RESEARCH ARTICLE

Impact of agricultural subsidies on biodiversity at the landscape level

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Abstract Agricultural management is a major factor driving the change of faunal richness in anthropogenic landscapes. Thus, there is an urgent need to develop tools that allow decision-makers to understand better intended and unintended effects of agricultural policy measures on biodiversity. Here we demonstrate the potential of such a tool by combining a socio-economic model with the biodiversity model GEPARD to forecast the response of bird and carabid species richness to two scenarios of agricultural subsidies: (1) subsidies based on production levels and prices and (2) direct income support that is independent of production levels. We focussed on farmland of the Lahn-Dill area, Germany, as an example of European regions with low intensity farming. GEPARD predicts faunal richness and is based on multi-scaled resource-selection functions. Under both scenarios the area of predicted losses in species richness of birds and carabids was larger than the area of predicted gains in species richness. However, the area with predicted losses of avian richness was smaller under the direct income support scenario than under the production-based subsidy scenario, whereas the area with predicted losses of carabid species richness was smaller under the production-based subsidy scenario than under the direct income support. Yet locally, richness gains of up to four species were predicted for carabids under both scenarios. We conclude that the sometimes contrasting and heterogeneous responses of birds and carabids at different localities suggest the need for spatially targeted subsidy schemes. With the help of the GIS-based approach presented in this study, prediction maps on potential changes in local and regional species richness can be easily generated.

Keywords Land use scenarios · Faunal diversity · Modelling · Multiple spatial scales · GIS

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Introduction

Modern agricultural management critically impacts faunal richness (Krebs et al. 1999; Donald et al. 2001). Though agriculture is often driven by subsidies, the impact of this financial support on biological richness is still poorly understood (Mayrand et al. 2003) and controversially

discussed (Green et al. 2005; Vandermeer and Perfecto 2005). Agricultural subsidies fall into two general categories (World Trade Organisation, 2002): (1) support based on production levels or prices (sometimes including limits to production) and (2) direct income support. Since the latter decouples subsidies from production quantities or prices, it has been hypothesized to enhance environmental benefits and support biodiversity by increasing producer flexibility and by allowing farmers to devise a least-cost approach to meeting environmental improvements (Claassen et al. 2001; Firbank 2005). The shift of the EU common agricultural policy (CAP) from production-based subsidies ("old CAP" or "Agenda 2000") to an income support program ("CAP reform"; European Commission 2004) was used to investigate the associated effect on biodiversity. So far, agri-environmental policies of the EU have not been very successful in protecting farmland biodiversity (Kleijn et al. 2001, 2004) due to unforeseen effects on habitat conditions and resource availability (Benton et al. 2003; Gaston et al. 2003). This points to the urgent need for predictive tools that permit a scenario-based approach allowing decision-makers to link policy, land-use, and biodiversity (Mattison and Norris 2005).

Our main objective was to determine the long-term effects of the two types of subsidies—"Agenda 2000" and the "CAP reform"—on the species richness of birds and carabids in a so-called 'marginal region' of low intensity farming in Europe, Germany (Hellegers and Godeschalk 1998). To do so, we developed the GIS-based model GEPARD (Geographically Explicit Prediction of Animal Richness Distributions), which is based on multi-scaled resource-selection functions (Manly et al. 2002). GEPARD was used to predict the distribution of species richness of birds and carabids under land-use scenarios that were devised by a landscape-specific socio-economic model. Rather than solely using the predicted species richness in the evaluation of subsidy effects on biodiversity, we quantified the changes in species richness between the present and the predicted situations. A marginal region was chosen as these regions are generally of high nature and landscape conservation value (European

Environment Agency 2004). Birds and carabids were chosen as they provide key ecosystem services, such as biological pest control (Kromp 1999; Tremblay et al. 2001), and are known to rapidly respond to changes in land-use intensity or landscape structure (Furness and Greenwood 1993; Gregory et al. 2004). Similar to other approaches, we focused on overall and functional group species richness (Fraser 1998; Sala et al. 2000; H-Acevedo and Currie 2003; Ferrier et al. 2004; Mitchell et al. 2006). In addition to assessing changes in species richness of birds and carabids under both subsidy schemes, we discuss the potential environmental factors such as land use type, slope, and matrix conditions that affect faunal species richness, and the spatial scales at what these environmental factors have an effect.

Methods

Study site and diversity sampling

The study was carried out in the Lahn-Dill-Bergland (Hesse, Germany), a low mountain range covering about 644 km^2. The area is characterised by a small-scale mosaic of forest (60% total cover), grassland (18% total cover), low-input arable land (5% total cover), fallow (5% total cover), and small amounts of various others land use types. Open land which includes arable land, grassland and fallow is restricted to an area of 177 km^2.

