**CHARLES UNIVERSITY IN PRAGUE**

Faculty of Science

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# HUMAN IMPACTS ON ECOSYSTEMS: APPROPRIATION OF PRIMARY PRODUCTION AND BIODIVERSITY IN THE CZECH REPUBLIC

Doctoral Thesis

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2010

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Hereby I declare that I have not been awarded other degree or diploma for the thesis or its substantial part. I certify that I have written doctoral thesis by myself, only using references and data presented in the thesis.

30 May 2010, Prague

# Abstract

The aim of this thesis is to explore relationship between selected indicators of human pressures and biological diversity in the Czech Republic. I assessed human impacts on ecosystems by calculating the fraction of aboveground net primary production appropriated by humans (aHANPP) in a cultural landscape of the Czech Republic. The human appropriation of aboveground net primary production reached 21.5 Tg C in aggregate or 56% of the potential natural productivity in 2006. I found the aHANPP to be a suitable indicator of human impacts on ecosystems as it detect trends and enables spatial mapping of human impacts. Furthermore, I tested hypothesis about a positive spatial relationship between human pressure indicators and biodiversity at species and ecosystem/landscape levels. I found a positive spatial coincidence ($r_s$=0.361) of people (measured by human population density and extent of urban areas) and species richness (measured by richness of 10 taxonomic groups of vertebrates, invertebrates and plants). Although aHANPP was not related to species richness, diversity at the landscape level (measured by Shannon landscape diversity index) was significantly negatively related to the intensity of land and ecosystem use (indicated by aHANPP). The hump-shaped relationship is reflecting an intermediate disturbance hypothesis. Presented analysis contributes to the discussion about the relationship between human activity and biodiversity in human dominated regions.

# Keywords

Human appropriation of net primary production; Biodiversity; Land cover change; Ecosystem use; Biophysical indicators; Human pressures; Czech Republic

# Acknowledgments

It is a pleasure to thank those who made this thesis possible. First and foremost, it is an honor for me to thank to a supervisor of my doctoral thesis, Prof. Bedřich Moldan, whose advice, support and guidance were indispensable for completing a thesis. I am also grateful to Dr. Jan Plesník (AOPK ČR), who provided valuable advice and support especially during initial phases of my doctoral thesis preparation.

I thank to colleagues who provided guidance and advice on various topics addressed in a thesis. I thank especially to Prof. Helmut Haberl (IFF, Vienna) for advice on HANPP indicator and to Dr. Ben ten Brink (PBL, Netherlands) for cooperation on biodiversity indicators in the framework of the Convention on Biological Diversity. My thanks also go to Dr. Jonathan Baillie (ZSL, London), Dr. Jonathan Loh (WWF) and Dr. Belinda Reyers (CSIR South Africa).

It is my pleasure to thank to Dr. Karel Chobot (AOPK ČR) for cooperation on research on biodiversity data and monitoring. Special acknowledgment goes also to many other colleagues who gather data on biodiversity in the Czech Republic and make them available. I also thank to Mrs. Erika Orlitová and Mr. Ondřej Nálevka (GISAT) for valuable insights and help with GIS analysis. I would like to thank to colleagues at the Charles University Environment Center, namely to Dr. Tomáš Hák, Dr. Jan Kovanda and Mr. Miroslav Havránek, for cooperation on projects, useful experiences exchanges and discussions.

Last but not least, I am indebted to my family, especially my wife Lenka and all daughters for their support, patience and encouragement during this work.

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# List of abbreviations

| | |
|---|---|
| AGRI | Agricultural areas |
| aHANPP | Human Appropriation of Aboveground Net Primary Production |
| AMPHI | Amphibians |
| BARE | Open spaces with spare vegetation or bare land |
| BEF | Biomass Expansion Factor |
| BII | Biodiversity Intactness Index |
| BUTTER | Butterflies |
| CARAB | Carabids or ground beetles (Carabidae) |
| CERAMB | Longhorn beetles or Cerambycidae |
| CLC | Corine Land Cover |
| CSR | Combined Species Richness |
| DGVM | Dynamic Global Vegetation Models |
| DMI | Dry Matter Intake |
| $D_W$ | Wood Specific Density |
| EF | Ecological Footprint |
| EKC | Environmental Kuznets Curve |
| ELATERID | Click beetles or Elateridae |
| GIS | Geographical Information Systems |
| GNP | Gross National Product |
| GRASS | Natural grassland and heathland |
| GSV | Growing Stock Volume |
| HANPP | Human Appropriation of Net Primary Production |
| HF | Human Footprint |
| HI | Harvest Index, Harvest Factor |
| HPD | Human Population Density |
| IBI | Index of Biotic Integrity |
| IBP | International Biological Programme |
| IDH | Intermediate Disturbance Hypothesis |
| INVERTEB | Invertebrate combined species richness |
| KFME | Mapping grid - Kartierung der Flora MittelEuropas |
| LPI | Living Planet Index |
| LUCC | Land Use and Land Cover Change |

| | |
|---|---|
| MA | Millennium Ecosystem Assessment |
| MAMM | Mammals |
| MMU | Minimum Mapping Unit |
| MSA | Mean Species Abundance |
| MTI | Marine Trophic Index |
| NBP | Net Biome Production |
| NCI | Natural Capital Index |
| NDVI | Normalized Difference Vegetation Index |
| NEP | Net Ecosystem Production |
| NPP | Net Primary Production |
| $NPP_0$ | Potential Natural Net Primary Productivity |
| $NPP_{ACT}$ | Actual Net Primary Productivity |
| $NPP_H$ | Harvested Equivalent of Net Primary Productivity |
| $NPP_T$ | Net Primary Productivity remaining in ecosystems after harvest |
| ORNL DAAC | Oak Ridge National Laboratory Distributed Active Archive Center |
| PAArea | Areal extent of specially protected areas |
| PAST | Pastures |
| REPT | Reptiles |
| RLI | Red List Index |
| SAR | Species-Area Relationship |
| SER | Species-Energy Relationship |
| SHLDI | Shannon Landscape Diversity Index |
| SR | Substitution Rate |
| SRIndex | Weighted Species Richness Index |
| URBAN | Urbanized areas |
| VERTEB | Vertebrate combined species richness |
| WATER | Water bodies and water courses |
| WET | Wetlands |
| $\Delta aNPP_{LC}$ | Net Primary Productivity lost by human induced land conversion |

# 1. Introduction and aims

Biodiversity and ecosystems are considered to be an irreplaceable component of sustainable development discussion and natural capital accounting as well (Sachs et al., 2005; UNEP, 2007). Despite the rising technological and economical improvements, humans have not escaped the dependence on the natural environment. The complexity of ecosystems and nature-society interactions evokes the need for relatively simple measures accounting for the extent of human alteration of the natural environment. Until recently, ecosystem changes had been only partially accounted as a component of national wealth or had not been accounted at all. However, as recognized by the Millennium Ecosystem Assessment (MA, 2005), ecosystem services and biodiversity closely associate with many aspects of human well-being. Therefore, quantitative indicators and accounting of human interactions with ecosystems and biodiversity are required which would contribute to measuring impacts of human impacts on nature.

Humans deliberately change the characteristics of natural ecosystems to harness food, fibre and energy (Vitousek et al., 1997). While some changes benefit human society, others have undesirable consequences and undermine the capacity of ecosystems to provide life-support services (MA, 2005). Changes in land cover and land ad ecosystem use are known to be responsible for the alteration of biogeochemical cycles, regional climate and biodiversity (Foley et al., 2005). The net primary production (NPP) has been recognized for a long time as an important indicator of the structure of food webs and nutrient cycling in ecosystems (McNaughton et al., 1989; Odum, 1969). Recently, indicators estimating the extent of human domination of ecosystems in terms of net primary production have been developed (Haberl et al., 2007; Imhoff et al., 2004). The recurring question of scientific as well as policy concern is whether and to what extent human activity has affected natural systems and biodiversity (Foley et al., 2005; MA, 2005; Sala et al., 2000).

The general question framing this analysis was focused on indicators of human dominance and the relationship between human activity and biodiversity in a cultural landscape of the Czech Republic. As a leading indicator of the intensity of land and ecosystem use, the concept of Human Appropriation of Net Primary Production (HANPP) was further developed and calculated for the area of the Czech Republic. Indicators of HANPP and Human Population Density (HPD) were consecutively used for the testing of hypothesis about human impacts on biodiversity. Biodiversity was approached at the species level as the species richness of 10 groups of vertebrates, plants and invertebrates, and at the landscape level as landscape diversity (i.e. diversity of land cover and land use). We hypothesized that human activity and density is not related to aspects of biodiversity at species and habitat/ecosystem/landscape level.

The HANPP indicators is based on carbon accounting and I used and further developed the HANPP concept for the analysis of human dominance in a cultural landscape and explored HANPP links to biodiversity at species and landscape levels. I calculated the aboveground human appropriation of net primary production (aHANPP) for the area of the Czech Republic as an indicator of human dominance. We were interested to account for the interactions between human activity manifested by the observed biophysical land cover and ecosystem use manifested by harvest, and the potential natural vegetation which would prevail without human activity. Therefore, I applied and adjusted the HANPP methodology using Corine Land Cover and ecological data to analyze to what extent human activity dominates ecosystems. The aHANPP indicator shows which concrete economic activities manifested by concrete land cover and ecosystem use change the net primary production outcome of a particular area.

Another aim of this work was to contribute to the understanding of the relationship between human population density, land and ecosystem use and biodiversity in a cultural landscape. Chapter 2.1 reviews existing approaches to indications of human impacts on biodiversity. As evident from the review of human pressures on biodiversity (Chapter 2.2), existing biodiversity indices reflect human pressures only partially. Therefore, we develop HANPP indicator as a composite indicator for the comprehension of patterns of human dominance of ecosystems (Chapter 3.1). HANPP approach is complemented by Human Population Density to test hypothesis about patterns of human impacts on biodiversity (Chapter 3.2). Selected indicators of biodiversity at species richness and landscape diversity levels are tested as response variables to human activity indicators. Chapter 4 summarizes the main results of our analysis and Chapter 5 discusses important aspects of our results. The work aims to contribute to current debate about the human impacts on biodiversity, especially in the context of changing cultural landscape, where diverse array of ecosystem services is required and biodiversity conservation is balanced against other land and ecosystem uses.

# 2. Human impacts on ecosystems and biodiversity - a general framework

There is a general recognition that humans are degrading the Earth´s ecosystems and leading biodiversity to extinction (Balmford et al., 2003, 2005a; Pimm et al., 2001; Vitousek et al., 1997). Biodiversity has been recognized as one of the factors supporting the ecosystem resilience (Loreau et al., 2001; Naeem and Li, 1997; Tilman et al., 2006) and provision of ecosystem services (Balvanera et al., 2006) as well as contributing to the performance of economic systems and human well-being in general (Balmford & Bond, 2005; Costanza et al., 1997; MA, 2005). Therefore, we could ask whether there are unbiased indicators available which would translate biodiversity loss and degradation into policy responses (Reid et al. 1993). These indicators can be regarded as societal mechanisms, which indicate the risks and limits of the exploitation of biodiversity and ecosystem services. As many ecosystems could reach a threshold beyond which they behave in different modes of functioning (Scheffer et al., 2001), society should protect itself against biodiversity perturbations affecting ecosystem services flows. While a suite of indicators has been proposed and developed (Balmford et al., 2005a; Biggs et al., 2007; ten Brink et al., 2007; Brooks & Kennedy, 2004; CBD, 2003a; EEA, 2007; Mace & Baillie, 2007; Reid et al., 1993; Walpole et al., 2009), their contribution to the assessment of human impacts on nature is still widely discussed (Royal Society, 2003; Spangenberg, 2007; Vackar et al., 2010a).

Biodiversity is a multidimensional and hierarchical concept (Allen & Hoekstra 1992; CBD, 2003a) and no existing indicator covers the complexity of living world (Biggs et al., 2007; Noss, 1990). Biodiversity could be defined as the complexity of living systems at all organisation levels (Figure 1). Many definitions are valid within the context of their specific use, and no simple definition can cover all aspects: natural versus human-altered diversity; evenness versus richness; the various spatial ($\alpha$, $\beta$ and $\gamma$ biodiversity) and temporal dimensions (phylogenetic biodiversity); and the biological incompatibilities of increasing diversity at all organisation levels simultaneously. The aspects of biodiversity can be defined at the supra-organism scale (the ecosystem), organism scale (species richness and abundance) and the sub-organism scale (the gene) (Allen &Hoekstra, 1992). Biodiversity also covers landscape diversity as a representation of habitat types and ecosystems within a landscape. A landscape that is a mixture of forest, grassland and cropland is compositionally, structurally and functionally more diverse than one which is forest only.

The difficulties in establishing operational indicators of biodiversity stem from three main sources: firstly, inadequacy of much of the data; secondly, the loss of information that occurs when a complex and multi-dimensioned concept is reduced to a one dimensional indicator; and finally, our rudimentary understanding of the causal links between human activities and biodiversity change (Biggs et al., 2007). Despite these obstacles, several biodiversity indicators approaches have been promoted. These approaches are based on the integration and aggregation of large-scale information representing probable trends in biodiversity. However, many of these basic approaches are based on pressures on biodiversity rather than biodiversity information itself.

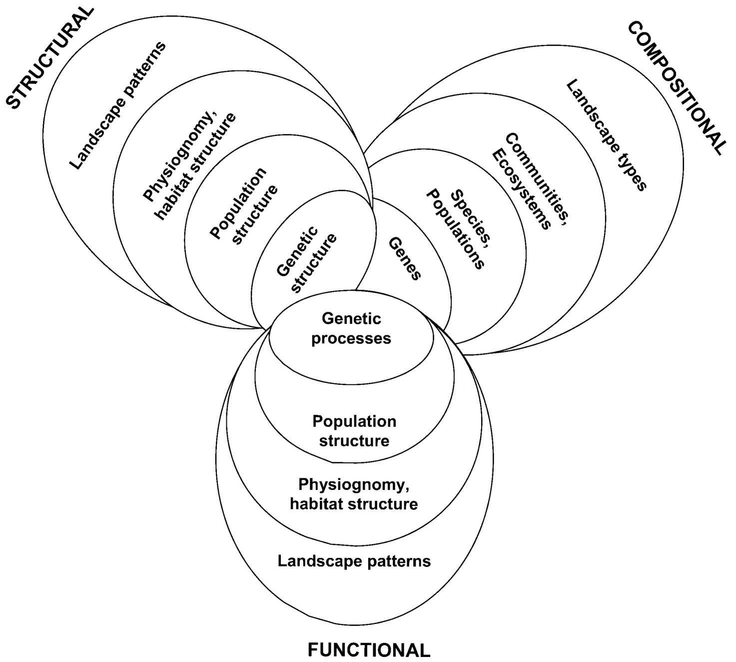

**Figure 1. Biodiversity covers complexity of different aspects of life at different organizational levels. Biodiversity thus includes not only genetic and species diversity but also ecosystems and landscape diversity. However, the development of biodiversity indicators is limited by data availability and insufficiency of evidence about causal (functional) relationship between human activities and biodiversity change. Scheme: Noss 1990.**

## 2.1. Biodiversity indicators frameworks

In this part, leading biodiversity indices and approaches used for the assessments of human impacts on biodiversity are reviewed and compared. Indices analyzed include species and populations based indicators, such as Living Planet Index (LPI) and Red List Index (RLI), as well as land use and ecosystem based indicators like Mean Species Abundance (MSA) and Biodiversity Intactness Index (BII). Measures of biological integrity such as Marine Trophic Index (MTI) and Index of Biotic Integrity (IBI) are also included in a review. Biodiversity indices should show the extent to which humans activities are coupled with the state of nature. However, existing indices are reflecting human interactions with nature only in a limited way, especially through the land use impacts on species abundance.

Basic components of existing biodiversity indices (i.e. biodiversity indicators that show relative trends, but without units) are reviewed and compared. The main interest is in indicators expressing broader biodiversity status and trends in the context of human pressures and impacts. We are interested to see whether there could be evidence for “decoupling” of human activity from biodiversity deterioration at the global level.

### 2.1.1. Living Planet Index

The Living Planet Index (LPI) was developed as an indicator of the changing state of the world’s biodiversity (Loh et al., 2005). The conceptual model of the indicator is based on tracking the abundance (measured as population count, index, density measure or measure per unit effort) of wild populations. If populations are declining, we are losing natural capital and conservation measures should be accepted in response. The LPI indicates trends in wild nature using populations of vertebrate species, for which time-series data are widely available.

Data are extracted from published sources, online databases and also from grey literature.

The LPI aggregates trends in over 7,100 populations of about 2,300 vertebrate species from different world regions into a single index (J. Loh, *personal communication*). Numbers of populations/species included in the index have been steadily rising since its introduction in 1998. The LPI is calculated as the geometrical average of separate indices that measure trends in populations of tropical and temperate terrestrial, freshwater and marine species. The LPI can be disaggregated for different biomes or ecosystems. Index values are generated by a chain method and a generalized additive modelling (see Collen et al. 2008 for detailed methodology). Although vertebrates represent only a fraction of all known species, it is assumed that their population trends are typical of global biodiversity as a whole. Between 1970 and 2006 (the most recent year for which satisfactory data are available) the LPI showed a 30% decrease.

The LPI represents an indicator from a family of indices measuring trend in selected species. These indices are usually denoted as Species Trend Indices (STI) and can include a broad range of species and populations. The most commonly used species trend indices, especially in Europe, are common bird indicators (Gregory et al., 2005). The population index of common farmland birds has been included as a headline indicator for biodiversity and natural resources in the European Union (EEA, 2007). Common bird indicators are supported by a well-developed monitoring scheme (Pan-European Common Bird Monitoring). However, species trend indices can be sensitive to the shifting baseline syndrome (see section 3.2.5).

### 2.1.2. Red List Index

The Red List Index (RLI) is an indicator measuring changes in extinction risk (Butchart et al. 2004, 2007), i.e. whether the aggregate conservation status of species is improving or deteriorating. The conceptual model is based on a species risk of extinction, which is categorized using a set of standardized and quantitative criteria based on range size, structure and trend, and population size, structure and trend (IUCN 2001) The IUCN Red List of Threatened Species is regarded as the most authoritative and objective system for classifying species by their risk of extinction (Rodrigues et al., 2006).

