



Human appropriation of net primary production and species diversity in agricultural landscapes

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Abstract

The relationship between land-use induced changes in production ecology and species diversity was analyzed based on a transect of 38 squares (600 m × 600 m) in landscapes of eastern Austria. “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 calculated, considering aboveground processes only. HANPP is an indicator of changes in the production ecology induced by land-use which takes ecosystem productivity and harvest into account. NPP_{act}, NPP_t, and HANPP were correlated with data on species richness of vascular plants, bryophytes, orthopterans, gastropods, spiders, ants, and ground beetles. NPP_{act} and HANPP were inversely correlated with species diversity, whereas NPP_t was positively correlated with species diversity. Results were compatible with the species-energy hypothesis which predicts a positive relationship between energy flow and species diversity. The analysis of the relationship between HANPP and species diversity may yield results that are relevant in terms of ecological theory and biodiversity conservation.

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1. Introduction

Land-use fundamentally alters the production ecology of terrestrial ecosystems, reducing or increasing

the net primary production (NPP) of ecosystems. Harvest removes NPP from ecosystems so that only a fraction of the actual NPP (termed NPP_t in this paper) remains in the ecosystem. The notion of “human appropriation of net primary production” (HANPP; Vitousek et al., 1986) is defined as the difference between NPP₀ and NPP_t (Haberl, 1997; Haberl et al., 2002).

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On a global level, HANPP amounts to 20–40% of the potential vegetation's NPP (NPP_0 ; Vitousek et al., 1986; Wright, 1990) and is probably higher than 40% in many industrialized countries. Human appropriation of aboveground NPP in Austria is currently at about 50% on average, but may reach up to 90% in intensively cropped regions (Haberl et al., 2001). Over the next 50 years global population growth is thought to result in a further global expansion of agricultural areas by about 10^9 ha (Tilman et al., 2001). This could lead to further increases in HANPP and hence in human "domination" (Vitousek et al., 1997) or "colonization" (Haberl et al., 2001) of ecosystems. The question of the impact human-induced changes in production ecology are likely to have on biodiversity is therefore of great interest (Chapin et al., 2000; Sala et al., 1999). This paper intends to test the so-called "species-energy hypothesis" (Wright, 1983, 1987, 1990) that HANPP could contribute to species loss.

This paper presents an empirical analysis of the relationship between NPP_{act} , NPP_t , HANPP, and species diversity in intensively managed agricultural landscapes of eastern Austria. Such an analysis is relevant in terms of ecological biodiversity theory (Huston, 1994; Rosenzweig, 1995; Ricklefs and Schluter, 1993) and could also allow for biodiversity patterns to be predicted from maps of HANPP, NPP_{act} or NPP_t derived from satellite imagery, land-cover surveys and statistical data (Haberl et al., 2001). The analysis was based on a correlation analysis between HANPP and indices of species diversity of seven groups (vascular plants, bryophytes, orthopterans, gastropods, spiders, ants and ground beetles) in 38 observation squares of a transect through eastern Austria.

2. Methods

Data were obtained from 38 randomly selected squares $600\text{ m} \times 600\text{ m}$ on a transect through eastern Austria (Fig. 1) at altitudes of 120–620 m a.s.l. Mean annual precipitation was 528–1115 mm, mean annual temperature 6.3–10.7 °C. Land-cover was dominated by croplands including fallow areas (57% total square area), grasslands (17%), forests (15%), built-up and urban areas (3%), and other ecologically valuable habitats (8%). For details, see Sauberer et al. (2003).

Considering only the aboveground compartment, the following parameters were assessed: potential net primary productivity (NPP_0), actual NPP (NPP_{act}), biomass harvest (NPP_h) and NPP remaining in the ecosystem after harvest (NPP_t). HANPP was defined as the difference between NPP_0 and NPP_t . 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). HANPP% expresses HANPP as a percentage of NPP_0 .

