



Human appropriation of net primary production as determinant of avifauna diversity in Austria

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Abstract

The relationship between land-use induced changes in production ecology and avifauna diversity was analysed using a GIS land cover dataset on a 0.25 km × 0.25 km grid covering Austria's national territory. Considering only aboveground processes, the "human appropriation of net primary production" (HANPP = potential NPP – NPP_t), actual NPP (NPP_{act}), harvest (NPP_h) and NPP_t (= NPP_{act} – harvest) were recalculated based on existing datasets. Elevation as well as indicators of land cover heterogeneity and landscape heterogeneity were also considered. Correlation analyses were performed between these potential determinants of avifauna diversity and breeding bird species richness data as well as the percentage of endangered breeding birds included in the Austrian red list. Four spatial scales—0.25 km × 0.25 km, 1 km × 1 km, 4 km × 4 km and 16 × 16 km, were analysed. It was shown that breeding bird species richness was more strongly correlated with production ecological indicators and elevation than with heterogeneity indicators. A residual analysis in which the effect of elevation (a proxy for climate) on species richness and its potential determinants was removed confirmed the importance of the availability of trophic energy (NPP) for bird diversity patterns. The results support the species-energy hypothesis, thus confirming the notion that HANPP could be a useful pressure indicator for biodiversity loss.

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1. Introduction

Human-caused biodiversity loss is a pervasive global process generally thought to jeopardize sustainability (Heywood and Watson, 1995; Pimm et al., 1995). Developing effective policies to slow the

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rate with which biodiversity is being depleted requires a better understanding of human pressures on biodiversity. Above all, the relative importance of different pressures on biodiversity is currently only incompletely understood (Chapin et al., 2001; McNeely et al., 1995; Sala et al., 2000).

It is well established that land-use is an important, may be even the most important, cause of biodiversity loss (Chapin et al., 2001; Sala et al., 2000). Land-use, however, is a multi-faceted notion that includes activities as diverse as clear-cutting or burning of original forest cover, ploughing, sowing, planting of seedlings, weeding, application of pesticides and fertilizers, soil sealing through construction of buildings and infrastructure, establishment of gardens or parks, afforestation, grazing of domesticated animals, crop, grass or wood harvest, and many more (Meyer and Turner, 1994; Turner et al., 1990). Land-use results in various changes in ecosystems on different spatial scales that include, among others, changes in land cover and landscape structure, changes in productivity and biomass stocks, changes in biogeochemical cycles of water, nutrients, carbon, etc. (Forman and Godron, 1986; Naveh and Liebermann, 1994) that are relevant for biodiversity (Waldhardt, 2003).

Much evidence has been accumulated to demonstrate that spatial patterns of landscapes such as landscape complexity or heterogeneity are strongly correlated with species richness, implying that land-use related changes in landscape heterogeneity may exert an important pressure on biodiversity (Benton et al., 2003; Hoffmann et al., 2001; Honnay et al., 2003; Moser et al., 2002; Steiner and Köhler, 2003; Zechmeister et al., 2003). The possible impact of land-use induced changes in production ecology on biodiversity has, however, received less attention (Haberl et al., 2004; Wr̀bka et al., 2004), although the concern that a reduction of energy availability in ecosystems due to the “human appropriation of net primary production” (HANPP) might be an important pressure on biodiversity was raised more than a decade ago (Vitousek et al., 1986; Wright, 1987, 1990). This concern was based on the species-energy hypothesis, i.e., the notion that the amount of energy available in ecosystems may be an important factor determining species diversity (Allen et al., 2002; Brown, 1988, 1995; Gaston, 2000; Hutchinson, 1959; Worm and Duffy, 2003; Wright, 1983).

As global human population growth is likely to require more agricultural area (Tilman et al., 2001), further increases in HANPP over the present value of about 20–40% (Vitousek et al., 1986) might be expected. The likely consequences of such trends for biodiversity are therefore of great interest. Moreover, there is an urgent need for feasible, reliable, and empirically validated pressure indicators for biodiversity loss, i.e., to parameters that can be unequivocally linked to socio-economic processes on the one hand, and to biodiversity on the other. As global (DeFries, 2002; Imhoff et al., 2004) and regional (Haberl et al., 2001) assessments of HANPP or its components are becoming increasingly available, HANPP is at least a promising candidate for such an indicator, and the research presented here may also serve to supply scientific backing for the development of such indicators.

In order to assess the relation between production ecology and biodiversity this paper presents an empirical study of the relationship between various production ecological parameters and Austria’s breeding bird species richness. Some simple indicators of landscape heterogeneity as well as an indicator of bird species endangerment (species included in the red list of Austria’s breeding birds) were also analysed. The analysis was conducted on four nested spatial scales and covered all of Austria.

2. Methods

The study was based on a land cover dataset covering Austria’s whole area of about 83,000 km² (Hollaus and Suppan, 2004; Peterseil et al., 2004; Wr̀bka et al., 1998, 2002). A 0.25 km × 0.25 km grid ($N = 1.3$ mio. cells) was used as basic unit; that is, 0.25 km × 0.25 km cells were considered homogeneous with respect to land cover, landscape type, production ecology, elevation and bird assemblage. Avifauna and elevation data were already available on that grid whereas production ecological parameters, land cover and landscape types were recalculated on that grid in order to avoid spatial distortions.