The survey of faunal species richness was conducted on a total of 319 study plots. Birds were recorded on 203 plots (arable land: $N = 68$, grassland: $N = 71$, deciduous forest: $N = 39$, coniferous forest: $N = 25$) by using Distance Sampling based on five-minute Point Counts (Bibby et al. 2000; Buckland et al. 2001). In 2004 and 2005 each plot was surveyed for birds five times between April and June. The analysis was restricted to birds that were observed within a distance of 200 m from survey points.

Carabids were investigated between 1997 and 2004 on 116 plots (arable land: $N = 46$, grassland: $N = 60$, fallow land: $N = 10$) using pitfall traps (Purtauf et al. 2004, 2005). All individuals were identified to species level and were assorted to

four feeding groups (carnivores, granivores, omnivores, phytophages) according to the literature (Lindroth 1992; Bezzel 1993; Ribera et al. 2001).

The socio-economic model

The socio-economic model ProLand produced maps of the potential spatial distribution of land-use types (arable field, grassland, forest) in the study region under conditions of both production-based subsidies and direct income support (see Kuhlmann et al. 2003 and Weinmann et al. 2006 for a detailed description of the ProLand approach). In short, the model is designed as a comparative static model, i.e. its results have to be interpreted as endpoints of adaptation processes. Regional land-use patterns are predicted from parameters for physical, socio-economic, and legal conditions. Spatially explicit information on these parameters is used to predict the allocation of land-use types and management intensity after an implementation period of the two agricultural subsidy schemes of 30 years. The model assumes that land users will establish management systems that guarantee maximal profit. The resulting land-use scenarios were compared by quantifying the changes in area, diversity, and distribution of different land-use types with regard to the present situation. The diversity of land-use types was quantified by the Shannon index, their distribution and

fragmentation by the Interspersion and Juxtaposition Index (IJI). The Shannon index is influenced by the number of land-use types in the landscape and by their specific area shares. The index increases as the number of different land-use types increases and/or the proportional distribution of area among patch types becomes more equitable. The IJI is calculated by dividing the observed interspersion by the maximum interspersion for the land-use types in a landscape. The index approaches 100 when all land-use types are equally adjacent to all other land-use types (McGarigal and Marks 1995).

The biodiversity model

The model GEPARD was developed to predict species richness in those parts of open land within the study region that are targeted by agri-environment programs of the EU (i.e. excluding urban land, protected areas, etc.). The independent variables used in the model include (i) local variables measured at the plot level, and (ii) matrix variables measured at various spatial scales around the plot (Fig. 1). Local variables comprised height above sea level, slope, soil humidity, insolation, soil type, and land-use type. Soil humidity was calculated using the compound topographic index or wetness index (CTI; Beven and Kirkby 1979), which quantifies the effect of topography on the location and extension of water accumulation in soils. Insolation was

Fig. 1 Flow chart of the methodology of GEPARD
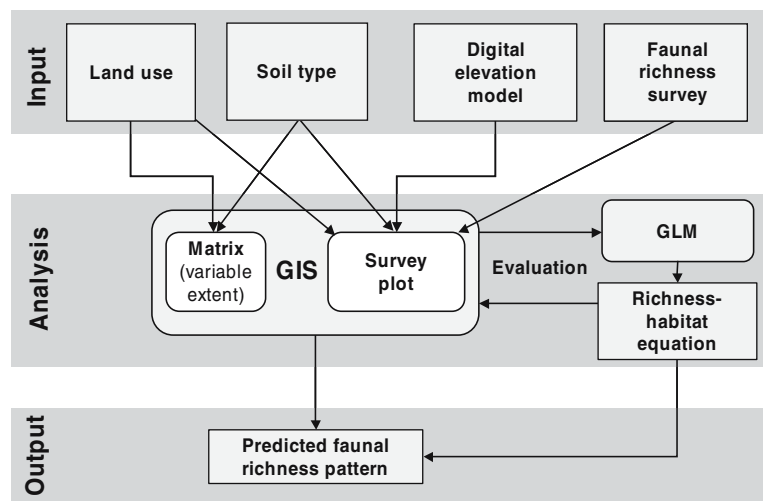
calculated as the mean annual intensity of solar radiation that reaches the earth surface (kW m^{-2}).

Matrix variables encompassed the share of the four major land-use types (arable land, grassland, fallow land, and forest) as well as measures of landscape fragmentation (effective mesh size) and diversity of both land-use and soil types (Shannon index, see above). The effective mesh size (Jaeger 2000) is a measure of fragmentation. It gives the area-weighted mean patch size, whereby the proportional area of each patch is based on the total landscape area. The lower limit of MESH is constrained by the cell size and is achieved when the landscape is maximally subdivided; that is, when every cell is a separate patch. MESH reaches its maximum when the landscape consists of a single patch (McGarigal and Marks 1995).