The 38 squares were mapped using orthophotos (years: 1992–1996, resolution 0.5 m) combined with field mapping in 1999 (Moser et al., 2002) which resulted in a total of 3305 distinct landscape elements each of which was classified into one of 75 land-cover classes. Potential NPP was calculated using factors for the average NPP per unit area of the potential vegetation of each square, considering vegetation type and climate (Haberl, 1995, 1997; Haberl et al., 2001). These factors had been derived by regression analyses of NPP data from the literature (Cannell, 1982; DeAngelis et al., 1981). For each landscape element classified as one of the cropland and meadow classes NPP_{act} was calculated using harvest indices (Singh and Stoskopf, 1971; Krausmann, 2001). 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 gives similar results as the extrapolation of forest NPP from wood increment data from the Austrian forest inventory (Haberl, 1997; Haberl et al., 2001). To assess NPP_h in forests the percentage of NPP_{act} harvested on average in the region was calculated using timber balances and the Austrian forest inventory (Haberl et al., 2001). For the remaining land-cover classes average values were derived from Haberl (1995) and Schulz (1999). Data were expressed in Joule (J) per year.

Data on species diversity were collected at 10 randomly selected sampling points per square, avoiding human settlement or inaccessible terrain. A census was made in 1998 and 1999 of the species richness of seven taxa: vascular plants, bryophytes, orthopterans, gastropods, spiders, ants and ground beetles. Vascular plants and orthopterans were recorded within a radius of 20 m, bryophytes and gastropods within a radius of 10 m around the sampling point. The other arthropod

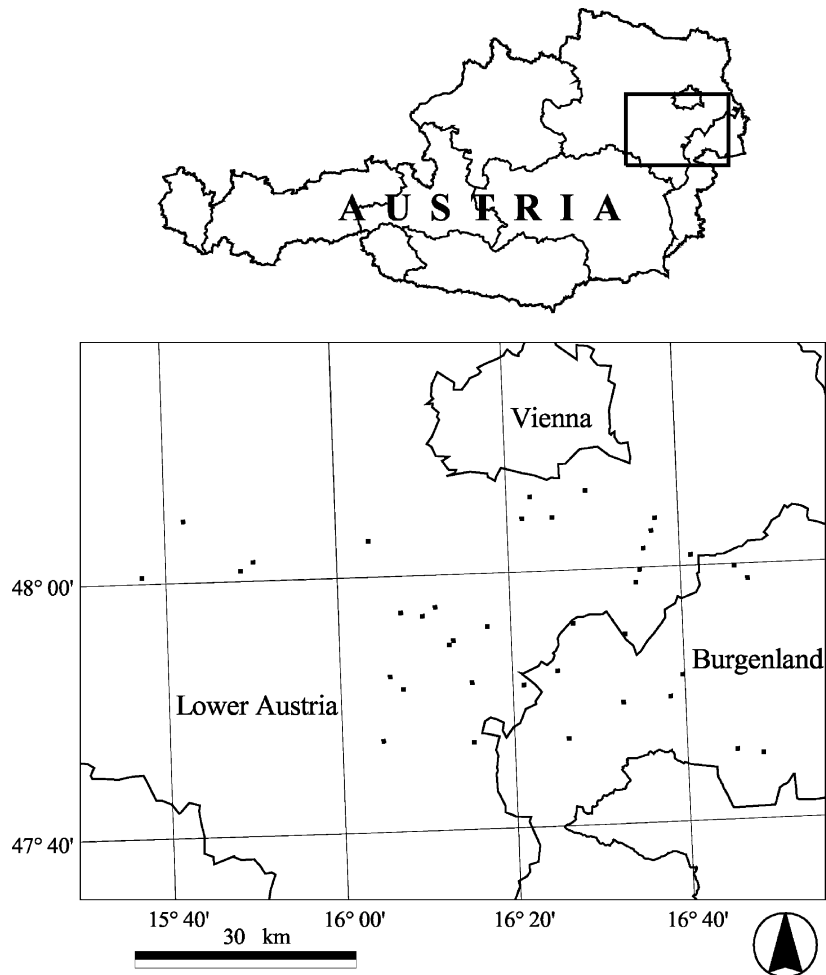


Fig. 1. Location of the study plots in eastern Austria.