The following parameters were analyzed as potential determinants of bird species diversity: elevation, actual NPP (NPP_{act}), human harvest of biomass (NPP_h), NPP remaining in the ecosystem after harvest (NPP_r), HANPP%, land cover heterogeneity (LC-Het) and

the Shannon-Wiener index (Krebs, 1989) of land cover types and of landscape types. HANPP was defined as the difference between NPP_0 and NPP_t , where NPP_0 denotes the NPP of the vegetation assumed to prevail in the absence of human intervention. HANPP reflects (1) the changes in productivity due to land-use and (2) the biomass removed from ecosystems at harvest (Haberl, 1997; Haberl et al., 2001; Vitousek et al., 1986; Wright, 1990). All NPP data were expressed in Joule [J] per year. HANPP% expresses HANPP as a percentage of NPP_0 . To avoid the large uncertainties related to belowground data, only the aboveground component was considered.

HANPP components (NPP_{act} , NPP_h , NPP_t and HANPP%) were recalculated from a previous study (Haberl et al., 2001) that had used a different land cover dataset with a similar land cover classification, but a different basic grid. NPP_0 was calculated using factors for the average NPP per unit area of different vegetation units, considering vegetation type and elevation as proxy for climate (Haberl, 1995, 1997; Haberl et al., 2001). The factors used were derived by regression analyses of NPP data from the literature (e.g., Cannell, 1982; DeAngelis et al., 1981). For cropland and meadows NPP_{act} was calculated using harvest indices (Krausmann, 2001; Singh and Stoskopf, 1971). Harvest data were obtained from agricultural statistics available at the district level for about 40 different crops (Statistik Austria, 1999). For forest ecosystems NPP_{act} was assumed to be identical to NPP_0 . This method gave similar results as the extrapolation of forest NPP from wood increment data from the Austrian forest inventory (Haberl, 1997; Haberl et al., 2001). As a refinement compared to the earlier study the calculation used here was based on disaggregated data on wood harvest in Austria's forest districts ($N = 85$) instead of one average figure for the percentage of forest NPP harvested in Austria's forests (Büchsenmeister et al., 1999). For the remaining land cover classes average values were derived from Haberl (1995) and Schulz (1999). Land cover heterogeneity (LC-Het) was calculated for each grid cell as the number of land cover classes present in the eight cells adjacent to each grid cell (variety of a 3×3 neighbourhood).

The avifauna data set covering Austria's total area was taken from an unpublished study by two of the authors (C. Plutzer and M. Pollheimer) in which

breeding bird species richness was extrapolated from Austria's bird inventory established by Birdlife Austria (Dvorak et al., 1993). In this study, a database of the spatial distribution of 213 breeding bird species in Austria was established. The distribution of 119 of these 213 species was assumed to be underrepresented; for these species a GIS-based expert system was used to fill spatial gaps caused by heterogeneous sampling efforts. The expert system was based on the field samples of the bird inventory and assumed for each of the species classified as underrepresented that areas without bird sightings in which environmental conditions were similar to those with bird sightings had a high probability of being inhabited by this species as well. An overlay of the 119 modelled distribution maps with the 94 distribution maps taken directly from the inventory resulted in the map of Austrian breeding bird species richness used in the analyses presented here. A comparison of this data set with detailed local field samples demonstrated its reliability and usefulness (linear correlation with $r^2 = 0.66$, $p < 0.001$, $N = 75$).

Since one aim of this study was to investigate whether there was any scale dependency in the relationships all analyses were carried out on four spatial scales, represented by four spatially hierarchical fishnets: $0.25 \text{ km} \times 0.25 \text{ km}$ ($N \cong 1.3 \text{ mio.}$), $1 \text{ km} \times 1 \text{ km}$ ($N \cong 84300$), $4 \text{ km} \times 4 \text{ km}$ ($N = 5510$) and $16 \text{ km} \times 16 \text{ km}$ ($N = 328$). More than 50% of the area of a $16 \text{ km} \times 16 \text{ km}$ square had to fall within Austria's borders for a square to be considered, for all other squares it had to be 100%. For grids larger than $0.25 \text{ km} \times 0.25 \text{ km}$ mean values were calculated for all variables. The Shannon-Wiener Indices (Krebs, 1989) of land cover (LC-Shannon) and landscape types (LSc-Shannon) were determined. Data on landscape types were taken from the literature (Wrbka et al., 2002). The corresponding Simpson Indices were also calculated, but results are not presented here because they performed worse than the Shannon-Wiener Indices. All data were log-transformed.