The Red List Index uses changes in the categories assigned to species in IUCN Red List assessments to track changes in the status of species. The RLI was initially designed and tested using data on all bird species and has been applied to amphibians, mammals, and corals. Other RLI applications are under preparation. The RLI can be disaggregated to show trends for species in different biogeographic realms, political units, ecosystems, taxonomic groups and for species relevant to different international agreements and treaties (Butchart et al., 2007). Currently, a Sampled Red List Index (SRLI) is being developed as a comprehensive approach to monitoring changing status of biodiversity worldwide (Baillie et al., 2008). The RLI has been endorsed by the Convention on Biological Diversity to assess the progress toward the 2010 target in the focal area of the status and trends in the components of biological diversity – change in the status of threatened species, and under the UN Millennium Development Goals to measure progress against the indicator "Proportion of species threatened with extinction".

A potential criticism of the RLI approach is that it may reflect changes in human knowledge of species status instead of actual change in extinction risk. Quayle and Ramsay (2005) suggested that the majority of changes in Red Lists for terrestrial vertebrates in British Columbia is attributable to changes in the knowledge available for the assessment of conservation status, refinements to assessment procedures, or reorganization of taxonomy rather than to genuine changes in status of species. However, the RLI excludes recategorisations owing to improved knowledge or taxonomy and includes only genuine improvements or deteriorations in the status of species (Butchart et al., 2006). Its principal weakness is that is has relatively coarse temporal resolution which is caused by the broad nature of the Red List categories. However, its principle advantage is that is globally representative in its coverage, rather than being biased to better known species or parts of the world.

### 2.1.3. Marine Trophic Index

Marine Trophic Index (MTI) was developed to measure the complex interactions between the fisheries and marine ecosystems. The conceptual model is based on the theory of "fishing down marine food webs" (Pauly et al., 1998). The mean trophic level characterizes the food web structure based on the trophic models of the ecosystem functioning. An organism's trophic level expresses its position in a food web relative to the primary producers. The Marine Trophic Index is based on the database of fish landings assembled by the UN Food and Agricultural Organisation (FAO). The database contains annual fish catches since 1950 for more than 200 species. The main assumption of MTI is that the fisheries landings correlate with the abundance of a species in ecosystems.

The resulting values of the MTI are interpreted as changes in the abundance of higher trophic fishes relative to lower trophic level fishes (Pauly & Watson, 2005). If the MTI is declining, then this trend indicates deterioration of fisheries. Marine Trophic Index is listed in the Convention on Biological Diversity 2010 target indicators, representing the focal area of the ecosystem integrity and ecosystem goods and services. MTI was listed as a sub-indicator of the 2008 Environmental Performance Index (EPI) in the objective Ecosystem Vitality, policy category Productive Natural Resources. MTI is also a component of the Commission on Sustainable Development (CSD) set of indicators for the area Oceans, seas and coasts/Marine environment.

One of the critiques of MTI is concerned with fact that changes in the mean trophic level in landings does not reflect changes in the underlying ecosystem, with the use of annual quantities of landings (excluding discarded catch) as abundance indicators (Caddy et al., 1998). However, the MTI is intended to be used as an indication of human impacts on ecosystems, i.e. fishing impact on harvest of economically important species. Moreover, catches usually reflect the relative abundance of species in a given ecosystem (Pauly & Watson, 2005).

### 2.1.4. Natural Capital Index and Mean Species Abundance

The Natural Capital Index (NCI) and the Mean Species Abundance (MSA) are coupled indicators introduced as measures of human impacts on biodiversity. The NCI is a flexible indicator framework for the assessment of biodiversity changes. This framework has two basic components: ecosystem quantity and ecosystem quality (ten Brink, 2000). The NCI has been defined as a product of these two aspects of the natural environment. The conceptual model is based on the notion that biodiversity loss is characterised as the decrease in abundance of many original species and the increase in abundance of a few other -often opportunistic- species as a result of human interventions. During this degradation process, species richness often increases initially as new species gradually replace the original ones. NCI intends to express this process by measuring the mean abundance of the original species, compared to the natural or low-impacted state. A pragmatical and flexible way to calculate NCI is first to calculate the remaining extent of an ecosystem due to cultivation (as % of the reference year; 'ecosystem quantity') and then to calculate the quality of this remaining ecosystem. The quality (%) is calculated as the mean of the current abundance/baseline abundance of a representative set of species. NCI is calculated as the product of these two factors (quantity x quality) with the dimension mean species abundance compared to the baseline year. Next, and separately from the NCI of natural areas, an NCI of agricultural (or urban) areas can be calculated, using extensive or traditional agriculture as a cultural baseline.

The issue of baselines is especially important for NCI. Conventionally, low-impacted or pre-industrial state has been selected as the baseline state for the NCI. Because NCI is a data demanding indicator (especially on current and baseline species abundance) a GLOBIO model (ten Brink et al., 2007; Alkemade et al.,

2009) has been developed  applying Mean Species Abundance (MSA) as indicator. The MSA uses data on the relationships between pressures and species trends, based on extensive literature reviews, to estimate mean abundance of original species relative to their abundance in undisturbed ecosystems (Alkemade et al., 2009). The pressures on biodiversity considered are agricultural intensity, forestry intensity, built-up land, climate change, atmospheric N-deposition, fragmentation and infrastructure development. At this stage, no specific MSA with a traditional agricultural baseline has been developed, as it has for the NCI.

Availability of data on changes in population abundance has been identified as one of the limiting factors in developing NCI. De Heer et al. (2005) attempted to mobilize data on trends on notably mammals, birds, butterflies, reptiles, fishes and vascular plants in Europe. Especially for butterflies authors mobilized dataset comparable with breeding birds. The current list of European biodiversity indicators (EEA, 2007) reflects data availability on butterflies by proposing an indicator on abundance and distribution changes. However, for a majority of the European countries, collecting and reconstructing distribution or abundance data on selected groups in current and baseline state require a major effort and cost.

### 2.1.5. Biodiversity Intactness Index

Biodiversity Intactness Index (BII) was proposed as an aggregate index providing synthetic information on biodiversity in a given area (Scholes & Biggs, 2005). The conceptual model behind the BII is equivalent to the NCI. However, BII is based on both species richness estimates as well as population abundance estimates. The BII estimates the average richness and area-weighted impact of a set of activities on the populations of a given group of organisms in a specific area.

The BII for Southern Africa made a total of 4,650 estimates of biodiversity impacts, comprising five broad taxonomic groups, six ecosystem types, an average of six land use activities and eight functional types (for full description of methodology see Scholes & Biggs, 2005). As species populations trend data are not always readily available, the BII uses expert judgment about population impacts from land use in different ecosystems. Scholes & Biggs (2005) estimated that BII has been reduced to 84% in comparison with the intact state in Southern Africa.

Although BII is multiscale (i.e. scalable to different levels of resolution), Rouget et al. (2006) recalculated BII for selected regions with detailed land cover data and found that coarse scale estimates could underestimate BII scores especially due to land degradation. Faith et al. (2008) criticized BII for focusing on abundance rather than variation from which biodiversity arises. Indeed, the majority of biodiversity indices are concerned with quantitative changes, that is changes in abundance, rather than variation in genetic, functional or ecological traits. Hui et al. (2008) developed a Biodiversity Intactness Variance (BIV) to estimate uncertainty associated with the population impacts estimates, which is the primary source of uncertainty and decisive term for calculating BII. The principal disadvantage of the BII is that it may be insensitive to slow and diffuse impacts on biodiversity, for instance the long term effects of habitat fragmentation, climate change or pollution.

### 2.1.6. Index of biotic integrity

Index of biotic integrity (IBI) was proposed to evaluate human impacts on ecosystems and resulting changes of ecological integrity, ecosystem health or ecological condition in aggregate index (Angermeier & Karr, 1994). The rationale behind the IBI is that ecosystems can be ranked according to the level of multifaceted human impacts. IBI aggregates and combines several ecosystem characteristics and compares them with a reference state. IBI usually includes indicators like species richness and composition, number and abundance of bioindicator species, trophic organization and function, reproductive behaviour, or condition of individual organisms (Jackson et al., 2000). The IBI has been denoted as a multimetric or composite index as it compounds different characteristics to a common scale.

The IBI has been developed in the context of environmental assessments of freshwater and estuarine ecosystems. Therefore, fish and benthos assemblages have been predominantly used to calculate biotic integrity indices (Pinto et al., 2009; Pont et al., 2006). It was proposed to extend the IBI concept to terrestrial systems (Andreasen et al., 2001) and has been applied in different terrestrial settings (grasslands, shrubs, forests) using a variety of species assemblages (Coppedge et al., 2006; Browder et al., 2002; Diffendorfer et al., 2007; Haeussler et al., 2007; Kimberling et al., 2001; Taft et al., 2006).

The concept of biotic integrity is closely linked to the concept of ecosystem health and biological monitoring and indicators. The use of bioindicators have long tradition in ecology and environmental science (Niemi & McDonald, 2004), but specific bioindicators are usually scale and taxon dependent (Boháč, 1999; Duelli & Obrist, 2003). Bioindicators have been used to detect responses to specific anthropogenic or natural stressors. Traditional diversity indices are not sensitive to complex changes in ecological communities following disturbance. Biotic indices faced criticism because they were relevant for small geographic areas. Suter (1993) criticized that indexes of heterogeneous variables of ecosystem health are meaningful and not applicable to most regulatory problems. Despite the relatively large data intensity of IBI approaches, results of integrity assessments have been already reported at landscape or regional levels (Brooks et al. 1998; McCormick et al. 2001; O'Connell et al. 2000; Pont et al. 2006). An advantage of the IBI is that it is able to take into account more qualitative characteristics of ecological assemblages exposed to human pressures, such as trophic structure, functional traits or disease.

## 2.2. Human pressures and impacts on biodiversity: theory and evidence

Previous section reviewed basic approaches to measuring biodiversity state and trends. Several of these approaches try to reflect increasing human dominance. Generally, these indicators doesn´t address the complexity of human-nature relationship. As evident from the comparison of existing biodiversity indices (Chapter 1.1.), there are clear trade-offs between the spatial and temporal coverage and the detail of information. Therefore, this part reviews an evidence of the relationship between the human activity and biodiversity. Biodiversity is treated especially at the species and landscape levels. Biodiversity can be defined not only as a variability of living world at different levels (species, landscape) but also as a abundance and distribution of species and condition and productivity of ecosystems (CBD, 2003b). Biodiversity loss therefore reaches beyond species extinction in this context.

The patterns of human impacts on biodiversity has been frequently discussed in the literature (Evans & Gaston, 2005; Haberl et al., 2005; Holdren & Ehrlich, 1974; Liu et al., 2003; Luck et al., 2004; McKinney, 2002; Vitousek et al., 1997; Wright, 1987). Numerous driving forces and pressures resulting from human activities have been considered in explaining the patterns of biodiversity (Spangenberg, 2007). The original equation established anthropogenic environmental impacts as a function of population, affluence of consumption and technological efficiency (Holdren & Ehrlich, 1974). These indirect drivers are manifested by energy consumption, material flows, land use change or ecosystem use. Direct anthropogenic pressures such as habitat loss and degradation, unsustainable exploitation, introduction of exotic species, climate change, UV-B radiation or N-deposition has been listed as causes of biodiversity loss (Spangenberg, 2007). However, there is no universal theory or model linking human pressures and biodiversity change.

The conceptual model of society and biodiversity interactions is based on extended pressure-state-response (PSR) framework (OECD, 2005), which represents a traditional model of biophysical and intangible exchanges between people (socio-economic system) and biodiversity (natural system) (Fig. 2). Biodiversity contributes significantly to the human economy as well as to human well-being. On the other hand, economic activity contributes to biodiversity deterioration, which is not fully taken into account in economic policy (Blaikie & Jeanrenaud, 1996; Spangenberg, 2007). Therefore, one of the aims of biodiversity indices is to detect interlinkages between human activities and biodiversity trends. This approach is in accord with the concept of sustainable development, which aims to balance the well-being of current and future generations with the health of nature (biodiversity and ecosystem services).

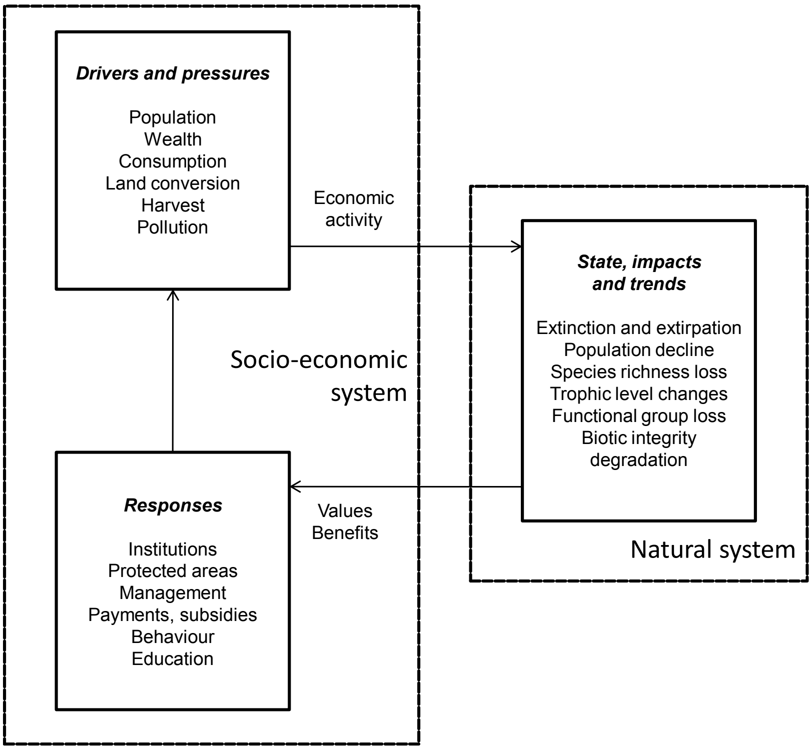

**Figure 2. Conceptual model of interactions between biodiversity and human society. Vackar et al., 2010.**

### 2.2.1. Biodiversity and sustainability

The concept of critical natural capital recognized that some of components of nature are not readily substitutable or replaceable (De Groot et al., 2003). Biodiversity provides many life-supporting services, including provisioning services (food and medicine), regulating services (control of production and rezilience of ecosystems), cultural services (aesthetic or recreational values) and supporting services (structural, compositional and functional diversity embodying evolutionary information) (Duraiappah & Naeem, 2005). However, the life-supporting functions of natural ecosystems escape the formal valuation and decision systems of human society as they are located outside of market operations or institutional arrangements (Nunes & van den Bergh, 2001). The result has been continuing depletion of biodiversity, which requires “defensive” responses such as protected areas designation or sustainable use incentive measures (UNEP-WCMC, 2008). Development of biodiversity indices has been driven in part by the need to “correct” existing societal decision making frameworks and accounts.

The relationship between human activity and biodiversity is far from being fully explained and described. Many pressures have been suggested as being responsible for biodiversity loss (Spangenberg, 2007). The size and growth of the human population are often cited as one of the key driving forces of biodiversity loss (Maurer, 1996), yet their contribution to the decline and extinction of other species has remained unclear.

One of the recurrent questions is to what extent biodiversity loss is induced by human activities and economic activity. Kerr & Currie (1995) tried to quantify effects of socioeconomic activity on species loss. They included gross national product (GNP), human population, birth rates, cropland area and $CO_2$ emissions as key driving forces, with protected areas included as a key response to biodiversity loss. They found that the number of threatened bird and mammalian species is related to several socioeconomic variables across countries analyzed. This analysis has been replicated in other recent studies (Asafu-Adjaye, 2003; Dietz & Adger, 2003; McKinney et al. 2009; Naidoo &

Adamowicz, 2001), especially in the light of Environmental Kuznets Curve (EKC) hypothesis.

The EKC is based on an empirical theory that increasing prosperity beyond a certain point doesn´t further promotes environmental degradation, i.e. environmental degradation is stopped or even reversed after reaching some optimal level of prosperity (Stern et al., 1996). Althoughan inverted-U shaped relationship was found between threatened birds and GNP (Naidoo & Adamowicz, 2001), generally the number of threatened species increases with increasing human population (Kerr & Currie, 1995; McKinney et al. 2009), per capita income or GNP (Asafu-Adjaye, 2003; Naidoo & Adamowicz, 2001), or proportion of urban population (McKinney et al., 2009) in cross-country analyses. However, on the response side, there is an indication that protected areas and international treaties could reverse biodiversity loss (Kerr & Currie, 1995; McKinney et al., 2009).

Despite the importance of the issue, biodiversity has been neglected in the mainstream of environmental accounting. Recently, biodiversity accounting has been considered in Land and Ecosystem Accounting (Weber, 2007) where integrated ecosystem accounts connect land, biodiversity and water information. Progress with biodiversity indicators has been spurred under the Convention on Biological Diversity framework (CBD, 2003a, 2003b) to achieve a significant reduction in biodiversity loss (Balmford et al., 2005a; Mace & Baillie, 2007). A suite of biodiversity indicators (see Chapter 2.1) was proposed and developed in several focal areas, including status and trend of biodiversity, sustainable use, ecosystem integrity, traditional knowledge and benefits. Existing biodiversity indices have made a considerable contribution to mapping the real state of nature. The main use of biodiversity indices can be seen in the socioeconomic and policy analysis where they have an irreplaceable role in complementing other leading indicators.

At the global level, we are interested in whether biodiversity degradation is coupled to the growth of human activities. To inspect trends in biodiversity indices in comparison with economic activity, we plotted selected biodiversity indices against selected indicators of socio-economic systems (Figure 3). A decoupling of environmental pressures should show a reduction in the rate of biodiversity loss with increasing development. A visual comparison of indicators suggests that biodiversity trends are not decoupled from socio-economic pressure. While human population numbers, economic output and ecological footprint are steadily increasing, indices measuring biodiversity trends are declining. Only the disaggregated LPI for Nearctic and Palearctic realms shows neutral and positive trend, respectively. These trends may reflect partial recovery of temperate biodiversity and a stabilization of trends after 1970 due to conservation measures (Humphrey et al., 2008). At the same time, the footprint of consumption in these regions has increased in the tropics.