taxa were caught by pitfall trapping. Bryophytes were evaluated in winter, vascular plants twice a year in spring and summer, recording all species found at a sample point. Spiders, ground beetles, and ants were identified based on pitfall trapping. Each pitfall (one per sample point, 4.5 cm diameter) was covered with a transparent roof, filled with ethylene glycol and exposed for three 14-day periods (September 1998, May 1999, June/July 1999). Gastropods were searched manually for 10 minutes, those caught by pitfall trapping being also determined. Four soil samples (10 cm × 10 cm, 5 cm deep) per sampling point were taken and any shell separated from soil samples by sifting through a series of sieves down to >2 mm.

Orthopterans were recorded in July–August 1999 for 10 minutes. Determination occurred according to morphological characteristics and using >20 kHz song detectors.

The species richness per square was calculated as the sum of the 10 sampling points; species recorded in more than one point were counted only once. To overcome disproportions in species numbers for the various groups considered (bryophytes: 215 species, vascular plants: 960, gastropods: 96, spiders: 215, orthopterans: 46, ground beetles: 196, ants: 40), each group was adjusted to 100%. The overall indices per square were calculated as the sum of the respective group index values divided by the number of groups.

Nine regressions between species diversity and each of the three variables NPP_{act} , NPP_t and $HANPP\%$ 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.

3. Results

Mean NPP_{act} values for the 38 squares ranged from 12.3 to 25.4 $MJ m^{-2}$ per year, mean NPP_h from

2.8 to 20.9 $MJ m^{-2}$ per year, mean NPP_t from 1.9 to 14.0 $MJ m^{-2}$ per year, mean $HANPP$ from 5.8 to 19.5 $MJ m^{-2}$ per year (about 45–95% of NPP_0). NPP_{act} was not correlated either with NPP_t or to $HANPP\%$, whereas NPP_t and $HANPP\%$ were highly correlated (-0.99 ; $P < 0.001$).

NPP_{act} was inversely correlated with the species diversity of all taxa, the regression coefficient being lowest for ground beetles ($r^2 = 0.118$) and highest for vascular plants ($r^2 = 0.408$). NPP_t was positively correlated with species diversity. In most cases, NPP_t gave a better fit than NPP_{act} , except for spiders and ground beetles, where both fits were about equal. The regression coefficient was between 0.132 (ground