The aim of this study was to test the species-energy hypothesis and its potential usefulness for developing pressure indicators for biodiversity loss, not to use potential determinants of species richness to derive a best-fit model of Austrian breeding bird species richness. Therefore neither multivariate methods nor variable reducing methods (e.g., principal component

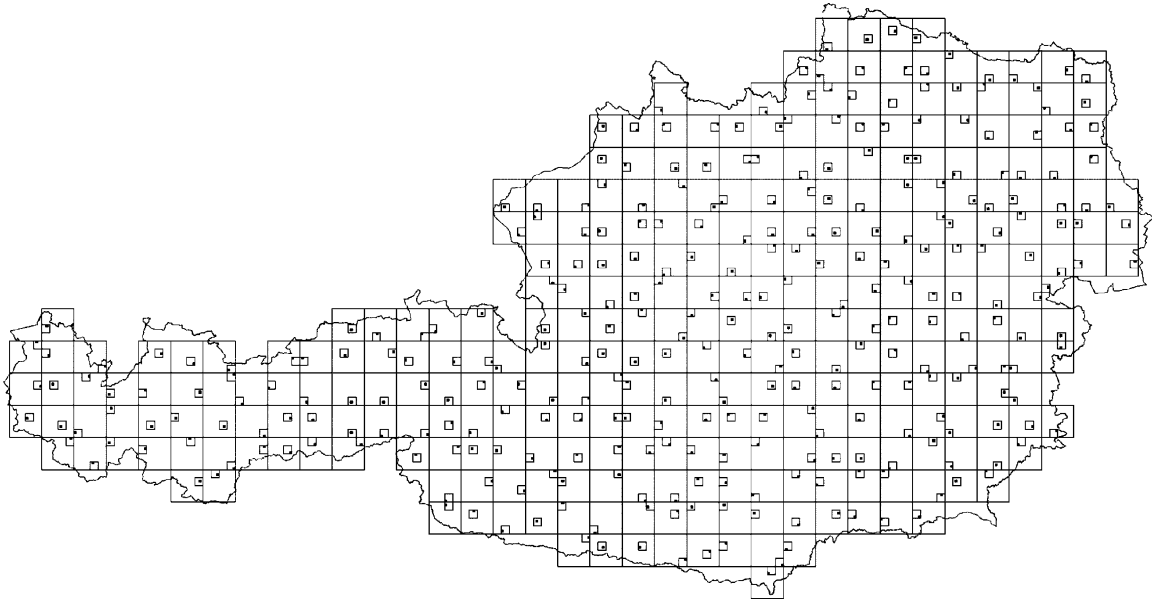


Fig. 1. Location of the 328 squares sized 16 km × 16 km, 4 km × 4 km and 1 km × 1 km, respectively, of the representative sample analysed most intensively in this paper (see text for explanation). The squares sized 0.25 km × 0.25 km were too small to be visualized in this map.

or factor analysis) were used. Instead, regressions were performed to determine the correlation between these parameters and data describing Austria's avifauna richness. In order to obtain samples of the same size (N) for each of the four spatial scales 10 random samples were taken using the following procedure: all 16 km × 16 km squares meeting the above-specified requirement were included. Within each 16 km × 16 km square one 0.25 km × 0.25 km square was randomly chosen. The 1 km × 1 km and 4 km × 4 km squares in which the selected 0.25 km × 0.25 km square was located were used so that each of the 10 iterations represented a nested sample with identical $N = 328$ for all four spatial scales. Regressions between avifauna richness and its potential determinants were made, using both a linear model ($Y = A + BX$) and a quadratic polynomial model ($Y = A + BX + CX^2$). Polynomial models resulted in a higher Pearson's ' r ' than linear models, but their degrees of freedom were larger. To decide which model to select the Akaike Information Criterion (AIC; Sakamoto et al., 1986) was used. All regressions were Bonferroni-corrected.

As this analysis had shown that the correlations were stable for all well-performing indicators, a

representative random sample was chosen from the 10 samples for all subsequent analyses. The selection was based on a χ^2 -test designed to determine the sample in which the distribution of land cover classes best matched that in all 0.25 km × 0.25 km grid cells. Land cover classes were aggregated to 10 classes in order to reduce the number of less frequent land cover classes, because less frequent classes would have distorted the χ^2 -test. The location of the squares of this representative sample is shown in Fig. 1. This sample was used in all scatter plots presented in Figs. 2 and 3, for the analysis of the percentage of endangered (red list categories 0, 1, 2 and 3 according to Frühauf, 2005) species, and for the residual analysis described below.

Land-use causes considerable deviation of actually prevailing conditions from production-ecological patterns that would be expected in the absence of human intervention; i.e., from a pattern that would to a large extent be determined by climate and thus elevation (Haberl et al., 2001). The next question was therefore whether, and to what extent, deviations of the observed bird species richness patterns from those predicted by elevation could be explained by deviations in production-ecological parameters from

the production ecological pattern that would be predicted by elevation. This analysis was performed as follows: using the AIC the best-performing model, linear or quadratic, for the dependency of all variables on elevation was determined and residuals, i.e., the deviation of data from the value predicted by the model, were calculated. For both production ecology and bird species richness these residuals were used as new, elevation-independent variables. The same correlation analysis as described above was performed to detect interrelations between these residuals.

3. Results

Table 1 presents the results of the correlation analyses between breeding bird species richness and its various potential determinants for all four spatial scales. For each scale the first column shows whether the AIC preferred the quadratic (Q) or the linear (L) model and, for all scales below $16 \text{ km} \times 16 \text{ km}$, how often each of the two models was chosen. Mean r^2 was the mean r -squared of all 10 regressions of the model type preferred by the AIC, r^2 range the range of r^2 (largest r^2 – smallest r^2) in the 10 samples.