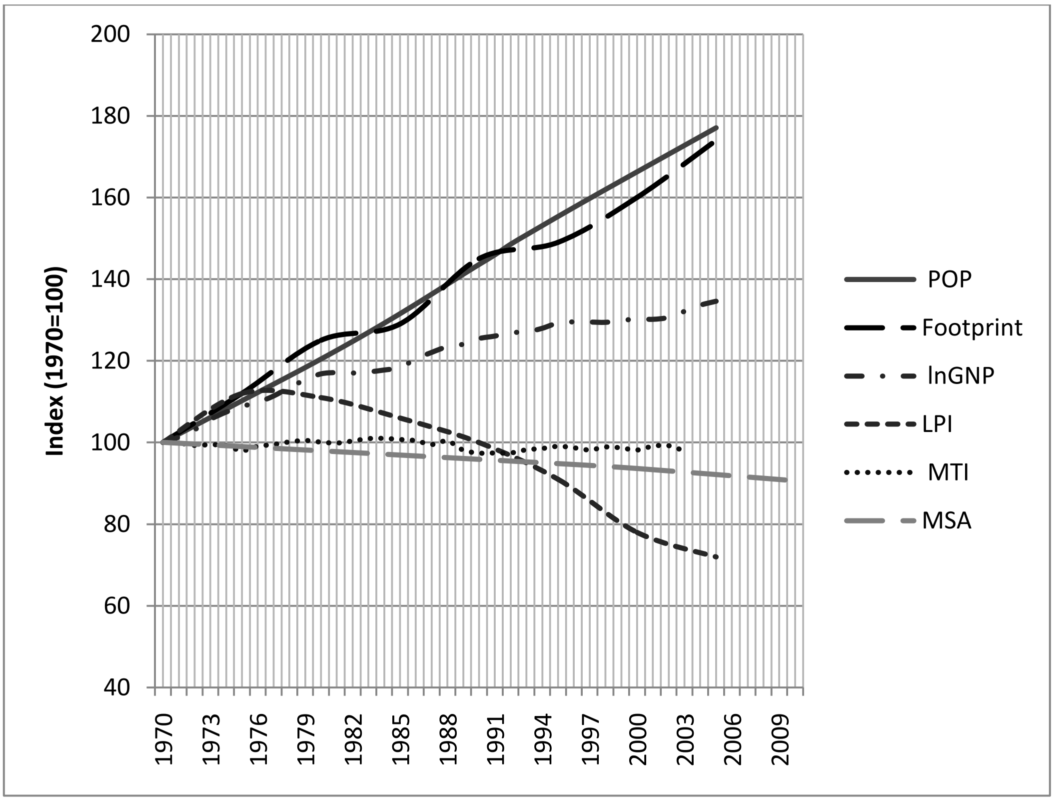

**Figure 3. Trends in selected indicators of human activity (population, GNP, Footprint) and response in biodiversity and ecosystem indicators (Living Planet Index, Marine Trophic Index, Mean Species Abundance). Vackar et al., 2010.**

### 2.2.2. Biodiversity and human population density

The size and growth of the human population are often cited as key driving forces behind the Earth's biodiversity loss (Maurer, 1996), yet the extent of their contribution to the endangerment and extinction of other species has remained unclear. The most biodiverse regions of each continent are also considered to be the most threatened by high human population densities and consumption (Liu et al., 2003), but this relationship is not straightforward. Globalization means that people may consume products and resources from all over the world, and so the impacts of their consumption do not necessarily occur in the places where the consumers live. Similarly, climatic changes are occurring most rapidly in the polar regions, where human population density is lowest.

Human settlements increasingly interact with biodiversity. A positive spatial relationship between the human population density and species biological diversity has been detected at different regions and spatial scales (Luck, 2007). Many studies suggest that human population density may be a useful surrogate measure of the impact on biodiversity of a range of activities associated with human settlements. Human density correlates with removal of natural habitat, damage to the environment, and extinction of species (Harcourt et al., 2001). The number of people in a given area is frequently considered as a primary cause of declines in species and ecosystems, with higher human densities leading to higher levels of influence on nature.

Human population density has been found positively correlating with species richness in sub-Saharan Africa (Balmford et al., 2001) and in Australia and North America (Luck et al., 2004). The correlation of biodiversity with human population density was confirmed also for majority of taxa on the European continent, although the correlation of breeding bird richness with population density was weak (Araújo, 2003). These coincidence patterns can be interpreted either as the threat of human population density to biodiversity or as the effect of increasing diversity with higher population densities, for example as a result of the introduction of novel species. The relationship between biodiversity and human density has been studied also at the regional and landscape scale. Spatial congruence of species richness and human population was found in South Africa (Hugo & van Rensburg, 2008) or Canada (White & Kerr, 2007).

Luck et al. (2004) tried to characterize the level of spatial overlap between densely populated and biodiverse areas and to evaluate options for alleviating potential conflict. They found that human population density strongly positively correlate with species richness and thus the most biodiverse regions are also the most threatened by human impacts. Liu et al. (2003) report significant growth of household numbers, manifested as urban sprawl, in six representative biodiversity hotspots. Sanderson et al. (2002) used in their approach of Human Footprint (HF) population density as one of the basic parameters. The maximum values of HF are logically found in areas with high settlement density, especially in big cities, while minimum scores were attained in large tracts of primeval forests, deserts and tundra. They also found that majority of the land (60 %) lies along the continuum between these two extremes, in areas of moderate but variable human influence.

### 2.2.3. Biodiversity, land cover change and ecosystem use

Land cover and land use change (LUCC) are considered to be a major factor contributing to biodiversity loss (Sala et al., 2000; Foley et al., 2005). Land cover can be defined as the observed biophysical cover on the earth´s surface. Land use is then characterized by the arrangements, activities and inputs people undertake in a certain land cover type to produce, change or maintain it. Definition of land use in this way establishes a direct link between land cover and the actions of people in their environment (Di Gregorio & Jansen, 2000). Land use change transforms the amount of materials and energy available in ecosystems and human activities further regulate the dynamics of ecological processes in ecosystems (Foley et al. 2005). Land use activities convert natural ecosystems to human managed systems and change management practices on managed land. We prefer the term “ecosystem use” to describe complex changes in ecosystem structure and function as a result of human induced land cover and land use change. Land cover change and ecosystem use are coupled aspects of human activities. This has been recently reflected by the development of Land and Ecosystem Accounting within the European Environment Agency (Weber, 2007).

As noted by the Millennium Ecosystem Assessment (MA, 2005), over the past 50 years, humans have changed ecosystems more rapidly and extensively than in any comparable period of time in human history, largely to meet rapidly growing demands for natural resources and related ecosystem services. This has resulted in a substantial depletion of services provided to humans by ecosystems and largely irreversible loss of biodiversity. The emerging consumers in developing and transition countries will require additional land for production of food, fiber and fuel. Moreover, with fossil fuel shortages and insecurity of supply, many countries depart on the strategy of biomass substitution. Whereas much current biomass energy is derived as a by-product of other crops, energy production from biomass on a much larger scale will require energy crops (Kheshgi et al., 2000). As many current agricultural yields surpass yields attainable under the natural conditions, the production of energy crops can have substantial implications for the biological productivity of land.

Relationship between land use intensity and biodiversity has not been extensively documented, despite the widespread apprehension of the land use as a leading pressure governing biodiversity changes (Haines-Young, 2009). Human impacts on land and biodiversity can be characterized by the theoretical foundations of species-area relationship (SAR) (MacArthur & Wilson, 1967), species-energy relationship (SER) (Storch et al., 2005) and intermediate disturbance hypothesis (IDH) (Connel, 1978). These theories provide mechanistic explanation of the relationship between human induced land use change, ecosystem use and biodiversity. Humans appropriate area and energy and generate disturbance which influence biodiversity through land and ecosystem use activities. Species area relationship (SAR) and species energy relationship (SER) have been documented across different spatial scales and taxonomic groups (Storch et al., 2005). The disturbance influences biodiversity in a hump-shaped relationship (Rosenzweig, 1995). The intermediate disturbance hypothesis states that moderate levels of disturbance maximize species diversity because competitively dominant species exclude subordinate species at low disturbance. That means diversity peaks at intermediate disturbance frequencies. Evidence suggest that high biodiversity (at the species level or landscape heterogeneity level) is correlated with the intermediate levels of human impact (Wrbka et al., 2004). Humans are raising the diversity of habitat types in the mosaic of different land uses and thus enabling the coexistence of species with different ecological requirements.

Land cover and land use change are influencing the biodiversity at the most basic level. Habitat modification is considered to be the main driving force of biodiversity loss. To account for impacts of land use changes on biodiversity, actual levels of biodiversity are usually compared to some reference levels. This is an approach of NCI and BII (see Chapter 2.1 for details). Currently, impacts on biodiversity resulting from land use changes are promoted in LCA methodology (Lindeijer, 2000; Köllner, 2000). Characterization factors are being developed which would express the effect of land use on biodiversity (Schmidt, 2008). The biodiversity was approached especially by the diversity of vascular plant species, mainly due to data availability. Characterization factors are deviced from species-are curves for land cover types and comparison of actual species levels to potential ones.

### 2.2.4. Net primary production and biodiversity

Net primary production (NPP) has been often used as an indicator of ecosystem functioning and services provided by ecosystems (Costanza et al., 1997, de Groot et al., 2002, Naeem et al., 2009). NPP has been defined as a rate of carbon accumulation in an ecosystem. Primary productivity thus represents the major input of carbon and energy into ecosystems and has been often proposed as an integrative indicator of ecosystem functioning (McNaughton et al., 1989; National Academy of Sciences, 2000; Odum, 1969).  Concepts related to NPP and relevant for accounting of carbon flows in ecosystem are Net Ecosystem Production (NEP) and Net Biome Production (NBP) (Schulze et al., 2000a). NEP is defined as a difference between gross primary production and total ecosystem respiration (Lovett et al., 2006). NBP takes into account also long-term biome dynamics, including broader-scale processes of carbon lost from harvest or fires or carbon accumulated due to lateral transfers. NPP is directly related to biomass production and biomass yield, concepts used mainly in agriculture and forestry. Photosynthetic production is critical for the sustainability of human society (Nátr, 2002).

There is established evidence that the relationship between net primary production and biodiversity is bidirectional. Productivity, usually expressed as net primary production, has been traditionally considered as one of the basic factors influencing biodiversity (Waide et al., 1999). The relationship is usually unimodal, i.e. biodiversity peaks at intermediate productivity levels. However, relatively novel but established stream in modern ecology considers biodiversity to be a factor influencing net primary productivity as a basic measure of the performance of ecosystems (Loreau et al., 2001; Naeem & Li, 1997; Tilman et al., 1996; see Vačkář & Plesník, 2005 for review in Czech). Multispecies communities utilize environmental resources more effectively (due to overyielding and sampling effects) and provide buffering against environmental perturbations. Therefore, biodiverse assemblages are able to achieve higher productivity in longer-term perspective. Biodiversity has been therefore related to stability and sustainability of ecosystems, although the relationship between diversity and stability is complex (Ives & Carpenter, 2007). Recent synthesis suggest that biodiversity of functional groups rather than that of species is important (Cardinale et al., 2006) and that declining biodiversity alters performance of ecosystems and influence ecosystem services and human well-being (Balvanera et al., 2006; Naeem et al., 2009).

Net primary productivity at larger spatial scales cannot be measured directly. Therefore, models and approximations have been usually used to estimate NPP at larger spatial scales, e.g. biome or regional level. The first global model of terrestrial ecosystems was developed in the early 1970s (Lieth, 1975), based on a large amount of observational data from the International Biological Programme (Ajtay et al., 1979). The MIAMI model provided a good approximation of the global distribution of potential vegetation productivity. Model has been extended to productivity models to simulate the entire carbon cycle, including biomass growth and soil carbon dynamics. Currently, several global biogeochemical models or dynamic global vegetation models (DGVMs) provide estimates of primary productivity related parameters (Cramer et al., 1999).

Two basic approaches for estimating the NPP include: (i) a book-keeping model (Houghton et al. 1999, 2000a, 2000b). The book-keeping model has been used to calculate changes in terrestrial carbon storage following changes in land use. The model included response curves that defined the annual changes in live and dead vegetation and soil carbon that occur on a unit area of land following a change in land use. In the book-keeping model, the NPP is spatially transferred as a function of land cover and unit productivity. The productivity data are transferred from NPP studies conducted in equivalent settings (i.e. ecoregion and/or climatic variables). (ii) models based on remotely sensed parameters. These models enable large-scale estimations of NPP. However, calibration and validation of satellite data is based on ground-based measurements which are limiting factor in reliable satellite NPP estimates.

One of the models used for the estimation of NPP is based on Monteinth´s equation and is given by a relationship between absorbed photosynthetic active radiation (APAR) and Normalized Difference Vegetation Index (NDVI):

$$NPP = \varepsilon \times \sum APAR,$$

where ε is light use efficiency (in g $MJ^{-1}$, grams per megajoule). NDVI is then scaled to APAR as the fraction of photosynthetically active radiation that is absorbed. This approach to NPP estimation is used in NPP models which use remotely sensed information, such as for example CASA model (Field et al., 1998).

Several indicators have been proposed in connection to net primary productivity, yield and carbon accounting. These include Net Carbon Storage NCS (Schimel et al., 2000; Pacala et al., 2001), Ecological Footprint EF (Haberl et al., 2004;

Wackernagel et al., 2002) or Human Appropriation of Net Primary Production HANPP (Vitousek et al., 1987; Imhoff et al., 2004a; Haberl et al., 2007). Carbon-related indicators have been already related to biodiversity. Carbon storage and sequestration as one of the main regulation ecosystem services was assessed in relation to biodiversity conservation in a landscape model context (Nelson et al., 2009). Carbon storage and biodiversity conservation were found to be mutually complementary ecosystem services. Ecological Footprint and biodiversity were linked through the available biokapacity and number of threatened species at the global level, and urban footprints and land disturbance with species richness at the national level (Vackar, 2007). At the global level, Ecological Footprint is related to the Living Planet Index to illustrate trends in human pressures and state of biodiversity (Humphrey et al., 2008).

Net primary productivity (NPP) or its equivalents (for example, NDVI) has been used as an explanatory variable for the level of biodiversity, especially species richness component.

### 2.2.5. Human appropriation of net primary production

Human appropriation of net primary production (HANPP) is an aggregated measure of human impacts on ecosystem functioning, especially of impacts originating from land conversion and ecosystem use (Imhoff et al., 2004a, Haberl et al., 2007; Rojzstacer et al., 2001; Vitousek et al., 1986). HANPP gives consistent measure of human impacts on land as the indicator includes land conversion term which reflects conversion of natural ecosystems to agricultural or urban land. Moreover, HANPP considers human use of ecosystems as people harness ecosystems for food, fodder, fibres or timber. The concept of Human Appropriation of Net Primary Production (HANPP) was originally introduced by Peter Vitousek and colleagues (1986). They estimated the amount of net primary production (NPP) which human economic activity directly appropriates, co-opts or influences. The theoretical basis of the HANPP rests on calculating the fraction of NPP which humans appropriate from the total NPP bulk available in a given area. The HANPP is thus an important indicator of environmental sustainability, which aims to establish NPP balances of the socio-environmental metabolism of society (Haberl, 1997; Imhoff et al., 2004a; Haberl et al., 2007).

According to the original calculation of Vitousek et al. (1986), people globally appropriated 30.7% of terrestrial global NPP. This includes replacement of natural ecosystems with agricultural systems, conversion of forests to pastures, harvest and residues, and urbanization. Rojstazcer et al. (2001) recalculated the original HANPP estimate of Vitousek et al. (1986) and came to a similar result of 32% appropriated by humans. However, a high estimate could amount to 55% of NPP appropriated. DeFries et al. (1999, 2002) estimated that humans reduced NPP by 5% globally by land cover changes but with large regional disparities. Imhoff et al. (2004a) estimated on the basis of biological consumption data that people demanded 20.32% of global carbon supply provided by ecosystems. Haberl et al. (2007) found similar HANPP of 23.8% of potential NPP appropriated by socioeconomic activities. Land cover changes alone reduce NPP by 9.6% in aggregate but with large regional variations. Table 1 summarizes results of HANPP studies which have emerged as a result of interest in human influence on carbon and energy flows.

The study of HANPP in Austria (Haberl et al., 2001) found a difference of 200 PJ between the potential natural aboveground NPP and the NPP of actual vegetation cover and the overall HANPP amounted to 51%. Humans reduced the amount of net primary production by 13% through land cover changes. In Nova Scotia, O'Neill et al. (2007) detected a difference of 0.73 Mt or 5% between the potential and actual vegetation with HANPP reaching 25.5%. Some studies calculate only the fraction of NPP lost due to land use changes, notably urbanization as a widespread land use change pattern (Imhoff et al., 2004b; Milesi et al., 2003; Xu et al., 2007). Other HANPP studies conducted at regional or national levels do not include estimates of the productivity losses due to land conversions (Cardoch et al. 2002; Prasad & Badarinth 2004). They calculate the NPP appropriation considering only ecosystem use (harvest) data. Recently, HANPP was calculated for a suite of countries and these studies revealed considerable human impacts on primary production in different countries (see Erb et al. 2009 for summary of results).

HANPP indicator was tested as an indicator of human pressures on biodiversity. Haberl et al. (2005) found that ecological production indicators, expressed as components of HANPP, better predicted bird species richness in Austria than for example heterogeneity indicators. Another analysis found that actual primary production ($NPP_{ACT}$) and HANPP were inversely correlated with species richness while the amount of primary production remaining in ecosystems was positively correlated with species richness on a transect in eastern Austria (Haberl et al., 2004).