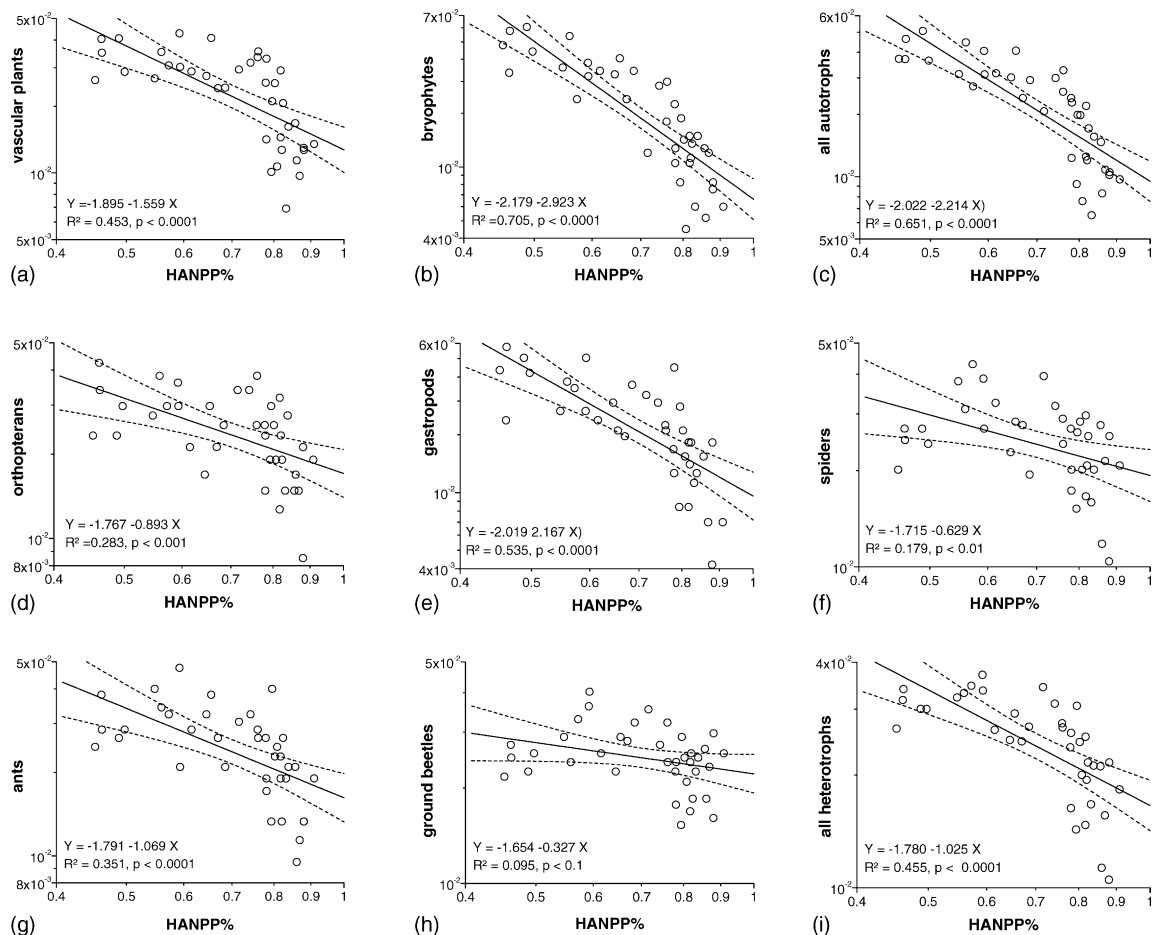


Fig. 2. The log–log scatter plots of the regression analyses between $HANPP\%$ as a percentage of NPP_0 ($HANPP\%$) and species diversity of (a) vascular plants, (b) bryophytes, (c) all autotrophs, (d) orthopterans, (e) gastropods, (f) spiders, (g) ants, (h) ground beetles, and (i) all heterotrophs. Dotted lines denote 95% confidence interval.

beetles) and 0.758 (bryophytes). HANPP% was inversely correlated with species diversity of all groups (Fig. 2). The data suggested that the pattern could be unimodal, but this was not confirmed by the AIC. The regression coefficient was between 0.095 (ground beetles) and 0.705 (bryophytes). Most fits were better than for NPP_{act} but worse than for NPP_t .

Autotrophs were generally better correlated to NPP_{act} , NPP_t , and HANPP% than heterotrophs. Bryophytes yielded better correlations than vascular plants, except for NPP_{act} which correlated better with vascular plants than with bryophytes. Among heterotrophs ground beetles, orthopterans and spiders gave lower correlations than groups with lower mobility.

4. Discussion and conclusions

Wright (1990) argued that HANPP could be expected to reduce species diversity. The species-energy hypothesis (Brown, 1981, 1995; Gaston, 2000; Hutchinson, 1959; Wright, 1983, 1987) suggests that increases in available energy should make it possible for more species to coexist, leading to a positive relation between energy availability and species diversity, and the species-energy hypothesis predicts a linear (or at least monotonous) positive correlation between NPP_t and species diversity. For heterotrophs species numbers should be positively correlated with the energy remaining in ecosystems. NPP_t and diversity were positively correlated as predicted by the linear orientation of the species-energy hypothesis. The present data suggest, however, that autotroph diversity was even more closely correlated with NPP_t than heterotroph diversity.