Table 1 shows that the ranges of r^2 were comparably small for well-performing regressions; therefore, all further analyses were based on the representative sample (sample #9) selected by the χ^2 -test. Elevation and HANPP components generally had much better explanative value than the heterogeneity indicators (LC-Het, LC-Shannon, LSc-Shannon). Correlations were best on the $1 \text{ km} \times 1 \text{ km}$ and $4 \text{ km} \times 4 \text{ km}$ scale and worst on the $0.25 \text{ km} \times 0.25 \text{ km}$ scale. Among the HANPP components, NPP_{act} was the best predictor of bird species richness on all scales. Whether NPP_{t} , NPP_{h} , or HANPP% worked second-best depended on scale, and differences between the mean r^2 were too small to favor one of these HANPP components over the other. All correlations of HANPP components and total bird numbers were unequivocally quadratic, except for NPP_{act} on the $0.25 \text{ km} \times 0.25 \text{ km}$ scale; here the AIC favored the linear model in two of the 10 samples. Fig. 2 shows scatterplots of the regressions (sample #9) between NPP_{act} and NPP_{t} on the four spatial scales, revealing monotonous relations between NPP_{act} and species richness on all four scales, and

monotonous relations between NPP_{t} and species richness on all scales except $16 \text{ km} \times 16 \text{ km}$.

The heterogeneity indicators did not only work worse than elevation and the HANPP components, they also did not produce stable patterns across scales, as visual inspection of the scatter diagrams (not shown here) revealed. For example, LC-Het, the best-performing heterogeneity indicator on all four scales, was linearly related to bird species numbers only on the smallest scale, but produced unimodal patterns on all other scales, contrary to the common assumption that more heterogenous squares should generally host more species.

Table 2 shows adjusted r^2 values of linear and quadratic correlations (sample #9) between the potential determinants of bird species diversity considered in this study. Elevation was significantly inversely correlated with all HANPP components. Linear regressions with elevation failed completely for NPP_{t} , but worked almost as well as quadratic ones for NPP_{h} and HANPP%. Heterogeneity indicators were neither linearly nor quadratically correlated with elevation. NPP_{act} was positively correlated with NPP_{h} as well as with NPP_{t} on all scales; as an example, Fig. 3a and b show these interrelations on the $1 \text{ km} \times 1 \text{ km}$ scale. In both cases linear regressions performed almost as well as quadratic, as confirmed by the scatterplot. HANPP% was also strongly related with NPP_{act} and NPP_{h} ; the linear regression only failed on the smallest scale for HANPP%'s relation to NPP_{act} . On the $1 \text{ km} \times 1 \text{ km}$ scale a clearly monotonous curve was found (Fig. 3c). The relationship between HANPP% and NPP_{t} , however, was clearly non-linear. In this case linear regressions yielded very low or even insignificant adjusted r^2 values, whereas a quadratic relation could be found on all four scales. Fig. 3d shows the scatterplot at the $1 \text{ km} \times 1 \text{ km}$ scale; a similar pattern was found on the other scales.

Correlations between HANPP components and the heterogeneity indicators were generally bad, with the exception of the relations between NPP_{t} and LC-Het (quadratic), HANPP% and LC-Het (linear and quadratic), as well as NPP_{t} and LSc-Shannon (quadratic at larger scales). LC-Het and LC-Shannon were strongly correlated ($0.51 < r^2 < 0.88$), LC-Het and LSc-Shannon as well as LC-Shannon and LSc-Shannon still considerably ($0.17 < r^2 < 0.32$).