**Table 1. Comparison of HANPP estimates from different studies conducted at the global, regional or national levels.**

| Region | Reference | Low | Intermediate | High |
|---|---|---|---|---|
| | | ***% of available or potential NPP*** | | |
| **World** | | | | |
| **World** | Vitousek et al. 1986 * | 3.9 | 30.7 | **38.8** |
| **World** | Rojstazcer et al. 2001 | 10 | 32 | **55** |
| **World** | Imhoff et al. 2004 | 14.10 | 20.32 | **26.06** |
| **World** | Haberl et al. 2007 | 8 [#] | 23.8 | **37 [#]** |
| **World** | DeFries et al. 1999 | | 5.66[§] | |
| | | | | |
| **World regions and** | | | | |
| **Africa** | Imhoff et al. 2004 | | 12.4 | |
| **Northern Africa and** | Haberl et al. 2007 | | 42 | |
| **Sub-Saharan Africa** | Haberl et al. 2007 | | 18 | |
| **East Asia** | Imhoff et al. 2004 | | 63.25 | |
| **South central Asia** | Imhoff et al. 2004 | | 80.39 | |
| **Central Asia and Russian** | Haberl et al. 2007 | | 12 | |
| **Eastern Asia** | Haberl et al. 2007 | | 35 | |
| **Southern Asia** | Haberl et al. 2007 | | 63 | |
| **Southeastern Asia** | Haberl et al. 2007 | | 30 | |
| **Western Europe** | Imhoff et al. 2004 | | 72.22 | |
| **Western Europe** | Haberl et al. 2007 | | 40 | |
| **Eastern and** | Haberl et al. 2007 | | 52 | |
| **North America** | Imhoff et al. 2004 | | 23.69 | |
| **Northern America** | Haberl et al. 2007 | | 22 | |
| **South America** | Imhoff et al. 2004 | | 6.09 | |
| **Latin America and the** | Haberl et al. 2007 | | 16 | |
| **Oceania and Australia** | Haberl et al. 2007 | | 11 | |
| | | | | |
| **National states** | | | | |
| **Austria** | Haberl et al. 2001 | | 51 | |
| **India** | Krishna Prasad and | | 42 | |
| **United Kingdom** | Musel 2009 | | 68 | |
| **Spain** | Schwarzlmüller 2009 | | 61 | |
| **Hungary** | Kohlheb and Krausmann | | 49 | |
| **Philippines** | Kastner 2009 | | 62 | |
| **Czech Republic** | Vackar et al. 2010 | | 55 | |
| | | | | |
| **Regions** | | | | |
| **Nova Scotia** | O'Neill et al. 2007 | | 25.5 | |
| **Ebro delta** | Cardoch et al. 2002 | | 35 | |
| **Jiangyin region** | Xu et al. 2007 | | 14.5[§] | |
| | | | | |

* Only terrestrial HANPP is considered

[#] Recalculation of Vitousek et al. (1986) estimates

[§] Only changes in NPP induced by land cover and land use change are considered

# 3. Methods and data

## 3.1. Calculation of HANPP indicator

In the calculation of the Human Appropriation of Net Primary Production (HANPP) indicator, only the aboveground components of NPP were considered. This is especially due to data limitations and uncertainties connected to belowground NPP component. Calculations using only aboveground NPP (aNPP) into considerations are consistent with current works on HANPP topic (Imhoff et al., 2004a; Haberl et al., 2007). The human appropriation of aboveground net primary production (aHANPP) has been conventionally defined as a difference between the aboveground potential natural vegetation of a given region and the aboveground biomass remaining in ecosystems after harvest (Haberl, 1997; Haberl et al., 2001; Haberl et al., 2007):

$$aHANPP = aNPP_0 - aNPP_T,$$

where $aNPP_0$ expresses the aboveground net primary productivity of the potential natural vegetation, i.e. reflects the potential NPP pool available in a given area, and $aNPP_T$ is fraction of NPP remaining in ecosystems after land use changes and biomass harvest.

The biomass remaining in ecosystems after harvest ($aNPP_T$) is the difference between the aboveground actual net primary production ($aNPP_{ACT}$), that is NPP produced by the actual land cover, and the aboveground harvest of biomass ($aNPP_H$), that is the biomass extracted from ecosystems by humans, which is economically used or discarded as harvest residues. The NPP remaining in ecosystems ($aNPP_T$) is therefore given by the difference between the actual NPP and harvested NPP (Haberl et al., 2007):

$$aNPP_T = aNPP_{ACT} - aNPP_H .$$

Another important process defining the extent of HANPP in a cultural landscape is the land conversion. Land conversion contributes to changes in NPP by introducing vegetation with different production characteristics. This process has been denoted as $\Delta NPP_{LC}$, or human induced land cover change, and is defined as difference between potential and actual vegetation (Haberl et al., 2001; 2007):

$$\Delta \; NPP_{LC} \; = \; aNPP_0 \; - \; aNPP_{ACT}.$$

The difference between the potential natural net primary production ($aNPP_0$) and the actual net primary production ($aNPP_{ACT}$) gives information about the human induced changes of net primary productivity (Haberl et al. 2007). HANPP indicators can be also expressed as the sum of productivity changes induced by land conversion (either negative or positive) and NPP equivalent of harvested biomass:

$$aHANPP \; = \; \Delta \; NPP_{LC} \; + \; aNPP_H \; .$$

We defined the aboveground human appropriation of net primary production (aHANPP) as a proportion of potential net primary productivity ($aNPP_0$) appropriated by humans. The novel aggregate mathematical formula defined in this work is based on the approach of Haberl (1997) and reflects the two main processes determining the NPP appropriation by humans. First process is the conversion of natural habitats to human-dominated land use, resulting in human-induced NPP changes. Second process is the direct harvest of biomass and generation of harvest residuals, resulting in direct appropriation of NPP. HANPP was re-expressed as a ratio of NPP remaining in ecosystems ($NPP_T$) after biomass harvest ($NPP_H$) and the potential natural vegetation ($NPP_0$):

$$HANPP(\%) \; = \; \left[ 1 \; - \; \frac{(NPP_{ACT} \; - \; NPP_H)}{NPP_0} \right] \times \; 100$$

which gives

$$HANPP(\%) \; = \; \left[ 1 \; - \; \left( NPP_T \, / \, NPP_0 \right) \right] \times \; 100 \, .$$

### 3.1.1. NPP datasets

An extensive compilation of field data on net primary productivity (NPP) of natural and agricultural ecosystems worldwide was synthesized in the Oak Ridge National Laboratory Distributed Active Archive Center (ORNL DAAC) NPP database (http://daac.ornl.gov/). The NPP Database contains documented field measurements of NPP for global terrestrial sites compiled from published literature and other extant data sources. The NPP Database currently contains 82 NPP data sets available on-line, with information on NPP in different biomes and ecosystems. A major goal of the data compilation is to use consistent and standard well-documented methods to estimate NPP from the field data. The NPP Database currently contains detailed data for over 60 intensive study sites. A majority of these sites are grasslands, the remainder being tropical forests, boreal forests, and tundra study sites. Climate and soils data are available for all sites in varying degrees of detail. Besides the intensive study sites, NPP Database contain multi-biome compilations of NPP data used in specific projects or models. The measurements of NPP in the database were categorized as either Class A, representing intensively studied or well-documented study sites; Class B, representing more numerous extensive sites with less documentation and site-specific information available, or Class C, representing regional collections of 0.5° latitude-longitude grid cells. The main NPP datasets which were extracted are multi-biome NPP data and include:

**The IBP (International Biological Programme) Woodlands Data Set**, 1955-1975 (DeAngelis et al., 1997) consists of contributions from 117 international forest research sites, predominantly associated with the IBP. The data were collected in the 1960s and early 1970s and compiled into a single data set at the Oak Ridge National Laboratory to facilitate comparisons involving the diverse woodland ecosystems. Data for up to 38 biomass compartments are presented in the data set, complemented by site description data, including edaphic characteristics, average meteorological conditions, and basic descriptive and quantitative data on the vegetation and plant characteristics. The data set represents the major forest types, especially Tropical, Mediterranean, Temperate and Boreal.

**Global Osnabrück Data**, 1937-1981 (Esser et al., 1998) presents an extensive compilation of field data on net primary productivity (NPP) of natural and agricultural ecosystems worldwide which was synthesized in the 1970s and 1980s. More than 700 single point estimates of NPP or biomass were extracted from the scientific literature, each with a geographical reference. Although this data set has not been updated since the 1980s, it was extensively used in NPP models development and validation. The aboveground NPP estimates range between 1 and 8530 g $m^{-2}$ per year (dry matter) or 2923 g $m^{-2}$ $year^{-1}$ in average, excluding uncertain values, wetlands, and crops/pastures and other likely managed systems. Each record includes a site identifier, latitude, longitude, author, country, NPP estimates, vegetation type, and other variables.

**Global Primary Production Data Initiative Products** (Olson et al., 2001a). This GPPDI NPP dataset was compiled for 2,523 sites and 5,164 half-degree grid cells. The GPPDI database includes NPP measurements collected over a long time period by many investigators using a variety of methods.

**Grassland, Boreal Forest, and Tropical Forest Sites**, 1939-1996
Terrestrial net primary productivity (NPP) estimates are compiled from the literature for 34 grasslands, 14 tropical forest sites, and 5 boreal forest sites. These 53 NPP estimates and associated site climate and biophysical characteristics were reviewed and documented to compile a series of web pages containing detailed data and to produce an overview synthesis paper (Scurlock & Olson, 2002).

**Gridded Estimates For Selected Regions Worldwide**, 1989-2001 (Zheng et al., 2003). Most field data for net primary productivity (NPP) are for relatively small field sites that are effectively points when considered at the 0.5 x 0.5 degree scale commonly used in global biogeochemical models. Thus, direct comparison between field data and coarse resolution model outputs can be misleading. Consistent estimates of NPP for 0.5x0.5 degree grid cells were developed from 15 studies representing NPP in croplands, sparse vegetation, shrublands, grasslands, and forests worldwide.

**PIK Data for Northern Eurasia**, 1940-1988 (based on Bazilevich dataset) (Denissenko et al., 2001). Dataset includes NPP values compiled by the Potsdam Institute for Climate Impact Research for the purposes of global model development and intercomparison (Cramer et al., 1999).

**NPP and Driver Data For Ecosystem Model-Data Intercomparison** (Olson et al., 2001b). The Ecosystem Model-Data Intercomparison (EMDI) provides the dataset for a wide range of global carbon cycle models to be compared with measured net primary productivity (NPP). The goals of EMDI are to compare model estimates of terrestrial carbon fluxes (NPP) to estimates from ground-based measurements and to improve understanding of environmental controls of carbon allocation.

### 3.1.2. NPP of potential vegetation

The area of potential vegetation was taken from the digitalized map of potential natural vegetation of the Czech Republic (Neuhäuslova et al., 1998), processed in the Geographical Information Systems (GIS). Together, 51 plant associations of the potential vegetation can be discerned. However, limited by the availability of NPP data, we grouped these classes into broader categories according to the dominant plant species (Table 2). Available NPP data were not able to catch differences within the broader vegetation units. A specific NPP values according to the dominant species were assigned to broader vegetation groups. The NPP of the aboveground potential vegetation ($aNPP_0$) was calculated as:

$$aNPP_0 = \sum_{i=1}^{n} A_i \times aNPP_i,$$

where $A_i$ denotes the area of potential vegetation class i and $aNPP_i$ denotes the aboveground NPP of vegetation class i per unit of area.

**Table 2. Average NPP, area and standard errors for different natural potential vegetation classes. The data were extracted from the ORNL DAAC database of the NPP in different world biomes and supplementary sources. Only the values for the vegetation of temperat and boreal regions with the species composition corresponding to the vegetation typical for the Czech Republic were considered. Data on managed forests were excluded where the meta-data identification was available. Lower values for spruce stands represent boreal-type forests.**

| Potential natural vegetation type | Area (ha) | Average NPP (g C $m^{-2}$ $yr^{-1}$) | Standard error (SE = SD/√N) |
|---|---|---|---|
| **Alluvial woodland** | 504 497 | 546.08 | 128.84 |
| **Hornbeam woodland** | 2 304 687 | 455.91 | 25.79 |
| **Beech woodland** | 2 831 643 | 527.90 | 34.57 |
| **Oak woodland** | 2 093 591 | 458.53 | 25.38 |
| **Pine woodland** | 3 105 | 353.90 | 52.27 |
| **Spruce woodland** | 109 787 | 359.24 | 38.65 |
| **Mires and peatlands** | 33 262 | 192.1 | 32.67 |

### 3.1.3. NPP of actual vegetation

Human activities change patterns in land cover and create heterogeneous land use mosaics with different influences on the NPP outcomes. The actual NPP for the area of the Czech Republic was calculated using the Corine Land Cover (CLC) data for periods 1990, 2000 and 2006 (EEA, 2006). CLC is an image based on satellite scanning of the Earth's surface. After processing and validation, satellite data are transformed into a map of land cover (Nunes de Lima, 2005). Together, 30 terrestrial land cover classes can be discerned on the area of the Czech Republic, spanning the continuum from anthropogenic surfaces to natural land cover. We considered water bodies only as contributing to land take as they are usually excluded from HANPP calculations (Haberl et al., 2001). We assigned specific values of aNPP to actual land cover, based on literature review and calculations. The actual $aNPP_{ACT}$ can be generally calculated as:

$$aNPP_{ACT} = \sum_{j=1}^{n} A_j \times \overline{aNPP_j},$$

where $A_j$ is an area of particular land cover or land use category j and $aNPP_j$ denotes specific aboveground NPP of vegetation class j per unit of area. We assigned specific NPP values to every land cover class to reflect specific net primary productivity influenced by humans. The following categories of land cover were considered for the calculation of NPP appropriation.

### *Artificial surfaces*

The majority of artificial surface classes were considered to be unproductive as they represent mainly sealed land. However, several urban areas contain a considerable proportion of vegetated surfaces. The dominating artificial class is the discontinuous urban fabric, which can contain approximately 30-50% of vegetation cover (Piringer et al., 2002; Svirejeva-Hopkins & Schellnhuber, 2006). Despite the negative effects of urbanization on net primary productivity (Imhoff et al., 2004b; Milesi et al., 2003), urban green areas such as lawns or parks are able to achieve relatively high levels of productivity because of resource inputs and management (Golubiewsky, 2006; Kaye et al., 2005). We used an average value of productivity reported from urban areas (539 g C $m^{-2}$, ± Standard Error SE = 94.3 g C $m^{-2}$), adjusted for the coverage of vegetated areas in a discontinuous urban fabric. Data for sport and leisure facilities were taken from Milesi et al. (2005). To airports we assigned the average grassland productivity adjusted for the proportion of vegetated surfaces. As NPP values for urban areas are limited, globally available values were used.

### *Agricultural land*

Agricultural land includes arable land, permanent crops, pastures and mosaic farmland. We calculated the productivity of arable land as an area-weighted average productivity of arable crops and permanent cultures which is 412 g C $m^2$. The harvest reported in the official statistics was adjusted to account for the components discarded in the economic production using harvest indices (Bradford et al., 2005; Johnson et al., 2006; Lobell et al., 2002; Prince et al., 2001). Permanent crops cover mainly fruit, berry and hop plantations and vineyards. The average yield of fruit trees and berry plantations was calculated as an area-weighted average of particular fruit and berry yields. The fruit yield has expanded in comparison with the partitioning ratios available in the literature (Palmer, 1988). Equivalently for fruits, grapes in vineyards are able to meet more than half of the total productivity. Therefore, we doubled the statistically reported grape yield. Pastures are defined as areas of dense grass cover, of floral composition dominated by graminaceae. We estimated the pasture productivity as the productivity of meadows which best match the definition of pastures (dense graminaceous cover, with the possibility of sedges present). The average productivity of pastures is 325 g C $m^{-2}$. Moreover, agricultural land includes mixed land cover classes classified as the complex cultivation pattern and land principally occupied by agriculture. The NPP estimate was gained by averaging the productivity of land cover types included in these mixed categories.

### *Forests*

We differentiated between coniferous, mixed and broadleaved forests. In the Czech Republic, coniferous stands cover approximately 77% of the timberland, with the majority covered by spruce (55%) and pine (17%). Our estimate of coniferous NPP based on available data 530 g C $m^{-2}$ $y^{-1}$. Stands classified as broadleaved forests cover 22.3% of the area, with beech and oak covering each around 6% of the timberland and birch, hornbeam, alder at other broadleaved species forming the remainder. The average NPP estimate for broadleaved forest species occurring on the territory of the Czech Republic is 545 g C $m^{-2}$ $y^{-1}$. According to the Corine Land Cover classification, approximately 275 kha of coniferous forests and 326,5 kha of broadleaved forests reported in forest statistics can be classified as mixed forests. The average value for natural and managed mixed forests based on the database search is 567 g C $m^{-2}$ $y^{-1}$. The specific land cover class is transitional woodland shrub, including not only young plantations but also forests damaged by clear-cutting, fire, wind or acid rain. The category can be dominated even by shrubs or herbaceous vegetation following the forest damage. Consequently, we estimated the productivity of this class as an average of forest and grassland productivity.

*Natural and semi-natural grassland*

The average NPP of natural grasslands from our database is 219 g C $m^{-2}$ $yr^{-1}$, which corresponds well to the above-ground NPP component of temperate meadows, provided that the above-ground and below-ground NPP is approximately similar. The below-ground component is not considered in this study. We assigned to the category of natural grassland the average productivity of steppe, moors and heathland, saline and alpine vegetation which form natural forest-free cover.

*Wetlands*

The land cover class of wetlands includes inland marshes and peatbogs. Inland marshes are among the most productive environments as they represent eutrophic ecosystems sustained by the high inputs of water and nutrients. Our mean estimate of wetland productivity is 707 g C $m^{-2}$ $yr^{-1}$. The number exceeds the average productivity of other land cover types. However, it shows the highest uncertainty (707 g C $m^{-2}$ ± 201 g C $m^{-2}$). The productivity of peatbogs was found to be considerably lower, with an average value of 192 g C $m^{-2}$ $yr^{-1}$. However, the data predominantly cover the above-ground components of mires and peatlands.

