landscape and local scale with increasing land-use intensity and decreasing amount and connectivity of semi-natural habitats (Hendrickx et al. 2007, unpubl.). However, we could show that this decrease in species richness is not evenly distributed across functional groups but depends on their characteristics. Several studies indicate that factors at the landscape scale affect arthropods differently depending upon the degree of specialisation and dispersal abilities (Hanski and Gilpin 1997, Jonsen and Fahrig 1997, Golden and Crist 1999). Specialists may need to move between habitat patches to acquire specific resources, and could be significantly affected by landscape-scale factors that inhibit dispersal. Generalists are more likely to find sufficient resources within a patch compared to specialists and, if highly mobile, they may perceive a fragmented landscape as sufficiently connected (Thomas 2000). Our study shows that this may also apply to entire functional groups which are dominated by species of a certain degree of specialisation or mobility. Hoverfly species richness within generalistic and highly mobile groups is more or less unaffected by any environmental variable at any spatial scale. Large scale gradients, land-use intensity, landscape structure, or local habitat features have very limited, if any, effects, indicating a potential compensation of adverse environmental conditions in intensively used agricultural landscapes by dispersal and/or niche breadth.

Both groups of common species with intermediate specialisation levels showed high dependence on landscape scale factors such as habitat fragmentation and crop diversity, while the effects of local habitat features were limited. These groups appear to be dispersal as well as resource limited as indicated by negative effects of fragmentation and positive effects of high crop diversity, whereas the crop diversity may act either directly on phytophages or indirectly on zoophages via increased prey diversity (Hunter and Price 1992, Siemann et al. 1998).

Unexpectedly, both groups containing mainly specialists did not predominantly react to landscape structure but were highly affected by factors that could be interpreted in terms of habitat quality: pesticide burden and fertilisation level. Hence, even well structured landscapes could not prevent those groups from the negative effects of high land-use intensity. The additional positive effect of habitat diversity at the landscape and local scale points to the great dependence of these species on (micro) habitat type and quality (Maibach and Goeldlin de Tiefenau 1994, Rotheray and MacGowan 2000, Rotheray et al. 2001). The importance of local habitat features and the lack of any evidence of large scale geographical structuring are most likely related to their rarity. Since rare species tend to be rare everywhere, their low numbers might prevent a

detection of spatial structuring either at the European or at the landscape scale.

Our first hypothesis was twofold. The first part which assumed that each functional group will be affected by land use was not supported since groups of mainly generalists were seemingly unaffected. The second part was supported, however, since the effects of land use differ between functional groups in such a way that groups characterised by resource or dispersal limitation are most susceptible. Consequently, ecological functions that are associated with such groups bear an increased risk of being lost when land use is increased.

Functional richness

Increasing land use indeed resulted in decreasing functional richness of local hoverfly communities, supporting our second hypothesis. Since species richness of generalist groups was nearly unaffected by land use factors, the observed loss of functional richness has to be attributed to specialised and intermediate groups, only. Whereas decreasing local habitat diversity and quality mainly affected groups with high proportions of specialists; decreasing crop diversity, percentage wood, and structure of herbaceous elements at the landscape level seem to cause local extinctions of groups containing rather common species with intermediate degrees of specialisation.

Theoretical, experimental and simulation studies suggest that the probability of losing functional diversity decreases with species richness (Tilman et al. 1996, 1997, Naeem and Li 1997, Yachi and Loreau 1999, Fonseca and Ganade 2001). However, the assumption that species richness affects the risk of extinction for a particular functional group was not supported by our analysis. The two most species rich groups (35 and 25 species; both with intermediate levels of specialisation and common species) were at a comparable risk of extinction as the two species poorest groups (15 and 11 species; both with predominantly specialised and rare species), while the unaffected groups of generalists contained intermediate numbers of species (22 and 18 species). In contrast to most experimental and simulation studies that are based on random extinction patterns or random draws from a species pool, our study on natural communities indicates non-random trait-dependent patterns of species extinction. Our findings are in accordance with recent studies which report that trait-dependent extinction causes greater than random loss of functional diversity (Petchey and Gaston 2002). This suggests that the theoretically and experimentally found evidence for insurance of functional diversity against environmental change due to species richness and redundancy must not necessarily apply to natural conditions. If particular environmental pressures act in a selective way they may cause trait-dependent extinction. Under such preconditions, the risk of losing a functional group merely depends on group characteristics such as dispersal and niche breadth rather than on species richness. These findings add to theoretical and other observational studies that found little evidence for a causal relationship between function and diversity but rather suggest that it is the specific features of the species that determine its function (Grime 1997, Wardle et al. 1997, Hooper and Vitousek 1997, Bengtsson 1998).

Conclusions

Our results show that species extinction in response to environmental pressures such as increasing land use is not random but depends on species traits related to resource or dispersal limitation. Functional groups wherein such traits are accumulated are at higher risk of extinction. This increased risk of extinction seems to depend little on the species richness within a particular group. There is general acceptance that 'biodiversity per se is a good thing and that its loss is bad' (Gaston 1996), but from our results we infer that high species richness within functional groups alone is no guarantee for maintaining functional richness. Even species rich groups can easily become extinct when particular environmental pressures affect their members in a similar manner. According to the insurance hypothesis (Lawton and Brown 1994), species of the same functional group perform the same ecological function, but should be as different as possible otherwise in order to buffer the impacts of different environmental pressures (Walker et al. 1999). When the members of a functional group are very similar in at least one aspect (which might also be the function they perform), environmental pressures that act on this very aspect might become group specific key factors that decide over maintaining or losing a whole functional group. For instance, increased pesticide application leads to the loss of specialised saprophagous hoverflies living on water plants (group 1), or increasing fragmentation of woody elements leads to the loss of intermediate specialised zoophages living on trees and their root zone (group 4). Thus, it is not species richness per se that improves insurance of functional diversity against environmental pressures but the degree of dissimilarity within each functional group in response to selective causes of extinction. These selective, trait-dependent causes of extinction may not only result in rapid loss of functional diversity, but they have the potential to reduce this diversity faster than most often assumed and tested random extinction patterns (Petchey and Gaston 2002). Therefore, future studies should not only focus

on overall species richness and random extinction patterns but also consider phylogenetic, morphologic, or general ecological trait similarity and trait-dependent extinction.

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