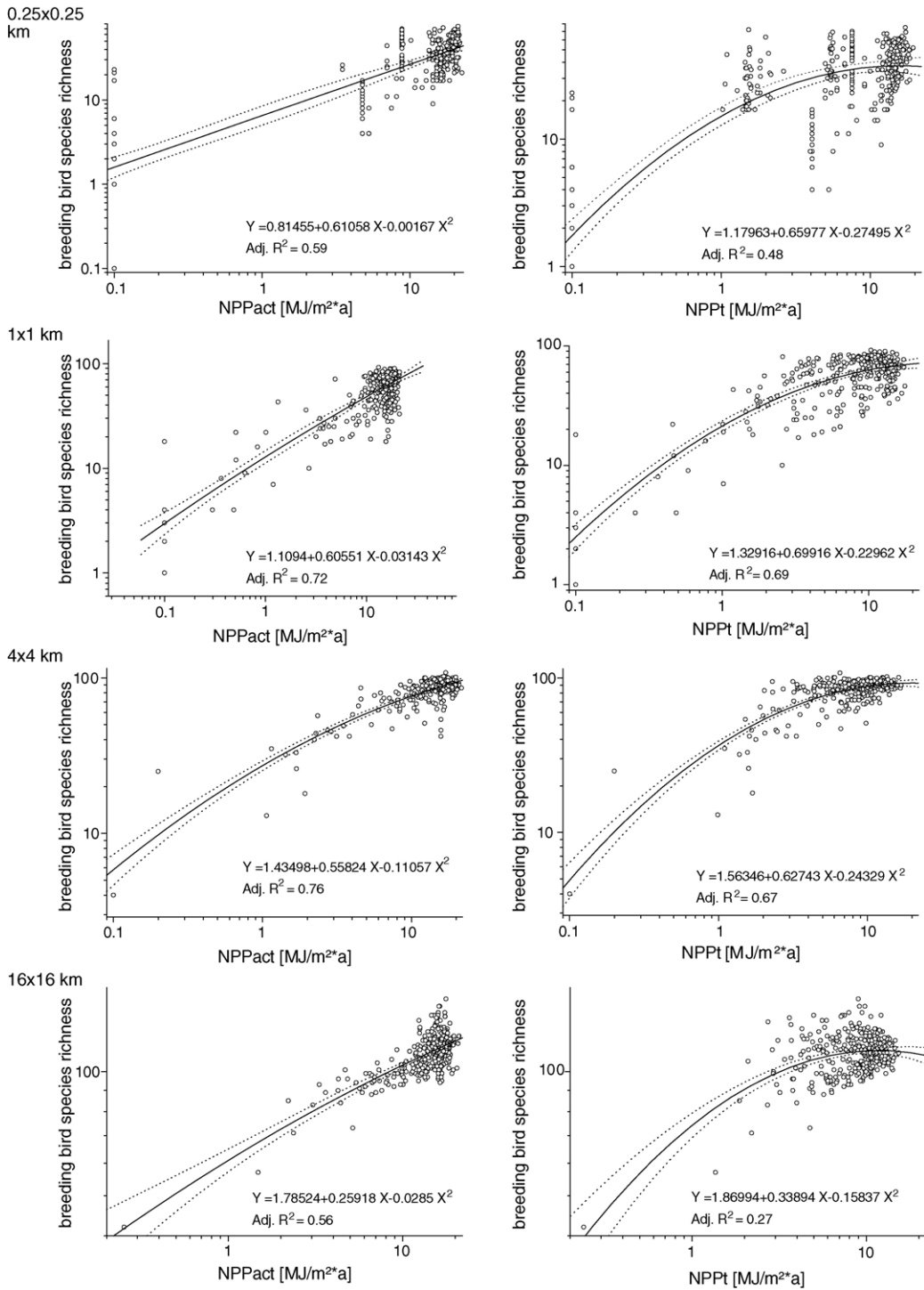


Fig. 2. Scatterplots of the regressions (representative sample #9) between NPP_{act} and breeding bird species richness (left column) and NPP_t and breeding bird species richness (right column) on all four spatial scales.

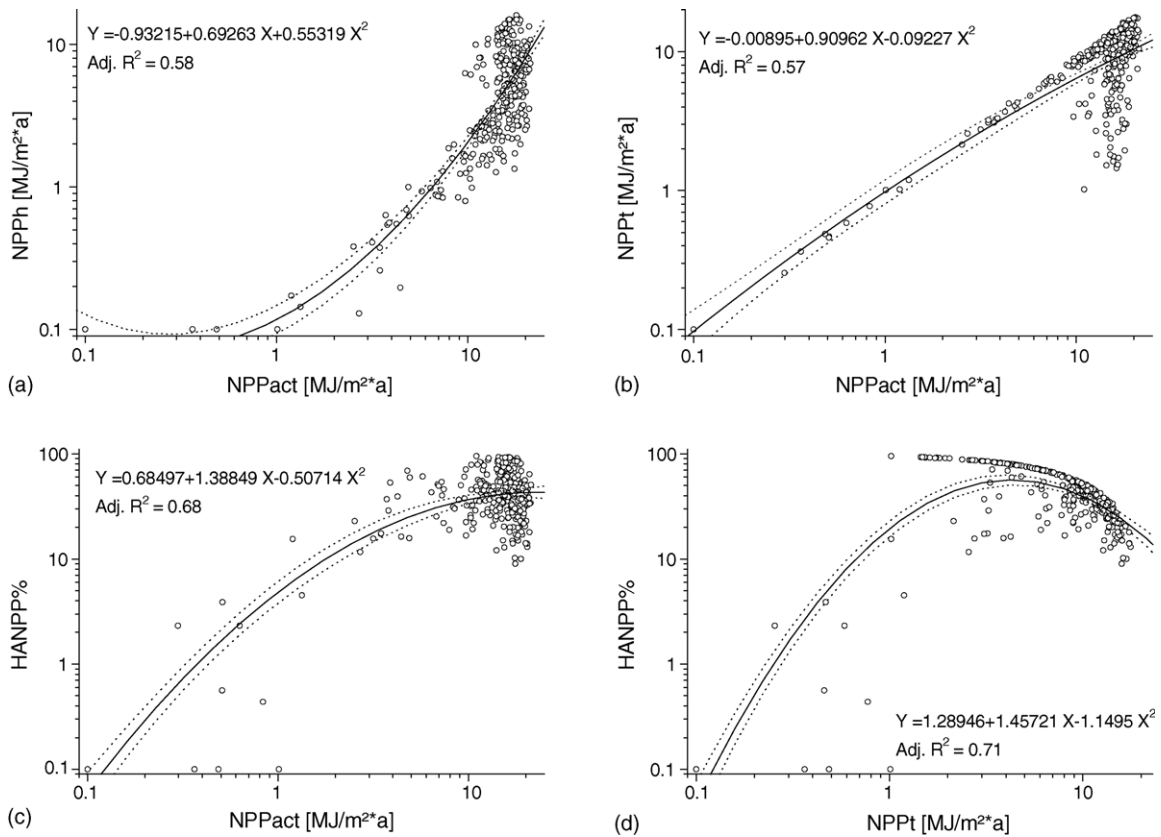


Fig. 3. Scatterplots of the relationships between HANPP components (representative sample #9) on the 1 km × 1 km scale: (a) NPP_{act} and NPP_h , (b) NPP_{act} and NPP_t , (c) NPP_{act} and HANPP%, (d) NPP_t and HANPP%.