### 3.1.4. NPP equivalent of harvested biomass

The last number required for the calculation of HANPP is the NPP fraction directly harvested or destroyed by humans. We call this NPP equivalent of harvest as harvest is usually reported as merchantable fraction of biomass extracted from ecosystems by humans. However, indispensable amounts of biomass are discarded or destroyed during harvest operations (Smil, 1999). The low NPP appropriation estimate represents the merchantable fraction of biomass used directly for economic production or consumption. These data are regularly reported by the agricultural and forestry statistics. The economic part of the harvest was adjusted for water content to get the dry matter estimate of the direct harvest. However, it is clear that people appropriate also the non-marketed part of the production, such are agricultural and forest residues – straw, bark, leaves etc. Some portion of these residues has other use or is burnt. We therefore included intermediate NPP appropriation estimate (Rojstaczer et al., 2001; Vitousek et al., 1986) to account for complete NPP fraction appropriated by harvest.

### *Agricultural harvest*

The overall harvested NPP appropriated by humans in agricultural systems is calculated as a ratio of biomass directly harvested, which is expressed as a product of the area covered by a particular harvested crop, $A_k$, and yield of that crop, $Y_k$, and of the harvest factor adjusting the harvested biomass to the total NPP required by humans to produce crop (Lobell et al., 2002; Prince et al., 2001). The harvested NPP of agricultural products can be expressed as:

$$NPPh_{agr} = \sum_{k=1}^{n} (A_k \times Y_k) \times (1 - MC_k) / HF_k \ ,$$

where $A_k$ represents the area covered by the particular crop, $Y_k$ stays for the yield achieved in a given year in a land use class $k$, $HF_k$ represents the appropriate harvest index capturing the ratio of economically utilized biomass to the overall aboveground biomass and $MC_k$ express the appropriate moisture (water) content of a crop $k$.

### *Harvest indices*

Large-scale NPP assessments are complicated by the insufficient spatial resolution and incompleteness of data (Lobell et al., 2002). In agroecosystems, only the economically important part of the phytomass production is directly counted and harvest residuals are usually not accounted for in harvest statistics. The most reliable estimates of agricultural NPP come indirectly from studies of harvest indices (Smil, 1999). The concept of harvest index is based on a general eco-physiological approach of the growth allocation into different organs. The breeding process leads to the increased allocation of dry matter into seeds and other economically utilized plant organs. The empirical basis for the study of harvest index has intensified in 1970's with the introduction of high-yielding varieties of cereals, rice and pulses.

The harvest index (HI) has been traditionally defined as a ratio of the economic (grain) yield of a crop ($Y_e$) and the total aboveground biomass of the crop (ABGB) (Hay 1995):

$$HI = \frac{Y_e \left[ g \cdot m^{-} \right]}{ABGB \left[ g \cdot m^{-} \right]},$$

or as a ratio of the economic yield of edible seeds, leaves, stalks or roots to the crop total aboveground biomass (Smil, 1999). The Harvest Index is based on empirical data from crop samples dried to constant weight (Table 3). The so called actual or nominal harvest index (Hay, 1995, Velayudhan et al., 1995) is based strictly on the aboveground biomass, while apparent harvest index is defined as a proportion of economic yield to the total biomass, including roots. However, the actual harvest index doesn't reflect the final processing of plants. Therefore, Velayudhan et al. (1995) in the context of controlled ecological life support systems introduced corrected harvest index which accounts for digestibility of plants. For example, the harvest index of rapeseed can reach 25% but approximately 40-45% of consumable product, canola oil, is extracted from the seeds. In lettuce, almost the whole plant is harvested (80%) but digestable fraction is estimated to be 30% giving the corrected HI of 0.23.

Values of harvest indices range from approximately 0.25 for oil crops to 0.6 for pulses (Table 3). Grains achieve in average HI values of 0.46, followed by maize (0.52) and legumes with values slightly higher than 0.55. Harvest indices for roots and tubers had also been established but their interpretation is ambiguous. For example, some authors report HI for sugar beet of 0.4 while other assign values even exceeding unity. Bondeau et al. (2007) found that HI for sugar beet is reaching the value of 2. The interpretation of this value is that the bellow-ground part of the plant is exceeding the aboveground components. According to the common definition of actual harvest index the HI values cannot exceed the maximum value of 1. The harvest indices for feed crops and hay may achieve values of 0.9-1. However, when both the aboveground and bellow-ground components are considered (the apparent harvest index) the harvest index can reach values higher than 1. The harvest index has been also defined for tree crops and defined as a proportion of fruit yield on annual dry matter production (Hay, 1995). We used average values of harvest indices extracted from the literature (Table 4).

**Table 3. Average values of Harvest Indices (HI) for agricultural crops. Values are extracted from following sources (see reference number in the table heading): 1. Bradford et al. 2005, 2. Bondeau et al. 2007, 3. Smil 1999, 4. Johnson et al. 2006, 5. Sinclair 1998, 6.Valeyudhan et al. 1995, 7. Prince et al. 2001, 8. Lobell et al. 2002.**

| Reference | 1. | 2. | 3. | 4. | 5. | 6. | 7. | 8. |
|---|---|---|---|---|---|---|---|---|
| **Cereals** | | 0.4 | 0.4 | | | | | |
| **Wheat** | 0.39 | | | 0.45 | 0.5 | 0.45 | 0.39 | 0.45 |
| **Wheat** | | | | | 0.37 | | | 0.4 |
| **Barley** | 0.49 | | | 0.5 | 0.48 | | 0.5 | 0.4 |
| **Oat** | 0.52 | | | 0.44 | | | 0.52 | 0.4 |
| **Rye** | 0.35 | | | | | | | |
| **Maize** | 0.52 | 0.5 | | 0.53 | 0.5 | 0.53 | | |
| **Legumes** | 0.55 | | 0.49 | | | | | |
| **Lentil** | | 0.6 | | | | | | |
| **Roots, tubers** | | | 0.4 | | | | | |
| **Potatoes** | 0.55 | | | | | 0.8 | | 0.5 |
| **Sugar beet** | | 2 | | | | | | 0.4 |
| **Oil crops** | | | 0.52 | | | | | |
| **Rapeseed** | | 0.3 | | | | 0.25 | | |
| **Sunflower** | 0.4 | 0.3 | | 0.4 | | | 0.27 | 0.35 |
| **Vegetables** | | | 0.38 | | | | | |
| **Lettuce** | | | | | | 0.8 | | |
| **Fruits** | | | 0.38 | | | | | |
| **Hay, alfalfa** | | | | | | | | 1 |
| **Other crops** | | | 0.28 | | | | | |

**Table 4. Harvest indices used for the calculation of HANPP in the Czech Republic.**

| Crop type | | Harvest index | Standard error |
|---|---|---|---|
| | | | |
| **Cereals** | | 0.46 | 0.01 |
| | Wheat | 0.43 | 0.01 |
| | Barley | 0.47 | 0.02 |
| | Oat | 0.47 | 0.03 |
| | Maize | 0.52 | 0.01 |
| **Legumes** | | 0.55 | 0.03 |
| | Beans | 0.55 | |
| | Pea | 0.50 | |
| | Lentil | 0.60 | |
| **Roots, tubers** | | 0.78 | 0.23 |
| | Potatoes | 0.62 | 0.08 |
| | Sugar beet | 1.2 | 0.57 |
| **Oil crops** | | 0.35 | 0.03 |
| | Rapeseed | 0.28 | 0.02 |
| | Sunflower | 0.34 | 0.02 |
| **Vegetables** | | 0.38 | 0.15 |
| | Lettuce | 0.80 | |
| **Fruits** | | 0.38 | |
| **Other crops** | | 0.28 | |

### *Pastures*

We were interested in what part of agricultural NPP appropriation can be attributed to the meat system. The main methodological problem of the calculation of NPP appropriation by meat system is the apportioning of the mixed production systems into the dietary components. Mixed systems rely on the combination of rangeland grazing, cultivated forages, harvested forages (hay and corn silages), crop residues and concentrate feeds. The final balance can be completed only if the total dietary requirements of animals are known.

One of the basic parameters to estimate the net primary production requirements of grazing livestock is the total dry matter intake (DMI), usually expressed as kg of DM per day. Vasquez and Smith (1999) found the average pasture dry matter intake of 11.6 kg DM (SD=2.95) based on the results of 27 previously published studies. When grazing cows are fed supplements, pasture DMI usually decreases, which is known as substitution rate. But total DMI usually increases when livestock is based on mixed pastures and concentrates feeding (Bargo et al., 2003). The substitution rate (SR) expresses the decrease in DMI when grazing cows are fed supplements. Substitution rate can be defined as the reduction in pasture DMI per kilogram of supplement.

The main methodological problem of the calculation of HANPP for meat system is the apportioning of the mixed or stratified production systems into the dietary components. Mixed systems rely on the combination of rangeland grazing, cultivated forages, harvested forages (hay and silages), crop residues and concentrate feeds. The final balance can be completed only if the total efficiency of meat production and total dietary requirement of animals are known.

The efficiency of meat production can be expressed by feed-to-meat ratios, commonly expressed by standards units of feed per unit of live weight. Equivalent approach is to express so called feed-to-gain ratio which measures the unit weight gain per unit of feed applied. Smil (2002) presents typical efficiencies of meat production based on the long-term data gathered by the US Department of Agriculture (Table 5). In some studies, the efficiency of grain-to-meat conversion in expressed per unit of edible final product.

**Table 5. Feed demand values for selected animals according to various sources.**

| | Feed (kg / kg live weight) Smil, 2002 | Grain per unit of product (CAST, 1999) | Feed demand (kg DM) Haberl et al., 2007 |
|---|---|---|---|
| **Poultry** | 2.5 | 2.2 | 3.0 |
| **Pork** | 5.0 | 3.7 | 5.0 |
| **Beef** | 10.0 | 2.6 | 9.2 |
| **Sheep and goat** | | 0.8 | 1.5 |

Elferink and Nonhebel (2007) developed a methodology for estimating land required to produce a unit amount of meat. They applied specific feeding rates to express the dietary requirements of livestock in Netherlands and calculated the amount of land required to produce the usual feed mixture with average yields. They found that chickens have the lowest land requirement (7.7 $m^2$ $kg^{-1}$), followed by pork (10.2 $m^2$ $kg^{-1}$) and beef (29 $m^2$ $kg^{-1}$).

One of the basic parameters to estimate the net primary production requirements of grazing livestock is the total dry matter intake (DMI), usually expressed as kg of DM per day. Dry matter intake (DMI) from pastures has been estimates at approximately 2.0 - 3.5% of body weight (BW). It corresponds approximately to 18 – 21 kg/d for grazing cows, provided sufficient pasture allowance of 50 kg DM per cow. However, average DMI is probably lower as results from field studies. Vasquez and Smith (1999) found the average pasture dry matter intake of 11.6 kg DM (SD=2.95) based on the results of 27 previously published studies. Furthermore, when grazing cows are fed supplements, pasture DMI usually decreases, which is known as substitution rate. But overall, pasture DMI decreased and total DMI increased by increasing the amount of concentrate (Bargo et al., 2003).

The substitution rate (SR) expresses the decrease in DMI when grazing cows are fed supplements (Bargo et al., 2003). Substitution rate can be defined as the reduction in pasture DMI per kilogram of supplement. Substitution rate is dependent on the type of supplements and is calculated according to the following formula:

$$SR(kg\ /\ kg) \ = \ \frac{(\text{pasture DMI UnSup - pasture DMI Sup})}{\text{Supplement DMI}}$$

where pasture DMI UnSup is DMI in unsupplemented treatment and DMI Sup is DMI in supplemented treatment. SR ranged from 0.84 to 1.02 kg/kg for grass silage supplementation and from 0.11 to 0.50 kg/kg for concentrate supplementation. Bargo et al. (2003) review the SR for different concentrate feeds. Overall, pasture DMI decreased and total DMI increased by increasing the amount of concentrate. Compared with diets based solely on pastures, increasing the amount of concentrate supplementation increased total DMI 24% (Bargo et al.

2003). Supplementation with nonforage fiber sources or processed corn did not affect total DMI.

We took the average of 35 SR values compiled in study of Bargo et al. (2003) which is 0.4 kg DMI from pasture per unit kg DMI from concentrates relative to the unsupplemented treatment. Therefore, we supposed that approximately third of the DMI is supplied by grazing and the remaining amount is supplied as feed concentrates or silage. To account for increasing DMI with mixed feeding, we increased average DMI from pastures 11.6 kg DM/d by substitution rate 0.4 for livestock, which gives estimate of DMI of 14 kg DM/d. Feed intakes for sheep, horses, pigs and poultry were taken from Haberl et al. (2007) (Table 5).

### *Forest harvest*

In contrary to agricultural systems, where harvest take place on a yearly basis and majority of biomass produced is harvested, forest ecosystems provides harvest in a specific rotation period, which is approximately 110 years in the Czech commercial forests (Institute for Forest Management, 2000). However, in aggregate the harvested biomass was considered as a fraction of annual NPP produced in forests. The NPP influenced by humans can be expressed at different levels equivalently to the agricultural systems. The low calculation considers only the volume of timber harvested annually which is adjusted for the biomass using wood density and moisture coefficients. At the intermediate level, the harvested biomass is estimated using biomass expansion factors ($B_{EF}$) which empirically link aboveground biomass density of trees to the merchantable volume. Following the method of Levy et al. (2004) we can express the intermediate NPP appropriation as the NPP of harvested trees:

$$NPP_{H\,for} = \sum_{i=1}^{n} B_{Hi} + \left( V_{Hi} \times D_{Wi} \times B_{EFi} \right),$$

where $V_H$ is the volume of timber harvested ($m^3$) of a particular tree species, $D_W$ is the specific density of wood (Mg C dry mass $m^{-3}$), and $B_{EF}$ represents the biomass expansion factor (Mg C $Mg^{-1}$). Term $B_H$ represents adjusted wood harvest. Biomass expansion factors adjust harvested wood to the overall biomass destroyed by the harvest, taking into account foliage, bark and branches. Several $B_{EF}$ values were extracted from the literature (Jenkins et al., 2003; Levy et al. 2004; Lehtonen et al., 2004).

### *Biomass Expansion factors (BEFs)*

Total forest biomass from timber data can be estimated using Biomass Expansion Factors (BEFs) (Table 6). Biomass expansion factors have been defined as a ratio of the aboveground tree or stand biomass or biomass of its components and the growing stock volume or merchantable timber volume (Brown & Schroeder, 1999; Fang et al., 2001; Lehtonen et al., 2004; Levy et al., 2004):

$$BEF = \frac{ABGB}{GSV},$$

where ABGB denotes aboveground biomass and GSV growing stock volume. Schroeder et al. (1997) observed BEF values ranging for spruce-fir forests from more than 2 Mg $m^{-3}$ for low-growing stock volumes to a low of 1 Mg $m^{-3}$ for high growing stock volumes. The values for the pine forest types were even higher, reaching 5.7 – 1.3 Mg $m^{-3}$ for low GSV but with values in the range of 1.3 – 0.7 for higher GSVs. For pine forest types with GSV higher than 100 $m^3$ $ha^{-1}$ they used constant BEF of 0.81. For hardwoods, Brown & Schroeder (1999) used a constant BEF of 1.0 for growing stock volumes higher than 200 $m^3$ $ha^{-1}$.

Lehtonen et al. (2004) define BEF as a ratio of dry weight of tree component $W_i$ (such as foliage, branches, stem, dead branches, bark) and stem volume, V:

$$BEF = W_i / V \; [\mathrm{Mg\ m^{-3}}].$$

They found that BEF is a declining function of age, with younger stands (less than 40 years) having higher BEF than older stands (more than 81 years). For Scots pine, the BEF ranges from 0.697 to 0.710, for Norway spruce from 0.777 to 0.862 and for broadleaved stands from 0.544 to 0.556. The mean age of coniferous and broadleaved stands in the Czech Republic is 62 and 63 years, which corresponds to BEFs of 0.710 for Scots pine, 0.790 for Norway spruce and 0.554 for broadleaved stands according to Lehtonen et al. (2004). Jalkanen et al. (2005) applied constant BEFs of 0.52 for Scots pine, 0.62 for Norway spruce and 0.64 for broad-leaved stands.

Levy et al. (2004) define BEF as a ratio of the total aboveground tree fresh mass ($M_{ag}$) and fresh mass of the merchantable timber ($M_{timber}$):

$$BEF = M_{ag} / M_{timber} \quad [\mathrm{Mg\ Mg^{-1}}].$$

The factors according to the definition of Levy et al. (2004) have values at different scale as they calculate BEFs on the dry mass basis rather than volume basis. They found that BEFs for coniferous species in Great Britain varied between 1.04 and 2.32, with a mean of 1.43.

BEF values are not constant but dependent on a growing stock density. Low growing-stock volumes have generally higher BEF than high growing-stock volumes and BEFs thus decrease with increasing growing-stock volume.
Fang et al. (2001) calculated BEF from the equation

$$BEF = a + b/x,$$

where *a* ($\mathrm{Mg\ m^{-3}}$) and *b* (Mg) are empirical constants depending on a forest type and x represents a stand timber volume based on direct field measurement. For example, mixed conifer and deciduous forests have factor values a=0.8136 $\mathrm{Mg\ m^{-3}}$ and b=18.466 Mg. Empirical factor a thus approaches traditional BEF definition, while factor b is a production of unity stand volume.

Brown & Schroeder (1999) found a functional relationship where BEF is a function of growing stock volume. Average growing stock volume in the Czech Republic was 247.07 $m^3$ $ha^{-1}$, in 1190 it was approximately 220 $m^3$ $ha^{-1}$. The growing stock volumes intensities are thus rather high and as empirical results show, BEFs are a saturating function of GSV. Expected values of BEF for the Czech Republic will probably lie in the lower range of values, approaching the values of 1 or even lower (1 – 0.7 Mg $m^{-3}$). Table 6 reviews biomass expansion factors derived from various studies.