All independent variables were processed in raster maps of 25 m resolution, which were generated from the following three source maps: (1) land-use, (2) soil type, (3) digital elevation model. The land-use map was classified from 1994 Landsat TM images and updated by intensive ground surveys in 2004 and 2005. Topographical variables were derived from a digital elevation model (HLBG 2005). Maps of the matrix variables were constructed using the circular moving-window approach within FRAGSTATS. A locational term (2nd order polynomial) that was a smooth surface of easting and northing was included as independent variables to imply responses of species richness to location and to control for spatial autocorrelation. Accounting for spatial autocorrelation in models can increase predictive accuracy and model versatility (Legendre 1993; Betts et al. 2006). Sample size was included for bias potentially resulting from different sampling efforts.

As species-habitat relationships are scale-dependent, the matrix parameters were calculated for areas with radii of 200 m, 500 m, and 1000 m around the plots using the software FRAGSTATS (McGarigal and Marks 1995). We focused on a range of spatial scales, which have been shown to be meaningful to birds (Hunter and Gutiérrez 1995; Jokimäki and Huhta 1996; Söderström and Pärt 2000) and carabids (Kinnunen et al. 1996; Weibull et al. 2003). Inclusion of three radii balances the risk of not identifying important parameters due to

the inclusion of too few scales and overfitting due to the inclusion of too many scales.

Dependent variables were total species richness of birds and carabids as well the species richness within feeding groups of birds (insectivores, granivores, omnivores) or carabids (carnivores, phytophages, omnivores).

GEPARD is based on generalized linear model (GLM) analysis, commonly applied in species distribution models (Miller and Cale 2000; Bustamante and Seoane 2004; Yen et al. 2004). Resource-selection functions (Manly et al. 2002) were obtained using a logarithmic link function and assuming a Gaussian error distribution. Three approaches were followed to optimize the model towards best prediction, as opposed to mechanistic explanation and hypothesis testing. (1) The Akaike Information Criterion (AIC, Akaike 1973) was applied for model selection to include the set of variables with the most relevant contribution to model fit. AIC overcomes the systematic sample-size dependence of significance-based selection methods, such as Forward Stepwise Selection, which tend to remove variables in cases of few samples giving rise to high *P*-values, and conversely retain too many variables in case of many samples giving rise to high degrees of freedom and hence low *P*-values (Anderson et al. 2000). We used AICc, a correction of AIC recommended if the number of survey sites divided by the number of parameters is less than 40 (Burnham and Anderson 2002). (2) To avoid overfitting and collinearity through spatial autocorrelation across scales, only one single scale was admitted for each independent variable in the final model. (3) Variables and scales were limited to those known to affect the distributions of birds (Hunter and Gutiérrez 1995; Jokimäki and Huhta 1996; Söderström and Pärt 2000) and carabids (Kinnunen et al. 1996; Weibull et al. 2003). We did not consider interaction terms to limit the number of models tested.

Prediction accuracy was quantified for each model run by means of a 1st order jack-knife permutation (Sokal and Rohlf 1995). Each sampling plot was specified in turn as ''unknown'' validation plot. The model was re-calibrated with all other plots, and the prediction error for the unknown plot was recorded. By repeating the

procedure for each plot, all possible cases of an unknown plot were covered. Thus, 203 validation runs were performed for the bird data, and 116 validation runs were performed for the carabid data. Compared to a split of the data into a calibration dataset and a separate validation dataset, the jack-knife approach minimizes deterioration of model calibration due to reduction of sample size, and maximizes exploration of the probability space of prediction error.

All geographical analyses and species predictions were conducted with the ArcInfo 9.0 GIS software (ESRI, Redlands, California). We implemented an interface to the statistical package R (R Development Core Team, 2006) into ArcInfo to automate GLM analysis and jack-knife permutation. In contrast to existing software such as GRASP (Lehmann et al. 2002) or BIOMOD (Thuiller 2003), in GEPARD the statistical analysis can be performed within the GIS environment and the results can be directly used to generate distribution maps.

First, GEPARD was applied to predict the distribution patterns of species richness in the entire study region using the environmental information of the present landscape situation. Then, land-use maps generated by ProLand were used to predict the distribution patterns of species richness under two contrasting agricultural policy scenarios. Changes in species richness in response to environmental change were calculated by subtracting the present species richness in each cell from the predicted species richness under both scenarios. Thus, positive values indicate areas with predicted gains in species richness and negative values indicate areas with predicted species losses as compared to the present situation.