As expected, linear models worked well in regressions between heterogeneity indicators.

Table 3 reports results of the correlation analyses for the percentage of endangered (red list 0–3) species.

Good quadratic, but very poor linear, correlations were found for elevation, NPP_h and HANPP%. Visual inspection of the scatter plots (not shown) revealed U-shaped patterns for these three parameters. NPP_{act}

Table 1
Results of the correlation analyses between different indicators and breeding bird species richness

	0.25 × 0.25			1 × 1			4 × 4			16 × 16	
	Lin/quad	Mean r^2	r^2 range	Lin/quad	Mean r^2	r^2 range	Lin/quad	Mean r^2	r^2 range	Lin/quad	r^2
Elevation	Q 0/10	(I) 0.670	0.113	Q 0/10	(I) 0.656	0.070	Q 0/10	(I) 0.511	0.119	Q	(I) 0.466
NPP_{act}	Q 2/8	0.574	0.209	Q 0/10	0.775	0.132	Q 0/10	0.821	0.162	Q	0.557
NPP_h	Q 0/10	0.571	0.160	Q 0/10	0.738	0.081	Q 0/10	0.645	0.112	Q	0.491
NPP_t	Q 0/10	0.461	0.240	Q 0/10	0.719	0.121	Q 0/10	0.731	0.142	Q	0.273
HANPP%	Q 0/10	0.374	0.211	Q 0/10	0.667	0.203	Q 0/10	0.714	0.270	Q	0.509
LC-Het	L 8/2	0.078	0.084	Q 0/10	0.201	0.141	Q 0/10	0.262	0.320	Q	0.296
LC-Shannon	n.a.	n.a.	n.a.	Q 0/10	0.143	0.119	n.s.	n.s.	n.s.	L	0.103
LSc-Shannon	n.a.	n.a.	n.a.	n.s.	n.s.	n.s.	Q 1/9	0.129	0.199	Q	0.239

The Lin/quad column reports how often the AIC favored the linear over the quadratic model or vice versa in the 10 samples. All regressions were Bonferroni-corrected, all r^2 values adjusted. n.a., not applicable; n.s., not significant ($p < 0.001$); Q, quadratic model more often supported by AIC; L, linear model more often supported by AIC; (I), inverse relationship, i.e., linear regression was also significant and inverse.

Table 2

Bonferroni-corrected, adjusted r^2 of linear and quadratic correlations between potential determinants of breeding bird species diversity considered in this study (representative sample #9)

	NPP _{act}		NPP _h		NPP _t		HANPP%		LC-Het		LC-Shannon		LSc-Shannon	
	Lin	Quad	Lin	Quad	Lin	Quad	Lin	Quad	Lin	Quad	Lin	Quad	Lin	Quad
Elevation														
0.25 × 0.25	(I) 0.24	0.46	(I) 0.56	0.58	n.s.	0.35	(I) 0.37	0.37	(I) 0.06	0.07	n.a.	n.a.	n.a.	n.a.
1 × 1	(I) 0.31	0.61	(I) 0.77	0.82	n.s.	0.47	(I) 0.42	0.49	(I) 0.11	0.13	(I) 0.06	0.07	n.s.	n.s.
4 × 4	(I) 0.36	0.69	(I) 0.83	0.87	n.s.	0.56	(I) 0.57	0.61	(I) 0.18	0.20	(I) 0.07	0.07	n.s.	n.s.
16 × 16	(I) 0.42	0.77	(I) 0.85	0.92	0.03	0.59	(I) 0.72	0.77	(I) 0.31	0.38	(I) 0.16	0.19	n.s.	0.13
NPP_{act}														
0.25 × 0.25			0.52	0.56	0.52	0.52	0.06	0.34	n.s.	0.06	n.a.	n.a.	n.a.	n.a.
1 × 1			0.54	0.58	0.57	0.57	0.52	0.68	0.03	0.16	n.s.	0.18	n.s.	0.11
4 × 4			0.55	0.61	0.44	0.45	0.48	0.52	n.s.	0.09	n.s.	0.12	n.s.	0.16
16 × 16			0.61	0.69	0.33	0.36	0.57	0.57	0.16	0.16	n.s.	0.05	0.08	0.13
NPP_h														
0.25 × 0.25					n.s.	0.85	0.31	0.37	n.s.	n.s.	n.a.	n.a.	n.a.	n.a.
1 × 1					n.s.	0.83	0.56	0.62	0.09	0.08	0.04	0.04	n.s.	n.s.
4 × 4					n.s.	0.80	0.71	0.72	0.17	0.18	0.04	0.09	n.s.	n.s.
16 × 16					n.s.	0.77	0.84	0.85	0.33	0.34	0.08	0.20	0.03	0.08
NPP_t														
0.25 × 0.25							(I) 0.09	0.79	n.s.	0.12	n.a.	n.a.	n.a.	n.a.
1 × 1							0.08	0.71	n.s.	0.44	n.s.	0.42	n.s.	0.11
4 × 4							n.s.	0.40	n.s.	0.43	(I) 0.04	0.54	n.s.	0.18
16 × 16							n.s.	0.23	n.s.	0.29	(I) 0.11	0.53	0.08	0.23
HANPP%														
0.25 × 0.25									0.09	0.10	n.a.	n.a.	n.a.	n.a.
1 × 1									0.24	0.26	0.20	0.21	0.05	0.05
4 × 4									0.31	0.32	0.14	0.15	n.s.	0.07
16 × 16									0.41	0.41	0.15	0.16	0.07	0.15
LC-Het														
0.25 × 0.25											n.a.	n.a.	n.a.	n.a.
1 × 1											0.88	0.88	0.25	0.26
4 × 4											0.78	0.81	0.17	0.27
16 × 16											0.51	0.55	0.23	0.32
LC-Shannon														
0.25 × .25													n.a.	n.a.
1 × 1													0.31	0.32
4 × 4													0.30	0.32
16 × 16													0.28	0.29