**Table 6. Biomass expansion factors based on empirical data from forest inventories and samples.**

| Species | | BEF | Unit | Reference |
|---|---|---|---|---|
| **Douglas fir** | Pseudotsuga menziesii | 1.486 | Mg $Mg^{-1}$ | Levy et al. 2004 |
| **European larch** | Larix decidua | 1.386 | Mg $Mg^{-1}$ | Levy et al. 2004 |
| **Norway spruce** | Picea abies | 1.546 | Mg $Mg^{-1}$ | Levy et al. 2004 |
| | | 0.62 | Mg $m^{-3}$ | Jalkanen et al. 2005 |
| | | 0.79 | Mg $m^{-3}$ | Lehtonen et al. 2004 |
| | | 1.00 | Mg $m^{-3}$ | Brown and Schroeder 1999 |
| | | | | |
| **Scots pine** | Pinus sylvestris | 1.39 | Mg $Mg^{-1}$ | Levy et al. 2004 |
| | | 0.52 | Mg $m^{-3}$ | Jalkanen et al. 2005 |
| | | 0.71 | Mg $m^{-3}$ | Lehtonen et al. 2004 |
| | | 0.81 | Mg $m^{-3}$ | Brown and Schroeder 1999 |
| | | | | |
| **Broadleaved** | | 0.64 | Mg $m^{-3}$ | Jalkanen et al. 2005 |
| | | 0.55 | Mg $m^{-3}$ | Lehtonen et al. 2004 |
| | | 1.00 | Mg $m^{-3}$ | Schroeder et al. 1997 |

### *Wood specific gravity*

Timber volume data reported in statistics are converted on the dry mass harvest values using wood specific gravity coefficients and wood moisture content data. We used a standard constant wood moisture content of 12% despite the fact that moisture content varies between different species (Forest Products Laboratory, 1999). However, the moisture content of the wood depends on the specific gravity, relative humidity and the proportion of sapwood and heartwood and the determination of moisture content factors would require extensive technical information. The density of most woods falls between about 320 and 720 kg $m^{-3}$ but the density varies greatly both within and between species (Forest Products Laboratory 1999). Table 7 lists specific gravity values of selected species at 12% moisture content.

**Table 7. Specific gravity values for selected wood species.**

| Species | Specific gravity (kg $m^{-3}$)[a] |
|---|---|
| Alder | 0.41 |
| Birch | 0.55 |
| Beech | 0.64 |
| Oak | 0.67 |
| Maple | 0.54 |
| Douglas fir | 0.48 |
| Fir | 0.39 |
| Larch | 0.52 |
| Pine | 0.47 |
| Spruce | 0.42 |

[a] Wood specific gravity values at 12% moisture content

## 3.2. Biodiversity and human pressures

The analysis aims to establish and estimate association (interdependence) between human population density (HPD) as a proxy for human pressures, appropriation of aboveground production (aHANPP) as a proxy for land cover change and ecosystem use impacts and species richness as a measure of biodiversity. The aim of this analysis is to explore the spatial patterns of human population density (HPD) and human appropriation of aboveground primary production (aHANPP) as an indicator proxy of human impacts and species richness in different taxa as a biodiversity indicator in a cultural landscape of a Central European country. The Czech Republic is a thoroughly surveyed country and biodiversity distribution for main plant, vertebrate as well as invertebrate taxa and trends for some flagship taxa (especially birds, butterflies and bats) are well known (Vackar et al., 2005). Distribution patterns and factors influencing species richness in the Czech Republic were analyzed for birds and butterflies (Storch et al., 2003), butterflies (Konvicka et al., 2003), invasive plants (Pysek et al., 2002), vertebrates (Krojerova-Prokesova et al., 2008). We expanded analyzed datasets using also invertebrate species and tested explicitly hypothesis about spatial coincidence of human population density and species richness. Moreover, we were interested to test a relationship between appropriation of aboveground net primary production (aHANPP) and species richness.

### 3.2.1. Species richness data

In the Czech Republic, there is a long tradition of biodiversity surveys for vertebrate, plant and invertebrate taxa as well. However, majority of data were available as published atlas data. Therefore, the available atlas data were synthesized (digitalized) into a GIS database of species presence in a mapping grid. The database basic mapping unit is a standard grid network of KFME (Kartierung der Flora MittelEuropas). The standard network divides the area of the Czech Republic into 676 grid squares (or quadrates/trapezoids) with slightly different area according to the latitude and longitude of a particular grid square.

Each grid square covers an area of 10' longitude and 6' latitude with the surface of approximately 133 km$^2$ (12 x 11.1 km).

Following datasets were utilized for the analysis of distribution and numbers of species richness in the Czech Republic (Table 8):

**Ground beetles (Carabidae)** (Skoupý, 2004)
Ground beetles (Carabids) are relatively well-known taxonomically and has been suggested as effective bioindicators of environmental impacts (Hůrka et al., 1995; Chobot et al., 2005).Total of 504 species of carabids has been documented on the area of the Czech Republic (Boháč, 2005). Our sample includes 244 species of carabids, i.e. nearly 50% of ground beetles recorded.

**Butterflies** (Beneš & Konvička, 2002)
Butterflies distribution are well documented at the European level and butterflies were proposed to indicate general trends in biodiversity (van Swaay et al., 2008). Our sample covers distribution of all (100%) butterfly species recorded on the area of the Czech Republic (Beneš & Konvička, 2002).

**Spiders** (Buchar & Růžička, 2002)
Spiders are used relatively scarcely as bioindicators of environmental quality. Our sample contains complete database of distribution of spiders in the Czech Republic according to Buchar & Růžička, 2002.

**Click beetles** (Elateridae) and **Longicorn beetles** (Cerambycidae) (Mertlik, 2004; Sláma, 1998).
Databases on the distribution of click and longicorn beetles has been recently made available. Datasets cover substantial part of species recorded in the Czech Republic.

**Mammals** (Anděra, 1995-2007)
Dataset on distribution of mammals in the Czech Republic includes all (100%) of mammal species recorded in the Czech Republic. Mammals are traditionally

subject of monitoring programs, including especially bat long-term monitoring network (Horáček et al., 2005).

**Amphibians and Reptiles** (Moravec et al., 1994; Mikátová et al., 2004)
Our dataset covers complete distribution of amphibians and reptiles in the Czech Republic.

**Birds** (Šťastný et al., 2006)
Birds are the best surveyed taxon due to popularity of bird watching and long-term data availability (Šťastný et al., 2005, 2006). We included only birds with proved nesting on the area of the Czech Republic (categories C and D).

**Plants** (Slavík, 1998)
We used data from Phytocartographical syntheses of the Czech Republic, compiled at the Institute of Botany of the Academy of Sciences. Considerable part of Czech flora is introduced. However, our sample cover approximately 40% of the native plants of the Czech Republic.

Data on the presence and absence of vertebrate taxa (mammals, birds, amphibians and reptiles), invertebrate taxa (butterflies, spiders, ground beetles, click beetles and longhorn beetles) and plants were summarized in GIS dataset spatially joined to the grid square layer. Therefore, the dataset contained information on estimated species richness of analyzed groups (Table 8).

We also applied a weighted species richness index (Luck et al., 2004) to account for inequitable share of species richness between different taxa. An index is calculated as:

$$Index(SR) = \frac{1}{10}\sum_{i=1}^{10}\frac{G_{SR\,i(g)}}{G_{SR\,i(t)}},$$

where $G_{i(g)}$ is the number of species of group *i* in the grid cell, and $G_{i(t)}$ is the total number of species of group *i* in a database. The index weights number of species in a grid as a proportion of the total species pool of given taxa.

**Table 8. Summary of species richness data and statistics for 10 species groups of invertebrates, vertebrates and plants in total numbers and mean grid numbers.**

| | **Total species richness** | | **Grid species richness** | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Number of species | Number of records | Range | Mean | Std. Error | Std. Deviation | Skewness | Kurtosis |
| **Invertebrates** | **1632** | **91 225** | | | | | | |
| Ground beetles (Carabidae) | 244 | 15 403 | 235.00 | 24.66 | 1.46 | 36.38 | 2.44 | 7.01 |
| Butterflies | 169 | 23 667 | 112.00 | 37.75 | 1.15 | 28.77 | 0.22 | -0.92 |
| Spiders | 830 | 34 342 | 381.00 | 54.31 | 2.80 | 69.73 | 1.81 | 3.33 |
| Click beetles (Elateridae) | 157 | 7 297 | 81.00 | 11.55 | 0.60 | 14.91 | 1.93 | 3.79 |
| Longicorn beetles (Cerambycidae) | 232 | 10 516 | 131.00 | 22.37 | 0.94 | 23.43 | 1.73 | 3.04 |
| **Vertebrates** | **330** | **86 848** | | | | | | |
| Mammals | 87 | 22 593 | 53.00 | 34.60 | 0.36 | 9.04 | -0.09 | 0.03 |
| Reptiles | 11 | 2 922 | 9.00 | 4.58 | 0.05 | 1.32 | -0.18 | 0.49 |
| Amphibians | 20 | 4 512 | 15.00 | 7.09 | 0.14 | 3.38 | 0.01 | -0.84 |
| Birds | 212 | 56 821 | 134.00 | 90.76 | 1.02 | 25.32 | -0.80 | 0.52 |
| **Plants** | **973** | **65 529** | 448.00 | 337.6 | 2.98 | 74.35 | 0.28 | -0.04 |

### 3.2.2. Gridded human population density

The examination of spatial relationship between the human population density (HPD) and biodiversity requires that comparable spatially explicit datasets be analyzed. However, population density data are usually reported in administrative census units (i.e., vector data) while biodiversity data are usually reported in a standardized gridded format. To be commensurable, the human population density dataset was transformed into standardized grid network. The dataset of human population numbers corresponding to human settlements administrative regions was transformed into the 1 km$^2$ scale and into the KFME grid, consequently. The input data on administrative unit boundaries and population numbers were used to produce gridded population density estimates showing the average number of people residing in each grid cell. The population density was modelled in GIS as an intersect function of population density dataset and grid polygon layer. That means each grid cell received an even portion of the administrative unit vector.

The gridded map of population density was created by spatial join function in GIS. Population density was calculated from the population statistics of settlements maintained by the Czech Statistical Office and administrative areas provided by the Czech Office for Surveying, Mapping and Cadastre. Table attributes of the population density were joined to the layer of administration boundaries provided and a new layer was gained form this operation. The new dataset was checked for consistency, as some areal data had not been corresponding to the real cadastre areas. New spatially-explicit dataset of human population density was then joined to KFME polygons to be comparable with biodiversity dataset. This operation was based on average population density of administrative units intersecting particular KFME grid.

### 3.2.3. Gridded aHANPP data

To calculate HANPP, three basic datasets are needed: (i) $NPP_0$ dataset of potential vegetation NPP, (ii) dataset of the NPP of actual land cover ($NPP_{ACT}$), and (iii) dataset of harvested biomass ($NPP_H$) (Haberl et al. 2007). Sample of NPP estimates from the Oak Ridge National Laboratory Distributed Active Archive Center (ORNL DAAC) NPP database (http://daac.ornl.gov/) was included in the bookkeeping NPP model integrated in GIS and supported by a geodatabase (see Chapter 3.1.1. for details). The NPP database contains documented field measurements of NPP for global terrestrial sites compiled from published literature and other extant data sources. Only NPP data corresponding to the composition of European Continental, Atlantic and Boreal vegetation had been selected. The raw NPP dataset generated by searching the ORNL datasets was biased towards the boreal forests data. Therefore, data were revised using especially temperature where available to remove outlier and non-representative NPP values. Boreal NPP values were retained only for vegetation in corresponding climatic conditions (e.g. mountains). The dataset was also checked with Cannel´s data on world forest biomass and primary production (Haberl et al., 2001). The ORNL DAAC NPP datasets were complemented by the search for other studies which reported NPP values for natural or anthropogenic ecosystem types. Where reported in different units, data were transformed into grams of carbon per square meter ($g\ C\ m^{-2}$) using the coefficient 0.475 for the calculation of average carbon content in organic matter, based on the average carbon content extracted from the available ORNL database records.

We calculated aHANPP separately for each grid cell in our dataset. Values on potential natural aboveground net primary production (aNPP), actual aNPP, harvested aNPP equivalent, amount of aNPP remaining in ecosystems, aNPP changes induced by land cover change and the percentage aHANPP in a grid cell were included. Aboveground HANPP for each grid square ($aHANPP_G$) was calculated as a ratio of aNPP remaining in ecosystems in a grid square ($aNPP_{TG}$) and the productivity of aboveground potential natural vegetation ($aNPP_{0G}$):

$$aHANPP_G\ (\%) = \left[1 - \left(aNPP_{T_G} / aNPP_{0_G}\right)\right] \times 100 .$$

Potential natural primary productivity was estimated according to distribution of 51 vegetation classes complemented by NPP data extracted from different sources. Actual aNPP was calculated based on Corine Land Cover information and estimates of actual aNPP values, using harvest indices on agricultural land and biomass expansion factors on forest land.

### 3.2.4. Landscape diversity data

Landscape diversity was calculated on the basis of Corine Land Cover (CLC) data for the year 2000. The basic aim of the CLC database is to provide an inventory of the Earth surface features for managing the environment (EEA, 2006). The approach of computer aided visual interpretation of satellite images have been chosen as mapping methodology. The basic choices of scale 1:100 000, minimum mapping unit (MMU) of 25 hectares and minimum width of linear elements 100 metres represent a trade-off between cost and detail of land cover information. The standard CLC nomenclature includes 44 land cover classes, from which 30 occurs on the area of the Czech Republic (Table 9). The CLC nomenclature is discriminated mainly by physiognomic attributes (shape, size, colour and pattern) of landscape objects (natural, modified – cultivated and artificial), as recorded on satellite images. Artificial surfaces and agricultural areas are also discerned by functional attributes and are related to land use.

The landscape diversity index was calculated according to the Shannon-Wiener information diversity formula. The Shannon Landscape Diversity Index (SHLDI) quantifies the diversity of the countryside based on two components: the number of different patch types and the proportional area distribution among patch types. Commonly the two components are named richness and evenness. Richness refers to the number of patch types (compositional component) and evenness to the area distribution of classes (structural component). The Shannon Index is calculated by adding for each patch type present the proportion of area covered, multiplied by that proportion expressed in natural logarithm, according to the formula:

$$SHLDI = -\sum_{i=1} CLC_i \ln pCLC_i ,$$

where $pCLC_i$ represents a proportion of land cover category $i$ from the sample of land cover categories present in a given grid. SHLDI increases as the number of different land cover classes increases and/or the proportional distribution of the area among patch types becomes more equitable. For a given number of classes, the maximum value of the SHLDI is reached when all classes have the same area. The following examples try to illustrate the influence of richness and evenness on the index.

**Table 9. Corine Land Cover categories for the area of the Czech Republic, which were used for the calculation of aHANPP and Landscape Diversity Index. Values of aNPP are summarized in a table, for explanation see text.**

| CLC code | CLC class | aNPP (g C $m^2$ yr) | Area (ha) | | |
|---|---|---|---|---|---|
| | | | CLC1990 | CLC2000 | CLC2006 |
| **111** | Continuous urban fabric | 0 | 1 464 | 1 464 | 1 567 |
| **112** | Discontinuous urban fabric | 278.45 | 357 850 | 362 585 | 377 384 |
| **121** | Industrial or commercial units | 0 | 52 120 | 54 773 | 59 935 |
| **122** | Road and rail networks and associated land | 0 | 4 807 | 5 273 | 6 253 |
| **123** | Port areas | 0 | 150 | 150 | 79 |
| **124** | Airports | 207 | 5 609 | 5 627 | 5 610 |
| **131** | Mineral extraction sites | 0 | 18 063 | 17 102 | 16 203 |
| **132** | Dump sites | 0 | 15 461 | 13 887 | 9 531 |
| **133** | Construction sites | 0 | 2 124 | 858 | 1 793 |
| **141** | Green urban areas | 539.12 | 6 526 | 6 555 | 6 620 |
| **142** | Sport and leisure facilities | 398.1 | 11 771 | 12 733 | 15 564 |
| **211** | Non-irrigated arable land | 412.09 | 3 554 095 | 3 262 160 | 3 010 914 |
| **221** | Vineyards | 178 | 11 077 | 11 942 | 15 767 |
| **222** | Fruit trees and berry plantations | 303.3 | 32 821 | 32 644 | 30 644 |
| **231** | Pastures | 325.58 | 252 762 | 531 705 | 700 797 |
| **242** | Complex cultivation | 292.37 | 41 534 | 42 954 | 47 441 |
| **243** | Land principally occupied by agriculture, with significant areas of natural vegetation | 360.77 | 673 617 | 674 768 | 706 699 |
| **311** | Broad-leaved forest | 545 | 249 524 | 252 740 | 278 240 |
| **312** | Coniferous forest | 530 | 1 655 186 | 1 699 256 | 1 722 050 |
| **313** | Mixed forest | 567 | 585 494 | 604 224 | 617 029 |
| **321** | Natural grassland | 219.21 | 40 464 | 39 204 | 27 051 |
| **322** | Moors and heathland | 140.48 | 2 652 | 2 739 | 1 823 |
| **324** | Transitional woodland shrub | 354.49 | 248 635 | 186 941 | 160 430 |
| **332** | Bare rock | 0 | 210 | 210 | 150 |
| **334** | Burnt areas | 0 | 117 | 116 | 115 |
| **411** | Inland marshes | 707.16 | 5 354 | 5 336 | 6 145 |
| **412** | Peatbogs | 192.1 | 3 750 | 3 711 | 4 223 |

### 3.2.5. Data analysis

Data for the analysis were transformed into the spatially-explicit dataset in GIS (ESRI ArcInfo 9.3). Only quadrates containing at least 75 % of the area of the Czech Republic were included in the analysis; quadrates outside the border with lower proportion have been removed from the dataset as they frequently included zero values of species richness and human population density. Total of 560 grid squares was included in the analysis. As majority of datasets was skewed, especially the human population density dataset, all data were log-transformed prior to the analysis. Before the log-transformation, we added the incremental value 1 to zero values in the dataset to make the log-transformation possible.

Pairwise Spearman´s rank correlation coefficients ($r_S$) were calculated for human population density and species richness of different taxa, including invertebrates, vertebrates, plants and all species combined. SPSS for Windows, Version 12.0.1 was used for statistical analysis of data. Correlation measures the amount of association between two variables (Quinn & Keough, 2002). Therefore, we were interested to determine whether human population density and species richness are interdependent or covary. Correlation coefficient detects possible linearity between examined variables. In other words, correlation analysis tests monotonic relationship between variables. Regression establishes a relationship where we want to determine predictor and response variable. The relationship between correlation and regression is more discussed in Chapter 5.2.