Results

According to the ProLand predictions, production dependent subsidies (i.e. continuation of the old CAP) would mainly increase in the area covered by arable land (+3.3%) at the expense of fallow land (–5.0%; Fig. 2). In contrast, a switch to income support (i.e. CAP reform) is predicted to mainly induce a shift from arable land (–1.4%), fallow (–5.0%) and forest (–4.2%) to grassland

(+12.6%). Conversion into forest has not been considered, as forest would generally yield less land rent than agricultural land in the focal region. The landscape developing under production dependent subsidies is predicted to be more fragmented (IJI index = 56.8) than under income support (IJI = 52.3). The Shannon index for present conditions is 1.58. Though it decreases in both scenarios, the level of landscape diversity will remain higher under production dependent subsidies (Shannon index = 1.51) than under income support (Shannon index = 1.43).

A total of 82 bird species and 113 carabid species was found. Feeding groups of birds include 56 insectivorous, 16 granivorous, and 10 omnivorous species, those of carabids 52 carnivorous, 30 phytophagous, and 11 omnivorous species, respectively. Twenty carabid species could not be allocated to any feeding group and were excluded from further analyses.

The GLMs explain 23–46% of the variation in the feeding group species richness. Landscape characteristics generally explain more variation
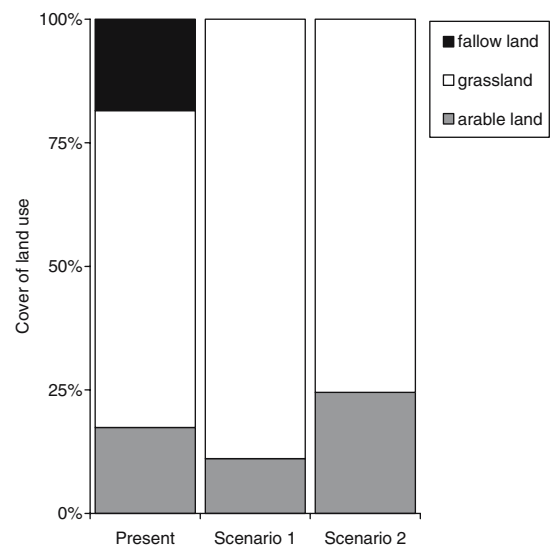

Fig. 2 Shares of the major types of open land. Stacked bars indicate the current condition within the study region (Lahn-Dill-Bergland, Germany) as well as the situation that are predicted by the socio-economic model ProLand to develop under two different EU agricultural policies based on production based subsidies (Agenda 2000 of the EU, Scenario 1) and on direct income support (CAP reform, Scenario 2)

than local habitat characteristics (Appendix 1). According to jack-knife calculations, the PA ranges from ±1.0 to ±2.3 species for the feeding groups of birds and from ±1.0 to ±2.8 species for the carabid groups.

Bird models contain landscape variables at comparatively small spatial scales, namely at the 200 m (4 variables) and 500 m radius (7 variables; Appendix 1). Landscape diversity has a positive effect on the species richness of granivorous and omnivorous birds (GLM: $P \le 0.01$), whereas the avian richness of all three groups decreases with increasing percent cover of most land-use types (GLM: $P \le 0.061$), in particular arable land (GLM: $P < 0.001$). The three carabid models mainly contain variables at the 200 m (3 variables) and 1000 m radius (3 variables; Appendix 1). However, GLM results do not indicate very strong and consistent habitat relationships across the various feeding groups. Whereas the richness of carnivorous carabid species is positively affected by the proportions of arable land at the 200 m scale (GLM: $P = 0.012$), the richness of phytophagous species is positively correlated with the cover of forests at the 500 m scale (GLM: $P = 0.002$). Landscape fragmentation was

retained in all three carabid models. It has a negative effect on phytophagous and carnivorous species (GLM: $P \le 0.06$), but a marginal positive influence on the species richness of omnivores (GLM: $P = 0.073$). Habitat conditions have a significant effect in only one case (altitude in the GLM of phytophages: $P = 0.007$). Variables accounting for spatial gradients or sampling bias in the data were retained in all bird and carabid models (GLM: $P \le 0.014$).

The cumulative amounts of areas with and without changes in species richness (Table 1, Fig. 3) show that (i) the area with species losses exceeds the area with species gains of carabids and birds under both scenarios, (ii) the area with no changes in species richness is particularly high for carabids under production based subsidies, and (iii) birds and carabids respond differently to agricultural policies according to the areas meeting the rigorous criterion of lying outside the taxon-specific uncertainty range (UR = 0 ± PA; see methods). The area with a marked loss of carabid richness is predicted to be larger under income support, while that with a marked loss of avian richness is predicted to be larger under production based subsidies.