n.a., not applicable; n.s., not significant ($p < 0.001$); (I), inverse linear correlation.

and NPP_t were inversely correlated with the percentage of endangered species; i.e., it was found that the percentage of endangered species was higher in plots with low NPP_{act} and NPP_t. NPP_t did not only give better fits (higher r^2), but was also much more stable across scales than NPP_{act} and gave unequivocally linear regression lines. The heterogeneity indicators did not work well with the possible exception of a positive

correlation between LC-Shannon and percentage of endangered bird species on the 16 km × 16 km scale.

Results of the residual analysis are shown in Table 4. It shows that, consistently across all scales, NPP_{act} and NPP_t retained considerable explanative power for species richness after removing the effect of elevation. HANPP as well as the heterogeneity indicators worked worse. Correlations were best on

Table 3

Bonferroni-corrected, adjusted r^2 values of the correlations between potential determinants of avifauna diversity with the percentage of endangered (red list 0–3) breeding species

	Elevation	NPP _{act}	NPP _h	NPP _t	HANPP%	LC-Het	LC-Shannon	LSc-Shannon
0.25 × 0.25								
Lin	0.09	(A) (I) 0.41	(I) 0.09	(A) (I) 0.44	n.s.	n.s.	n.a.	n.a.
Quad	(A) 0.46	0.41	(A) 0.46	0.44	(A) 0.27	n.s.	n.a.	n.a.
1 × 1								
Lin	(I) 0.01	(A) (I) 0.36	(I) 0.05	(A) (I) 0.48	(I) 0.04	n.s.	n.s.	n.s.
Quad	(A) 0.36	0.35	(A) 0.43	0.48	(A) 0.31	(A) 0.02	n.s.	n.s.
4 × 4								
Lin	(I) 0.06	(I) 0.13	n.s.	(A) (I) 0.42	n.s.	n.s.	(A) 0.06	n.s.
Quad	(A) 0.45	(A) 0.16	(A) 0.44	0.41	(A) 0.21	n.s.	0.06	n.s.
16 × 16								
Lin	(I) 0.16	(I) 0.01	0.07	(A) (I) 0.36	0.07	0.08	0.18	n.s.
Quad	(A) 0.42	(A) 0.05	(A) 0.39	0.36	(A) 0.38	(A) 0.09	(A) 0.19	(A) 0.04

n.a., not applicable; n.s., not significant ($p < 0.001$); (A), selected by the AIC; (I), inverse linear correlation.

Table 4

Bonferroni-corrected, adjusted r^2 values of the correlations between residuals of HANPP components or heterogeneity indicators with residuals of bird diversity indicators

	NPP _{act}	NPP _h	NPP _t	HANPP%	LC-Het	LC-Shannon	LSc-Shannon
(a) Number of all breeding bird species							
0.25 × 0.25							
Lin	0.27	n.s.	0.31	n.s.	n.s.	n.a.	n.a.
Quad	(A) 0.31	n.s.	(A) 0.32	n.s.	n.s.	n.a.	n.a.
1 × 1							
Lin	0.35	n.s.	0.39	0.17	0.12	0.14	(A) 0.14
Quad	(A) 0.36	n.s.	(A) 0.40	(A) 0.22	(A) 0.13	(A) 0.15	0.14
4 × 4							
Lin	0.42	n.s.	0.34	0.16	n.s.	n.s.	0.12
Quad	(A) 0.52	n.s.	(A) 0.42	(A) 0.27	(A) 0.10	(A) 0.11	(A) 0.18
16 × 16							
Lin	0.15	n.s.	0.17	n.s.	n.s.	0.08	0.15
Quad	(A) 0.20	n.s.	(A) 0.18	(A) 0.19	(A) 0.07	(A) 0.09	(A) 0.16
(b) Percentage of endangered (red list 0–3) breeding species							
0.25 × 0.25							
Lin	(I) 0.15	n.s.	(I) 0.28	(A) 0.09	n.s.	n.a.	n.a.
Quad	(A) 0.17	n.s.	(A) 0.29	0.09	n.s.	n.a.	n.a.
1 × 1							
Lin	(I) (A) 0.17	n.s.	(I) (A) 0.24	(A) 0.02	(A) 0.04	(A) 0.01	n.s.
Quad	0.17	n.s.	0.24	0.02	0.04	0.01	n.s.
4 × 4							
Lin	(I) (A) 0.14	n.s.	(I) (A) 0.10	n.s.	(A) 0.02	n.s.	n.s.
Quad	0.14	n.s.	0.10	n.s.	0.01	n.s.	n.s.
16 × 16							
Lin	(I) 0.07	n.s.	(I) (A) 0.09	0.02	(A) 0.11	n.s.	n.s.
Quad	(A) 0.08	n.s.	0.09	(A) 0.06	0.11	(A) 0.01	n.s.