# 4. Results

## 4.1. Human appropriation of aboveground net primary production

The potential natural aboveground net primary production ($aNPP_0$) is determined as 38 Tg C (Tera grams of carbon or $38 * 10^{12}$ grams of carbon) per year. The highest productivity of forest habitat types is reached in alluvial woodlands (Figure 4). However, beech woodlands contribute most to the overall productivity, as they occupy the largest area. The most productive environments are also those with the most variable parameters, reflecting also the small sample size. Productivity of pine and spruce natural vegetation is significantly lower than production of managed coniferous forests. Natural conifers in the Czech Republic are limited to mountainous, rocky, waterlogged and other extreme stands. Therefore, they are not as productive as managed coniferous forests replacing natural broadleaved stands.

The actual aboveground net primary production ($aNPP_{ACT}$) reaches ~34 Tg C (Figure 5). According to our results for years 1990, 2000 and 2006 the $NPP_{ACT}$ was relatively stable, reaching 34.1 Tg C and 33.9 Tg C, respectively (Figure 6). The actual primary production is dominated by non-irrigated arable land (15.6 Tg C), followed by coniferous forests (8.4 Tg C). Together, these dominant land uses contribute 66 % to the total actual aboveground primary productivity. Other land cover classes significantly contributing to the actual production are also linked to the agricultural and forestry production, especially mixed forests and agricultural mosaic with natural fragments. The most productive ecosystems are wetlands with 707 g C $m^{-2}$. Wetlands replacing other land uses contribute negatively to aHANPP, i.e. productivity is increased relative to natural state.

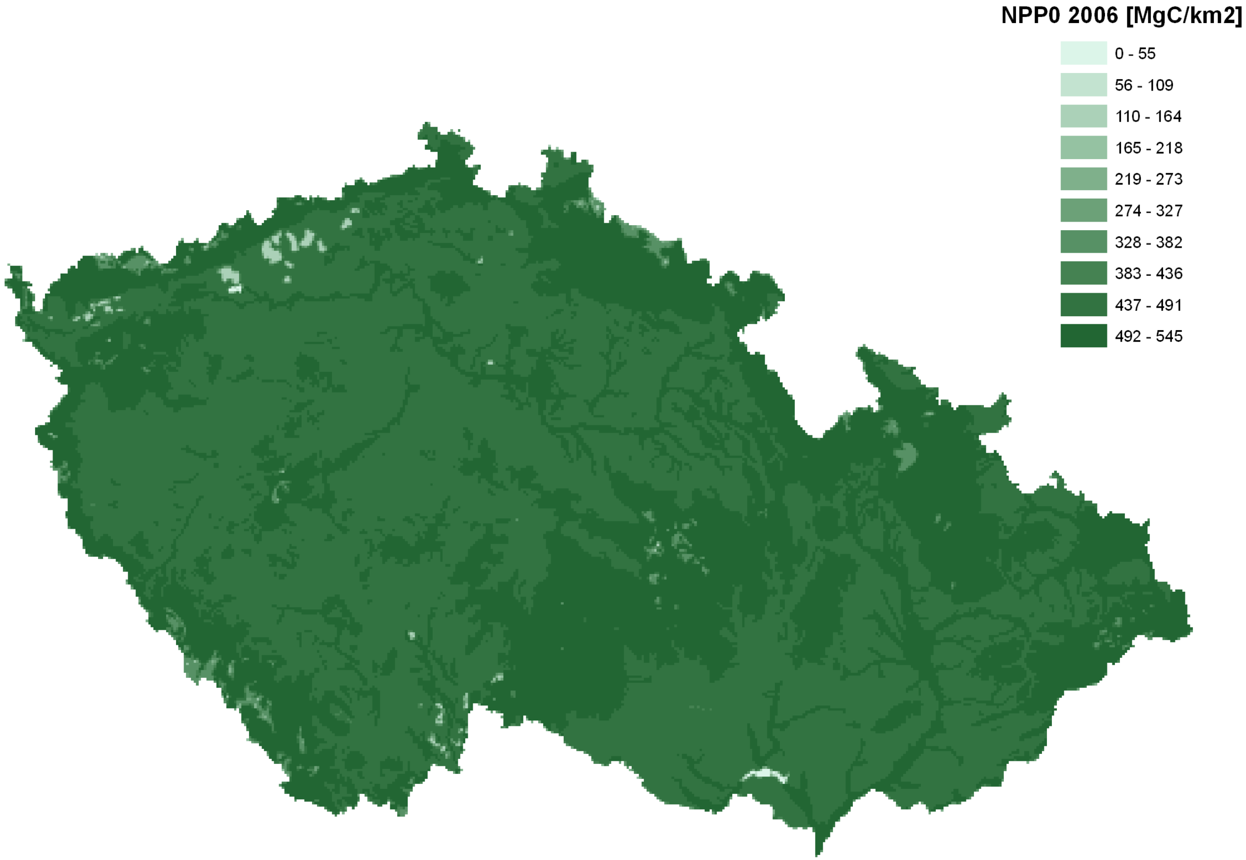

**Figure 4. Potential natural aboveground primary productivity (aNPP$_0$) for the Czech Republic. Places with low productivity (white colour) are water bodies or antropogenically influenced sites (e.g. coal mining).**

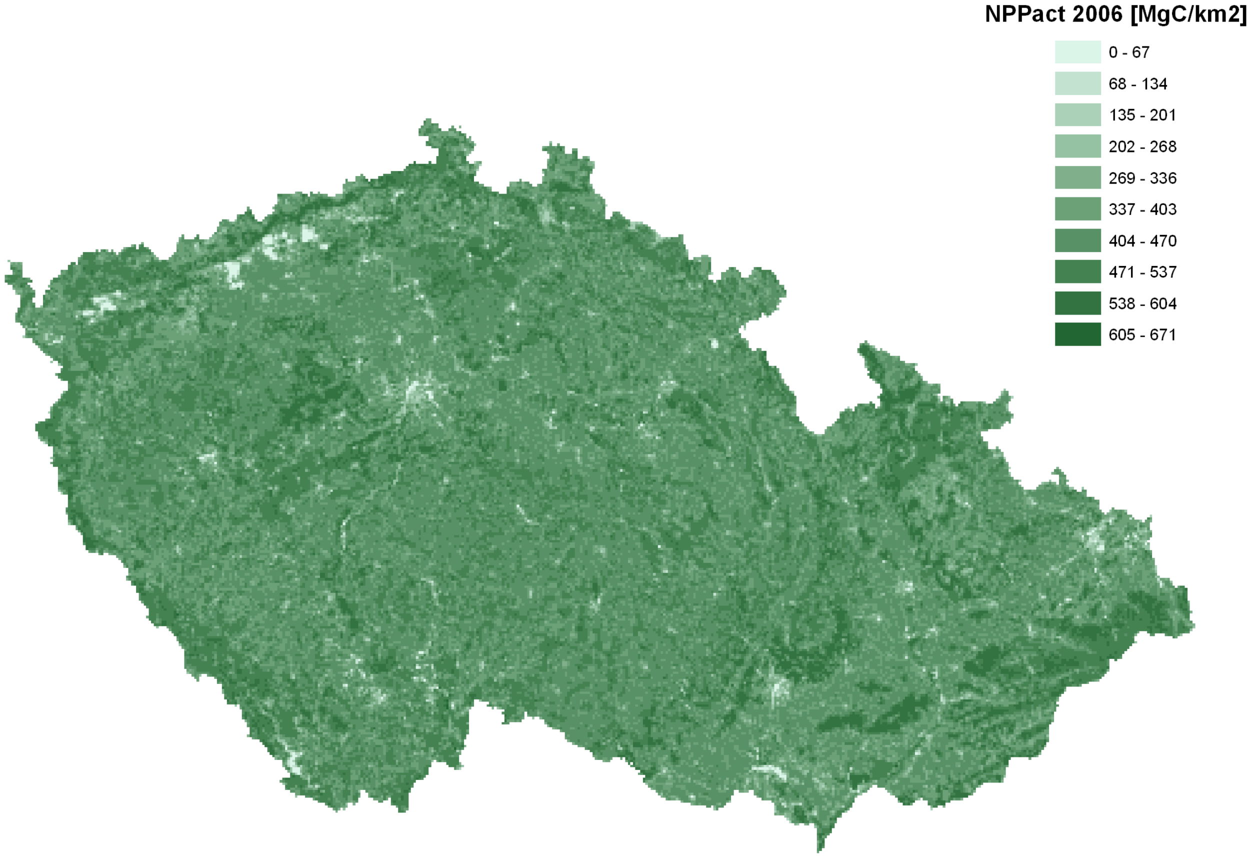

**Figure 5. Actual aboveground net primary production (aNPP$_{ACT}$) in the Czech Republic for the year 2006. Low productivity values are water bodies, urbanized areas and other anthropogenic sites significantly influenced by human activities.**

Human appropriation of aboveground net primary production (aHANPP) reached 55.16% in a cultural central-European landscape in the year 2000 and 56.4% in the year 2006 (Figure 7). This number reflects loss of productive capacity generated by natural ecosystems stock due to conversion to a mixture of cultural landscape types ($\Delta aNPP_{LC}$= 4.1 Tg C) (Figure 8) and harvest of biomass taking into account recovery rates ($aNPP_{H}$= 16.9 Tg C) (Figure 9). In aggregate, people have appropriated 21 Tg C annually in the Czech Republic while 17.1 Tg C (or amount corresponding to harvested NPP equivalent) remains in ecosystems (Figure 10). In other words, 10.8% of aNPP appropriation can be attributed to land conversion from natural vegetation to actual land cover ($\Delta aNPP_{LC}$) and harvesting of actual ecosystems is responsible for 44.2% of aNPP appropriation.

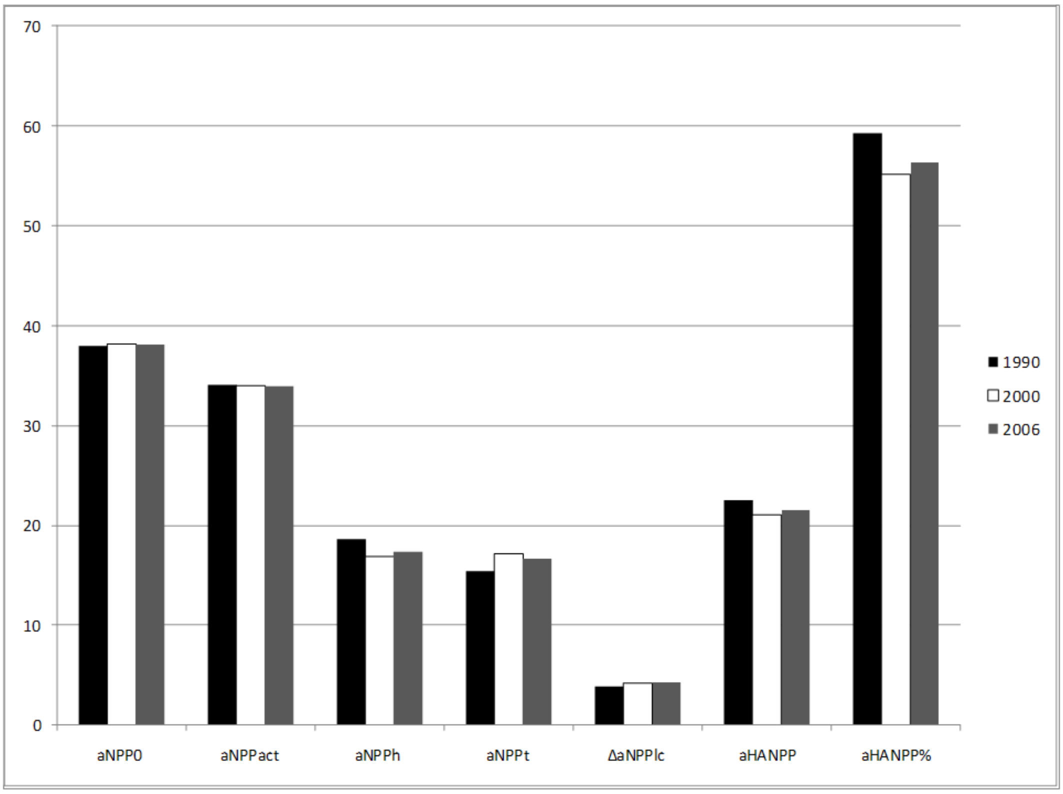

**Figure 6. Components of aHANPP for time horizons 1990, 2000 and 2006. Total aHANPP (%) decreased between 1990 and 2000 and slightly increased in 2006 to 56.4 %. Components of aHANPP are reported in Tg C $yr^{-1}$. In absolute terms, aHANPP of 55 % corresponds to 21 Tg C per year.**

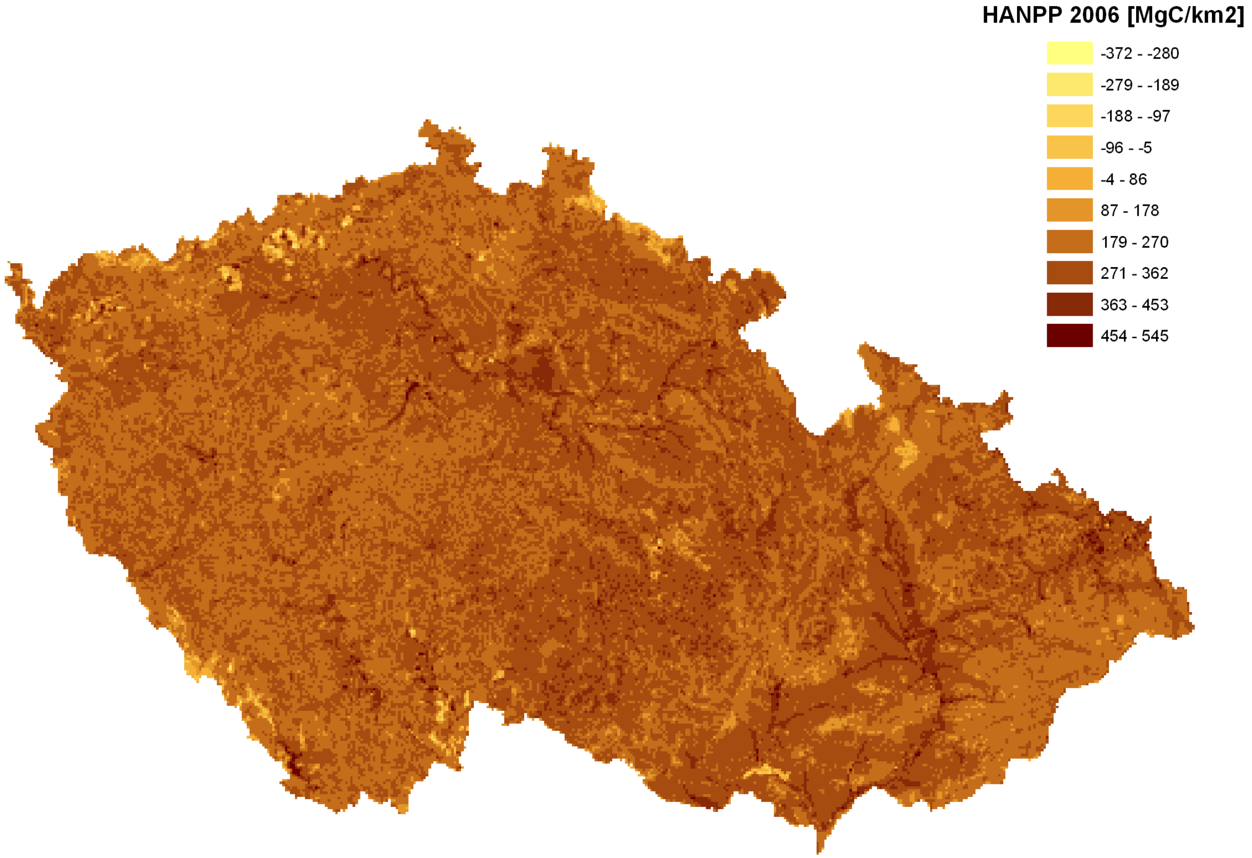

**Figure 7. Aboveground HANPP in the Czech Republic, 2006. Water bodies have no actual productivity and together with urbanized areas, these types of land conversion contribute maximally to the overall aHANPP.**