Table 1 Summary of the GEPARD predictions on changes in species numbers (S). Areas with gains and losses of species that lie outside the uncertainty range (UR) according to the prediction accuracy are displayed in italics (see section on methods). The Agenda 2000 scenario is based on production based subsidies and the CAP reform scenario is based on direct income support

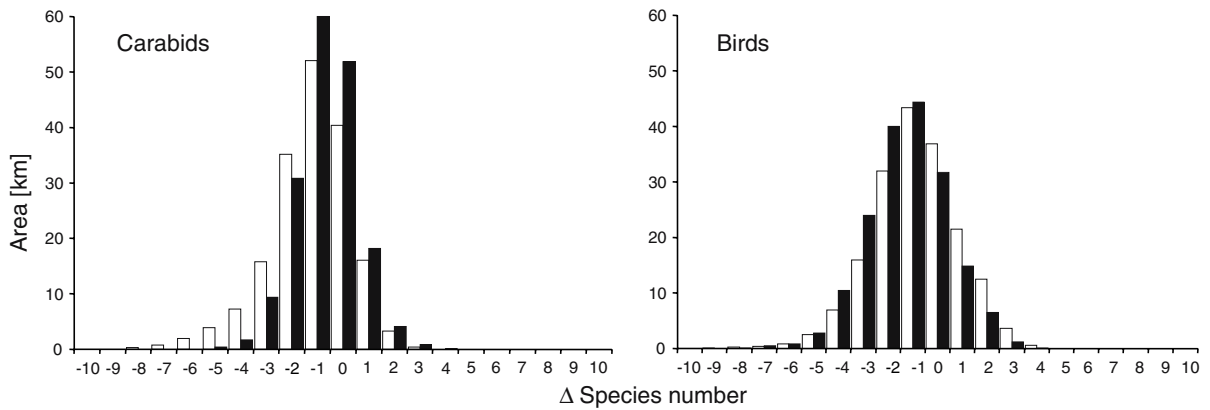| Taxon	Agenda 2000			CAP reform			UR (S)
	areas with		no change (km²)	areas with		no change (km²)	
	species gains (km²)	species losses (km²)		species gains (km²)	species losses (km²)		
Birds							
total	22.6	123.0	31.6	38.1	102.2	36.9	
	4.7	*62.3*		*11.0*	*44.5*		±1.88
insectivores	9.5	109.4	58.3	36.7	61.3	79.2	
	0	*7.9*		*1.3*	*5.3*		±2.27
granivores	0	62.4	114.8	0.1	59.8	117.3	
	0	*9.7*		*0*	*9.8*		±0.95
omnivores	2.1	95.7	79.4	2.4	114.0	60.8	
	0.1	*24.3*		*0.1*	*37.6*		±1.15
Carabids							
total	38.8	76.6	61.8	21.9	124.0	31.3	
	4.5	*2.0*		*3.0*	*16.9*		±2.16
carnivores	47.0	38.8	91.4	23.5	79.1	74.6	
	1.1	*0.8*		*0.9*	*10.0*		±2.85
phytophages	22.1	45.5	109.6	14.4	97.3	65.5	
	5.7	*7.5*		*5.1*	*30.3*		±1.40
omnivores	0	29.7	147.5	2.2	34.4	140.6	
	0	*2.4*		*0*	*3.4*		±1.01

Fig. 3 Distribution of the cumulative amount of area showing a predicted loss (–), gain (+), or no change (0) in species numbers of carabids and birds under two EU subsidy schemes: Agenda 2000 (production based subsidies: black columns) and CAP reform (direct income support: white columns) in a marginal agricultural landscape (Lahn-Dill-Bergland, Germany). The change in species richness was calculated by subtracting the prediction for the present distribution of species richness from the distributions predicted for the two scenarios. Distribution of predicted changes of species numbers in relation to the area

Spatially explicit projections of the modelling results under both scenarios reveal considerable regional differences in the response of carabids. Richness declines are particularly strong in the eastern part of the study region, while richness gains with up to 4 species occur in some other areas (Fig. 4).