n.s., not significant ($p < 0.001$); (A), selected by the AIC; (I), inverse linear correlation.

the 1 km × 1 km and 4 km × 4 km scales. Visual inspection of the scatterplots (not shown) revealed that residuals of both NPP_{act} and NPP_t were positively correlated with residuals of bird species numbers. Monotonous patterns prevailed with the exception of NPP_{act} at the scales 0.25 km × 0.25 km, 1 km × 1 km and 4 km × 4 km and NPP_t at the 1 km × 1 km scale, but even in these cases the elevation-corrected relation between energy availability and species numbers was positive over most of the interval spanned by the data. Table 4b shows that the residual analysis removed almost all effects besides those of NPP_{act} and NPP_t on the percentage of endangered species. (Almost) linear inverse correlations were found for the relations between NPP_{act}/NPP_t and the percentage of endangered species. NPP_t had a higher r^2 than NPP_{act} except on the 4 km × 4 km scale. The correlation was reasonably good for NPP_{act} only on the three smallest scales, and only on the two smallest scales for NPP_t .

4. Discussion and conclusions

Bird species richness was much better explained by production ecological parameters than by the landscape/land cover heterogeneity indicators included in this study. It cannot be ruled out, however, that more refined heterogeneity indicators would perform better than those considered here. It would therefore not be justified to use this result to question altogether the well-established positive relation between landscape heterogeneity and species richness (Benton et al., 2003; Gaston and Blackburn, 2000; Hoffmann et al., 2001; Honnay et al., 2003; Levin and Paine, 1974; MacArthur and MacArthur, 1961; Moser et al., 2002; Steiner and Köhler, 2003; Zechmeister et al., 2003).

Two different versions of the species-energy hypothesis have been proposed: (1) a linear or at least monotonous positive relation between energy availability and species richness (Allen et al., 2002; Brown, 1981, 1995; Wright, 1983), and (2) an unimodal (hump-shaped) curve (Rosenzweig, 1992; Rosenzweig and Abramsky, 1993). Metaanalyses of published studies did not clearly favor one of these two patterns over the other (Mittelbach et al., 2001, 2003; Waide et al., 1999). Many authors have argued that the form of the curve may be scale-dependent (Pastor et al., 1996; Rapson et al., 1997; Weiher, 1999;

Whittaker and Heegaard, 2003); and it has been proposed that unimodal patterns would prevail on smaller scales, monotonous patterns on larger scales (Chase and Leibold, 2002; Gaston, 2000). The data presented here support the monotonous version of the species-energy hypothesis on all four scales, i.e., on plots sized 0.06–256 km² (a factor of over 4000), suggesting a fairly general and stable pattern. This is further substantiated by the finding that NPP_{act} and NPP_t were able to explain much of the variation in bird species numbers after the effect of elevation had been removed in the residual analysis. The latter result implies, as theoretically predicted (Allen et al., 2002), that not only climate, but also the availability of trophic energy are relevant in determining bird species richness.

A direct test of the hypothesis proposed by Wright (1990) that HANPP is related to species loss was impossible because no data on species loss were available. Moreover, there is no linear relation between HANPP and NPP_t because NPP_t may be low due to low initial productivity (low NPP_0) or due to large harvest in a productive system (large NPP_0 , NPP_{act} and NPP_h). In this study the relationship between HANPP and NPP_t was unimodal (Fig. 3d). Because deviations of NPP_{act} and NPP_t from the pattern that would be expected as a result of elevation (climate) alone are to a large extent caused by land-use, the residual analysis indirectly supports the hypothesis that HANPP is related with species loss. No distinction could be drawn, however, between NPP_{act} and NPP_t , as these two parameters were highly correlated (linear regression with $0.32 < r^2 < 0.58$; Table 2).

The definition of red list species refers to their extinction probabilities (Mace and Lande, 1991). The results for endangered species therefore support the hypothesis that low energy availability results in high extinction probability (Brown, 1995). Both NPP_{act} and NPP_t were inversely and more or less linearly correlated with the percentage of endangered species. The U-shaped relation between elevation and the percentage of endangered species can be explained as follows: at high altitudes, bird species richness is low and species tend to be vulnerable (high extinction probability) due to their naturally low population densities. Intensive agriculture, a well-known determinant of bird endangerment (Chamberlain and

Fuller, 2000; Donald et al., 2001) resulting in high NPP_h and HANPP values, is concentrated in lowlands, thus the percentage of endangered bird species is high there. Intermediate elevations are characterized by comparably energy-rich, and species-rich ecosystems with few endangered bird species. NPP_h and HANPP were strongly inversely related to elevation and reproduced the same U-shaped pattern as elevation and were therefore eliminated in the residual analysis. That less energy availability (i.e., lower NPP_t and NPP_{act}) was correlated with a higher percentage of endangered species, and NPP_t worked better than NPP_{act} in the residual analysis, supports the species-energy hypothesis and is consistent with the notion that that human-caused changes in energy availability contribute to species endangerment.

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