The inverse correlation between NPP_{act} and diversity was difficult to explain. One explanation could be that fertile plots were harvested more intensively. Another explanation could be a possible negative impact of high NPP levels on species diversity (Rosenzweig, 1992; Rosenzweig and Abramsky, 1993). The possibility that diversity could saturate or even decline at high NPP_t or low HANPP% levels cannot be excluded. Testing this possibility would require data that include highly productive plots with low HANPP (high NPP_t) and plots with no or little HANPP and low NPP_t .

The bad fit of the data obtained for ground beetles and spiders could be due to their high mobility. An explanation for the better fit of autotrophs as compared to heterotrophs could be that they included species from all kinds of habitats, whereas heterotrophic groups were mainly surface-active invertebrates.

At least at levels above 50% HANPP has negative consequences in terms of biodiversity, as predicted by the species-energy hypothesis. This confirms the conventional wisdom of conservationists that species diversity is negatively correlated with the intensity of land-use (Hoffmann et al., 2001; Zechmeister and Moser, 2001). The approach taken in this paper could lead to results of potentially great value in the discussions around land-use changes as a driving force of biodiversity loss, and on scenarios of future changes in biodiversity (Chapin et al., 2000; Sala et al., 1999). Another practical use of the correlations between HANPP and species diversity could be the development of indicators for socio-economic activities leading to biodiversity loss, so-called “pressure indicators” for biodiversity as currently developed within environmental reporting systems (Eurostat, 1999).

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References

- Brown, J.H., 1981. Two decades of homage to Santa Rosalia: toward a general theory of diversity. *Am. Zool.* 21, 877–888.
- Brown, J.H., 1995. *Macroecology*. Chicago University Press, Chicago.
- Cannell, M.G.R., 1982. *World Forest Biomass and Primary Production Data*. Academic Press, London.
- Chapin, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E.,