Under both agriculture policies and for all bird and carabid feeding groups except carnivorous carabids, the area with a predicted decline of species richness exceeds that with a predicted gain of species richness (Table 1). The extent of richness loss, however, differs between production based subsidies and direct income support.
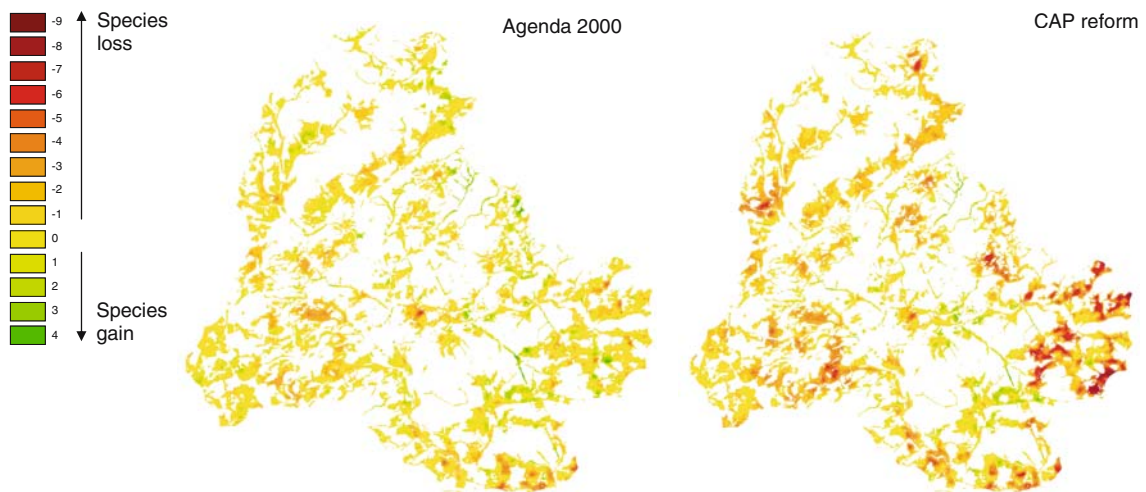

Fig. 4 Predicted changes in the distribution of carabid species richness on farmland in the Lahn-Dill-Bergland. Shown are the effects of (**a**) the Agenda 2000 of the EU (scenario 1, production based subsidies) and (**b**) of the CAP reform (scenario 2, direct income support). Areas in red indicate regions with a loss in species richness and areas in green indicate regions with gains in species richness. White colour represents forests and urban areas that have not been considered

For insectivorous birds the predicted area with declines in species richness is considerably larger under production based subsidies than under income support. For omnivorous birds the opposite is the case. Carabids respond more consistently, with the area for which a decline in species richness is predicted being larger under income support than under production based subsidies for omnivores and phytophages. Model predictions for carnivorous carabids, in contrast, suggest that this group might even slightly profit from production based subsidies. Differences in the predicted response of granivorous birds and omnivorous carabids to both scenarios are small and the predicted area with no changes in species richness is exceptionally high for both groups. It should be noted, however, that the amount of area lying outside the uncertainty range is comparatively small for all feeding groups (Table 1).

Discussion

According to the socio-economic scenarios, the continuation of production-based subsidies would increase the area covered by arable land and the degree of fragmentation, while the switch to income support will increase the area covered by grassland in a more uniform landscape. GEPARD predicts both scenarios to have negative effects on the overall species richness of birds and carabids, yet to a differing extent. Hence, the management regime currently implemented in the marginal region of the Lahn-Dill-Bergland seems to affect biodiversity much more positively than the one expected to develop under any of the two subsidy schemes within the next thirty years. This probably is a consequence of farmers not carrying yields to the extreme, e.g. fallow land is still widespread and field sizes are smaller than in more intensively managed systems. Future conditions may thus vary depending on the degree of implementation of agriculture policies by local farmers, a factor that is difficult to be estimated in socio-economic models. Decreasing landscape diversity and the loss of fallow land—both consequences of maximizing agriculture production—have frequently

been shown to negatively affect species richness (Benton et al. 2003; Weibull et al. 2003; Fuller et al. 2004) and at least partly explain the predicted decline in species richness of birds and carabids under both subsidy scenarios in the future.

Taxon-specific differences in the response to agricultural policies have been identified. Carabids seem to respond less negatively to production based subsidies, while birds seem to respond less negatively to income support. The environmental variables generally explained only a small part of the total variance in the data. Their kind, the direction of their relationships with species richness, and the spatial scales at which environmental variables were selected, however, generally conform to previous studies (Thiele 1977, Altauri and de Luco 2001) and suggest that differences in the response to landscape change are likely to be related to different habitat requirements and/or spatial strategies of carabids and birds. Also, the differences in the response of functionally similar feeding groups, such as carnivorous carabids and insectivorous birds, to landscape change, are likely to be due to very different spatial niches and vastly different movement abilities that characterise these groups. These differences among or even within taxonomic or functional groups of species make it difficult to determine specific spatial scales that are relevant in predicting species richness (cf. Pearman 2002; Robinson et al. 2004; Mitchell et al. 2006) and explain why species richness may be found to be affected by environmental factors at various spatial scales (Bossenbroek et al. 2004).

The extension of arable fields under the production-based subsidies seems to favour phytophagous and carnivorous carabids. Phytophagous carabids are known to positively respond to the provision of certain seeds (in particular grasses, umbellifers, and crucifers; Thiele 1977) and carnivorous carabids to the high numbers of insects hosted by weeds in agricultural land (Marshall et al. 2003; Purtauf et al. 2004). In addition, phytophagous and carnivorous species respond negatively to landscape fragmentation (negative response to mesh size). Consequently, carabid species are predicted to show a pronounced

decline especially in the Eastern part of the study area, where, in response to the CAP reform, the landscape will become more monotonic and dominated by grassland.

Birds do not seem to be strongly affected by habitat fragmentation. This is probably due to the greater mobility of this taxon. Because birds perceive their environment at larger spatial scales, however, they react more strongly to landscape heterogeneity (cf. Böhning-Gaese 1997; Atauri and de Luco 2001; Mitchell et al. 2006). Consistent negative effects of increasing area percentages of single land use types on all three feeding groups of birds as well as an explicit positive effect of landscape diversity on granivorous and omnivorous birds underline the importance of structurally rich landscapes for bird species richness. Since insectivorous birds are known to positively respond to the increasing availability of both food- and plant-rich habitats in landscapes dominated by low-input grasslands (Henderson et al. 2004; Newton 2004), a higher gain of species richness under income-support than under production based subsidies may be assigned to the extension of grassland under the former scenario.

Taxon-, group- or even species-specific differences in life history traits, movement ability, and resource requirements also explain, why our predictive models only explained around 40% of the variation in species richness. Yet, this is well within the range of previous studies modelling the distribution of multiple or even single species distributions (Morrison et al. 1998). A substantial proportion of the variation in species richness of some groups was explained by latitudinal or longitudinal gradients or by patterns related to the sampling regime. This suggests that the spatial distribution of species richness is controlled by factors, which might not at all or only weakly be affected by changes in land-use and landscape structure. One example would be the effect of biotic and abiotic variables that are quantifiable only at finer spatial scale. Much of the agricultural biodiversity in marginal agricultural landscapes is being maintained in small-scale landscape elements and structures (e.g. ditch banks, field margins, hedgerows; Benton et al. 2003, Schweiger et al. 2005) and some of these structures may

not have been identified precisely enough given the resolution of the Landsat images used in this study (cf. Mack et al. 1997; Gottschalk et al. 2005). Edge structures, such as field- and path-margins are likely to be present more frequently in highly diverse landscapes. Therefore, the landscape diversity index may be also regarded as an indicator for the abundance of edge structures partly compensating for the lack of detailed knowledge of the distribution of these small scale elements.

Our data confirm that the effects of landscape changes are taxon-specific and impact species richness via local and regional processes (Dunford and Freemark 2005; Schweiger et al. 2005). Taxon-specific changes in species richness may considerably alter the composition of particular functional groups within agricultural landscapes. This in turn may substantially alter the provision of ecosystem services such as biocontrol (insectivorous birds and carnivorous carabids) and, as a consequence, may have negative effects in monetary terms (Östman et al. 2003). Stronger landscape- than habitat-specific effects on the predicted species richness within most functional groups of carabids and birds point to the need of including the landscape context into analyses of and predictions on faunal distribution patterns (Graf et al. 2005).

Modelling prospective changes in land-use and landscape structure given complex socio-economic conditions—like in marginal landscapes—undoubtedly involves uncertainties. Likewise does the absence of replication in other landscapes—though common in landscape ecology—represent a limitation to error-free and general conclusions. However, the negative effect on species diversity consistently predicted for both EU subsidy schemes and the observed differences in species' responses among structurally different parts of our study region strongly suggest that agri-environmental programs aiming at protecting biodiversity in agricultural landscapes should be landscape specific (e.g. targeted to marginal landscapes) in order to fulfil their aims.

In conclusion, our results show that the integrative modelling approach used in this study is a valuable tool for evaluating the effects of

agricultural subsidy schemes on species diversity in agricultural landscapes. We believe that our approach is well suited for fitting future agri-environmental schemes more specifically to the regional situation. By being spatially explicit it helps to identify areas in which the diversity of selected taxa is predicted to be particularly sensitive to the expected land-use changes. Adverse effects of landscape unification on bird and carabid species richness as well as taxon- and group-specific responses to changes in landscape structure highlight the risks associated with a mechanistic application of agricultural policies. Thus, our findings underline the need for complementing the implementation of agricultural subsidy schemes by regional forecasts of their ecological consequences (Robertson and Swinton 2005). We acknowledge that a richness-based approach has its shortcomings (Wolters et al. 2006) and that in some situations the inclusion of expert knowledge on the response of

selected specialist or endangered species may add to the value of spatially-explicit model predictions (Carter et al. 2006). Besides tailoring both the socio-economic and the biodiversity model even closer to the specific situation in marginal landscapes (e.g. increasing the spatial resolution of habitat maps) and testing GEPARD in different landscape situations, it will be a remaining challenge to take into account future changes in the environment caused by climate change or atmospheric deposition of nutrients.