- Hobbie, S.E., Mack, M.C., Diaz, S., 2000. Consequences of changing biodiversity. *Nature* 405, 234–242.
- DeAngelis, D.L., Gardner, R.H., Shugart, H.H., 1981. Productivity of forest ecosystems studied during the IBP: the woodland data set. In: Reichle, D.E. (Ed.), *Dynamics of Forest Ecosystems*. Cambridge University Press, Cambridge, pp. 567–672.
- Eurostat, 1999. Towards environmental pressure indicators for the EU. Office for Official Publications of the European Communities, Luxembourg.
- Gaston, K.L., 2000. Global patterns in biodiversity. *Nature* 405, 220–227.
- Haberl, H., 1995. Menschliche Eingriffe in den natürlichen Energiefluß von Ökosystemen. Working Paper Social Ecology No. 43, Vienna.
- Haberl, H., 1997. Human appropriation of net primary production as an environmental indicator: implications for sustainable development. *Ambio* 26, 143–146.
- Haberl, H., Erb, K.H., Krausmann, F., Loibl, W., Schulz, N., Weisz, H., 2001. Changes in ecosystem processes induced by land use: human appropriation of net primary production and its influence on standing crop in Austria. *Global Biogeochem. Cycles* 15, 929–942.
- Haberl, H., Krausmann, F., Erb, K.H., Schulz, N.B., Rojstaczer, S., Sterling, S.M., Moore, N., 2002. Human appropriation of net primary production. *Science* 296, 1968–1969.
- Hoffmann, J., Kretschmer, H., Pfeffer, H., 2001. Effects of patterning on biodiversity in northeast German agro-landscapes. In: Tenhunen, J.D., Lenz, R., Hantschel, R. (Eds.), *Ecosystem Approaches to Landscape Management in Central Europe*, Ecological Studies 147. Springer, Berlin, pp. 325–340.
- Huston, M., 1994. *Biological Diversity: The Coexistence of Species on Changing Landscapes*. Cambridge University Press, Cambridge.
- Hutchinson, G.E., 1959. Hommage to Santa Rosalia, or why are there so many kinds of animals? *Am. Nat.* 93, 145–159.
- Krausmann, F., 2001. Land use and industrial modernization, an empirical analysis of human influence on the functioning of ecosystems in Austria 1830–1995. *Land Use Policy* 18, 17–26.
- Moser, D., Zechmeister, H.G., Plutzer, C., Sauberer, N., Wrba, T., Grabherr, G., 2002. Landscape patch shape complexity as an effective measure for plant species richness in rural landscapes. *Landsc. Ecol.* 17, 657–669.
- Ricklefs, R.E., Schluter, D., 1993. *Species Diversity in Ecological Communities*. The University of Chicago Press, Chicago.
- Rosenzweig, M.L., 1992. Species diversity gradients: we know more and less than we thought. *J. Mammal.* 73, 715–730.
- Rosenzweig, M.L., 1995. *Species Diversity in Space and Time*. Cambridge University Press, Cambridge.
- Rosenzweig, M.L., Abramsky, Z., 1993. How Are Diversity and Productivity Related? In: Ricklefs, R.E., Schluter, D. (Eds.), *Species Diversity on Ecological Communities*. The University of Chicago Press, Chicago, pp. 52–65.
- Sakamoto, Y., Ishiguro, M., Kitagawa, G., 1986. *Akaike Information Criterion Statistics*. Reidel, Tokyo.
- Sala, O.E., Chapin III, F.S., Gardner, R.H., Lauenroth, W.K., Mooney, H.A., Ramakrishnan, P.S., 1999. Global change, biodiversity and ecological complexity. In: Walker, B., Steffen, W., Canadell, J., Ingram, J. (Eds.), *The Terrestrial Biosphere and Global Change, Implications for Natural and Managed Ecosystems*, IGBP Book Series 4. Cambridge University Press, Cambridge, pp. 304–328.
- Sauberer, N., Zulka, K.P., Abensperg-Traun, M., Berg, H.M., Bieringer, G., Milasowsky, N., Moser, D., Plutzer, C., Pollheimer, M., Storch, C., Tröstl, R., Zechmeister, H.G., Grabherr, G., 2003. Surrogate taxa for biodiversity in agricultural landscapes of eastern Austria. *Biol. Conserv.*, in press.
- Schulz, N., 1999. Auswirkungen von Landnutzung auf Ökosystemprozesse: Die menschliche Aneignung von Nettoprimärproduktion in Österreich, vergleichende Berechnung anhand verschiedener Datenquellen. Masters Thesis. University of Vienna, Vienna.
- Singh, I.D., Stoskopf, N.C., 1971. Harvest index in cereals. *Agron. J.* 63, 224–226.
- Statistik Austria, 1999. *Ergebnisse der landwirtschaftlichen Statistik 1998*. Statistik Austria, Vienna.
- Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A.P., Howarth, R.W., Schindler, D., Schlesinger, W.H., Simberloff, D., Swackhamer, D., 2001. Forecasting agriculturally driven global environmental change. *Science* 292, 281–284.
- Vitousek, P.M., Ehrlich, P.R., Ehrlich, A.H., Matson, P.A., 1986. Human appropriation of the products of photosynthesis. *BioScience* 36, 368–373.
- Vitousek, P.M., Mooney, H.A., Lubchenko, J., Melillo, J.M., 1997. Human domination of earth's ecosystems. *Science* 277, 494–499.
- Wright, D.H., 1983. Species-energy theory an extension of species-area theory. *Oikos* 41, 495–506.
- Wright, D.H., 1987. Estimating human effects on global extinction. *Int. J. Biometeorol.* 31, 293–299.
- Wright, D.H., 1990. Human impacts on the energy flow through natural ecosystems, and implications for species endangerment. *Ambio* 19, 189–194.
- Zechmeister, H.G., Moser, D., 2001. The influence of agricultural land-use intensity on bryophyte species richness. *Biodiversity Conserv.* 10, 1609–1625.