Appendix 1 Results of the GLMs on the relationship between species richness (s) and environmental variables

Dependent variables	Independent variables[a]	Scale[b] (m)	–/+[c]	EV[d]	P-value[e]	UR[f] (s)	Model R^2 [g]
Birds							
Granivores						1.0	0.23
	Habitat conditions (total EV = 0.08)						
	Height above sea level		(+)	0.05	0.000		
	Soil humidity		(–)	0.01	0.061		
	Curvature		(–)	0.02	0.021		
	Surrounding matrix (total EV = 0.13)						
	Arable land (%)	500	(–)	0.06	<0.001		
	Grassland (%)	500	(–)	0.01	0.061		
	Deciduous Forest (%)	500	(–)	0.02	0.025		
	Coniferous Forest (%)	1000	(–)	0.02	0.008		
	Landscape diversity	500	(+)	0.02	0.009		
	Location: Y (North-South)		(–)	0.02	0.014		
Insectivores						2.3	0.41
	Habitat conditions (total EV = 0.06)						
	Soil humidity		(+)	0.03	0.020		
	Curvature		(+)	0.03	0.030		
	Surrounding matrix (total EV = 0.28)						
	Arable land (%)	500	(–)	0.13	< 0.001		
	Deciduous Forest (%)	200	(–)	0.05	0.004		
	Coniferous Forest (%)	200	(–)	0.06	0.003		
	Mesh of land use types	500	(–)	0.02	0.057		
	Soil type diversity	200	(+)	0.02	0.090		
	Location: X^2 (East-West)		(–)	0.06	0.002		

Appendix 1 continued

Dependent variables	Independent variables[a]	Scale[b] (m)	–/+[c]	EV[d]	P-value[e]	UR[f] (s)	Model R^2 [g]
Omnivores						1.15	0.44
	Habitat conditions (total EV = 0.08)						
	Land-use types			0.08			
	Surrounding matrix (total EV = 0.17)						
	Arable land (%)	200	(–)	0.12	<0.001		
	Grassland (%)	1000	(–)	0.02	0.027		
	Landscape diversity	500	(+)	0.03	0.010		
	Location: X (East-West)		(–)	0.07	0.001		
	Location: Y (North-South)		(–)	0.12	0.001		
Carabids							
Phytophages						1.5	0.41
	Habitat conditions (total EV = 0.15)						
	Altitude		(+)	0.15	0.007		
	Surrounding matrix (total EV = 0.004)						
	Forests (%)	500	(+)	0.00	0.002		
	Soil type diversity	200	(–)	0.00	0.042		
	Mesh of land use types	1000	(–)	0.00	0.002		
	Location: Y^2 (North-South)		(–)	0.12	<0.001		
	Bias correction: Sampling effort		(+)	0.14	<0.001		
Omnivores						1.0	0.46
	Habitat conditions						
	No significant variable						
	Surrounding matrix (total EV = 0.004)						
	Landscape diversity	1000	(+)	0.00	0.805		
	Mesh of land use types	1000	(+)	0.00	0.073		
	Location: X (East-West)		(+)	0.05	0.003		
	Bias correction: Sampling effort		(+)	0.41	< 0.001		
Carnivores						2.8	0.41
	Habitat conditions						
	No significant variable						
	Surrounding matrix (total EV = 0.04)						
	Arable land (%)	200	(+)	0.01	0.012		
	Mesh of land use types	200	(–)	0.03	0.060		
	Location: X^2 (East-West)		(+)	0.33	0.004		
	Bias correction: Sampling effort		(+)	0.04	0.005		

[a] Independent variables of local habitat conditions were topographical parameters (height above sea level, slope, soil humidity, insolation), soil types, and land-use types (arable land, grassland, fallow land, forest). Independent variables of the surrounding matrix were the share of each of the four land-use types (arable land %, grassland %, fallow land %, forest %) as well as measures for the distribution of land-use types and soil types (Shannon index, IJI of land-use types, IJI of soil types). Location: spatial autocorrelation and spatial gradients were accounted for including two-dimensional geographic coordinates, completed by including all terms for a trend surface regression (X, Y, X^2, Y^2) into the models. Bias correction: differences in sampling effort were controlled by including sample size into the models

[b] The extent of the surrounding matrix within which a particular predictor variable took effect on the dependent variable

[c] Plus or minus sign indicates direction of relationship

[d] Explained variance (EV); quantifies the relative importance of each predictor variable

[e] Significance level of each predictor variable

[f] Leave-one-out Jack-knife Error estimation of the uncertainty range (UR); the regression equation was repeatedly recalculated, each time ignoring one of the survey plots. The residuals (observed-predicted) in the ignored plots were recorded and the absolute residual averaged across all ignored plots was taken as a measure of the average prediction error in an unknown plot

[g] Overall fit of the entire model

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