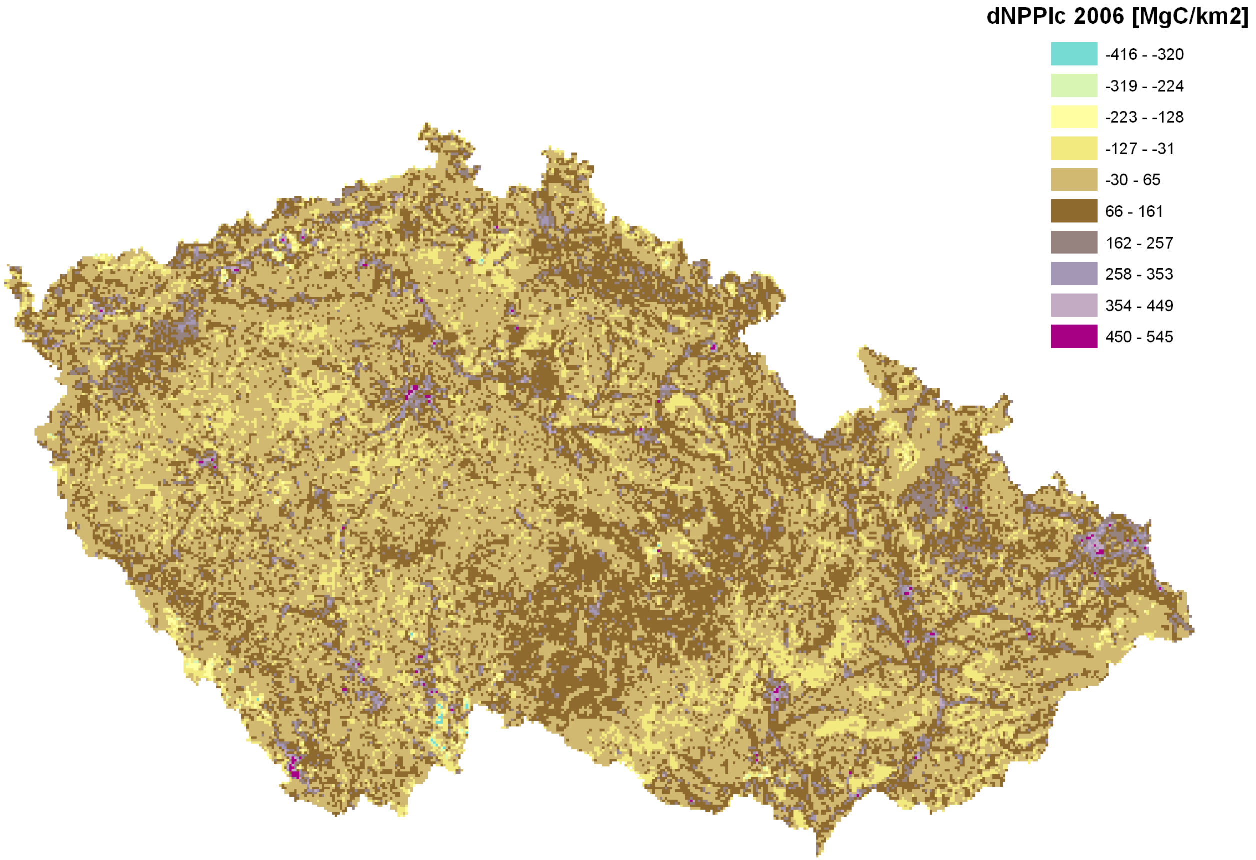

**Figure 8. Land conversion is a process contributing to the overall HANPP. Measure of $\Delta aNPP_{LC}$ express the amount of aNPP lost due to human induced land conversion. While urbanization and water reservoir building decreases available aNPP, managed forests and some agricultural areas increase available aNPP (negative values of $\Delta aNPP_{LC}$ on the map).**

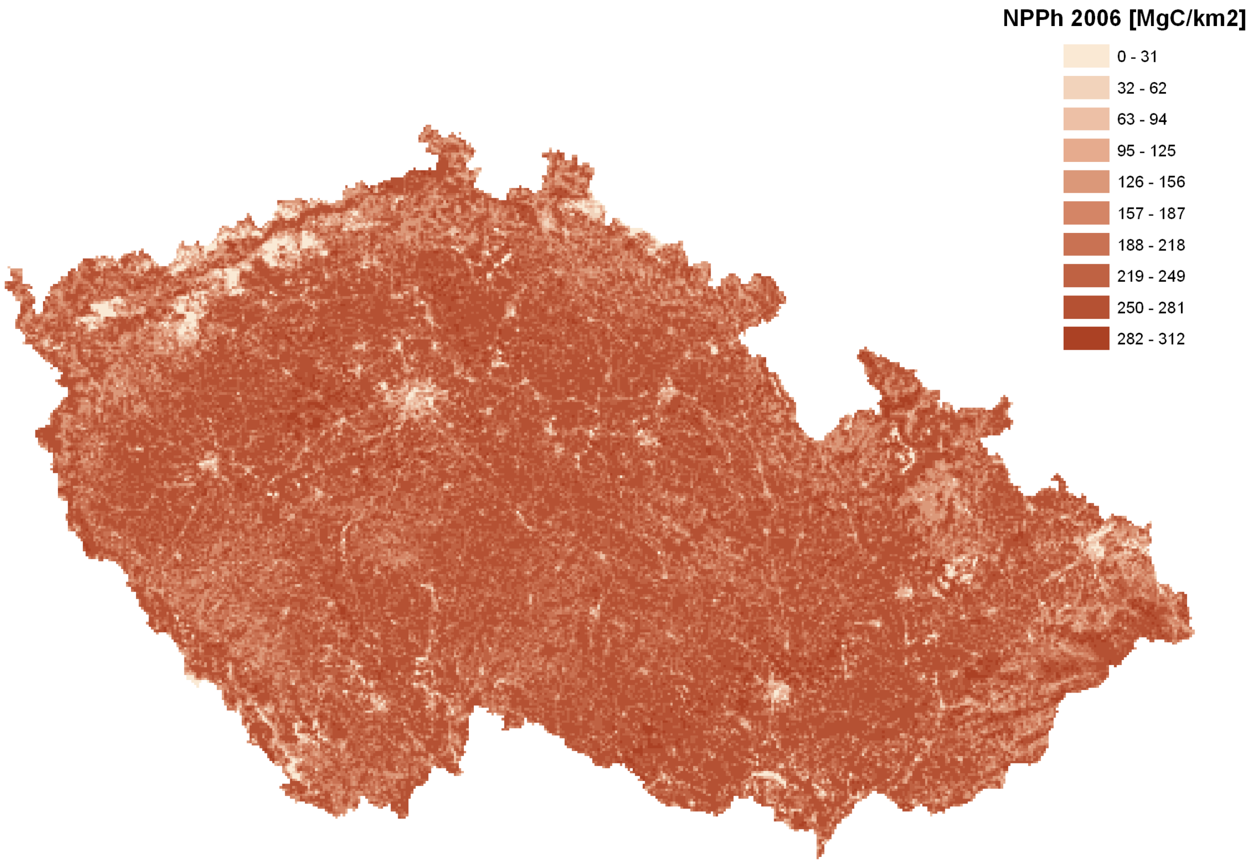

**Figure 9. Harvested aNPP equivalent ($NPP_h$), or NPP equivalent of harvested biomass, is distributed mainly on agricultural and forest land.**

**Figure 10. NPPt describes the amount of aNPP remaining in ecosystems after land conversion and harvest. aNPPt is besing considered as an indicator of energy available for biodiversity and natural processes.**

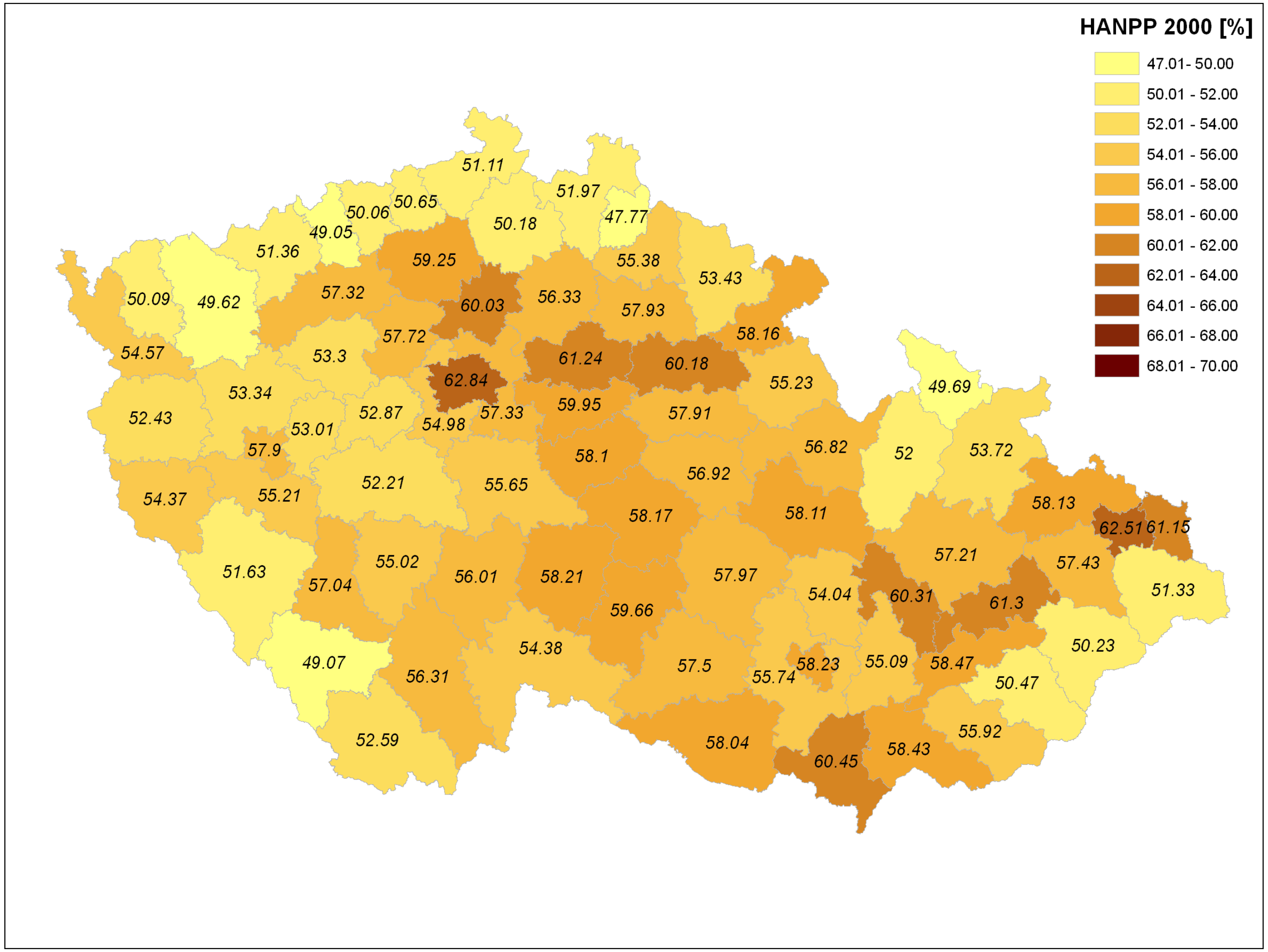

**Figure 11. HANPP values for Czech regions. Highest values are achieved in urbanized regions, while lowest values of aHANPP are typical especially for border regions with low population density.**

Concerning the aHANPP change during the period 1990 – 2006, aHANPP reached highest levels in 1990, declined in 2000 and slightly raised again in 2006 (Figure 6). Harvested NPP equivalent is mainly responsible for this trends, with 18.58 Tg C of NPP equivalent harvested annually in 1990, 16.9 Tg C in 2000 and 17.3 Tg C in 2006. The agricultural harvest dominates harvested biomass and it declined from 13.3 Tg C in 1990 to current level of 9.7 Tg C. This decline is partially attributable to decline of feed requirements of livestock. Meat system currently appropriates 4.6 Tg C according to dry matter requirements of livestock but in 1990 this appropriation amounted to 7.9 Tg C. However, decreasing agricultural output contributed to increased aHANPP on pastures. Decline in agricultural production has been also partially balanced by growth of forest aNPP equivalent harvest by 2.25 Tg C during the period 1990-2006. We also mapped patterns of aHANPP in Czech regions (Figure 11). Highest appropriation is reached in extensive urban agglomerations (Prague, Ostrava) and in regions with high proportion of agricultural land. Regions with high forest cover and low population density reach lower aHANPP values.

Results disaggregated according to land cover types reveal considerable human impact on ecosystems (Table 10). Built-up areas and infrastructure appropriate 100% of potential productivity as they provide minimal natural production functions. Exceptions from artificial habitats are discontinuous urban fabric, airports, green urban areas and sport and leisure facilities which contain remnants of productive surfaces (e.g. lots planted with exotic species, lawns, and trees). aHANPP on agricultural land exceeds 60% and even approaches 70% in intensively used land classes, including arable land and complex cultivation (Table 10). Agricultural land with significant areas of natural vegetation has relatively lower HANPP of 44% which reflects more extensive use of land. The aHANPP in forests oscillates around 40% of NPP appropriated by humans and is comparable between forest categories. Within forest categories, lowest aHANPP can be attributed to mixed forests while highest to broad-leaved forests.

HANPP in the forest and semi-natural land category is increased especially by transforming the natural forest into semi-natural grasslands, moors and heathlands, and by wood biomass harvesting. Forest planting increased aNPP per unit of area by 7 – 16 % in comparison with potential natural NPP. Harvest of aNPP equivalent from broad-leaved forests more than doubled while the area raised only slightly. This is reflected by

44% HANPP for broad-leaved forests while traditionally intensively managed coniferous forests reach the equivalent aHANPP of 43%. Also the harvest in coniferous and mixed forests increased by 1.5 Tg C and 0.4 Tg C, respectively. Together, forest aNPP harvest equivalent increased from 4.9 Tg C in 1990 to 7.1 Tg C in 2006, reflecting increasing demand on forests. Semi-natural habitats (natural grassland, moors and heathland, peatbogs) are not intensively harvested but contribute to HANPP as habitats converted from forest cover.

By overlapping the layers of the potential natural NPP and the actual NPP we were able to calculate the estimate of the NPP changes induced by land conversion ($\Delta aNPP_{LC}$) (Figure 8). The urbanization and land sealing are responsible for the maximal HANPP of 100% where zero natural productivity remains in ecosystem. However, some intensively managed areas can outperform the natural communities in productivity terms, such as green urban areas and sport and leisure facilities. The $\Delta aNPP_{LC}$ term can achieve negative terms, which means an increase of NPP in comparison with the natural potential vegetation. In aggregate, the green urban areas increase productivity by 11% in comparison with potential natural NPP expected on areas covered by green urban surfaces. While urban development takes land with highest potential productivity (~ 500 g C $m^{-2}$), mineral extraction sites and dump sites could occupy naturally less productive land (330-350 g C $m^{-2}$).

**Table 10. Aboveground HANPP (aHANPP) components for detailed Corine Land Cover classes, Czech Republic, 2006. Data are reported in Mg C per year or per area. Negative values are interpreted as enhancement of aNPP in comparison with potential natural state.**

| Code CLC | CLC class | $aNPP_0$ | $aNPP_{ACT}$ | $aNPP_H$ Mg C | $aNPP_T$ | $\Delta aNPP_{LC}$ | HANPP | HANPP Mg C/km$^2$ | HANPP % |
|---|---|---|---|---|---|---|---|---|---|
| **111** | Continuous urban fabric | 7 928 | 0 | 0 | 0 | 7 928 | 7 928 | 506 | 100 |
| **112** | Discontinuous urban fabric | 1 821 773 | 1 050 827 | 350 276 | 700 551 | 770 946 | 1 121 222 | 297 | 62 |
| **121** | Industrial or commercial units | 291 204 | 0 | 0 | 0 | 291 204 | 291 204 | 486 | 100 |
| **122** | Road and rail networks and | 29 837 | 0 | 0 | 0 | 29 837 | 29 837 | 477 | 100 |
| **123** | Port areas | 429 | 0 | 0 | 0 | 429 | 429 | 545 | 100 |
| **124** | Airports | 26 620 | 11 613 | 0 | 11 613 | 15 007 | 15 007 | 267 | 56 |
| **131** | Mineral extraction sites | 56 883 | 0 | 0 | 0 | 56 883 | 56 883 | 351 | 100 |
| **132** | Dump sites | 33 646 | 0 | 0 | 0 | 33 646 | 33 646 | 353 | 100 |
| **133** | Construction sites | 8 504 | 0 | 0 | 0 | 8 504 | 8 504 | 474 | 100 |
| **141** | Green urban areas | 32 226 | 35 689 | 17 845 | 17 845 | -3 463 | 14 381 | 217 | 45 |
| **142** | Sport and leisure facilities | 73 533 | 61 959 | 30 980 | 30 980 | 11 574 | 42 554 | 273 | 58 |
| **211** | Non-irrigated arable land | 14 352 779 | 12 407 676 | 7 834 366 | 4 573 310 | 1 945 103 | 9 779 469 | 325 | 68 |
| **221** | Vineyards | 72 482 | 28 066 | 4 460 | 23 606 | 44 417 | 48 877 | 310 | 67 |
| **222** | Fruit trees and berry plantations | 142 658 | 92 944 | 21 258 | 71 686 | 49 714 | 70 972 | 232 | 50 |
| **231** | Pastures | 3 450 231 | 2 281 655 | 897 776 | 1 383 879 | 1 168 576 | 2 066 351 | 295 | 60 |
| **242** | Complex cultivation | 225 182 | 185 256 | 123 440 | 61 816 | 39 926 | 163 366 | 344 | 73 |
| **243** | Land principally occupied by | 3 462 620 | 2 946 934 | 905 336 | 2 041 598 | 515 686 | 1 421 022 | 201 | 41 |
| **311** | Broad-leaved forest | 1 351 083 | 1 516 410 | 717 249 | 799 161 | -165 327 | 551 921 | 198 | 41 |
| **312** | Coniferous forest | 8 510 666 | 9 126 863 | 4 567 975 | 4 558 888 | -616 197 | 3 951 778 | 229 | 46 |
| **313** | Mixed forest | 3 004 663 | 3 498 552 | 1 825 273 | 1 673 278 | -493 889 | 1 331 385 | 216 | 44 |
| **321** | Natural grassland | 129 405 | 59 298 | 0 | 59 298 | 70 107 | 70 107 | 259 | 54 |
| **322** | Moors and heathland | 5 358 | 2 561 | 0 | 2 561 | 2 797 | 2 797 | 153 | 52 |
| **324** | Transitional woodland shrub | 747 378 | 568 708 | 0 | 568 708 | 178 671 | 178 671 | 111 | 24 |
| **332** | Bare rock | 551 | 0 | 0 | 0 | 551 | 551 | 368 | 100 |
| **333** | Sparsely vegetated areas | 349 | 0 | 0 | 0 | 349 | 349 | 303 | 100 |
| **411** | Inland marshes | 27 479 | 43 453 | 0 | 43 453 | -15 975 | -15 975 | -260 | -58 |
| **412** | Peatbogs | 14 744 | 8 113 | 0 | 8 113 | 6 631 | 6 631 | 157 | 45 |
|  | **Total** | 37 880 208 | 33 926 576 | 17 296 233 | 16 630 342 | 3 953 633 | 21 249 866 | 271 | 56 |

## 4.2. Human pressures and biodiversity

I found significant spatial correlations between majority of species groups and human population density (Figure 12; Table 13). Results give indications of possible interdependence and monotonic relationships between HPD and biodiversity. Therefore, we cannot reject a hypothesis about a positive spatial relationship between human population density and species richness. The patterns of spatial coincidence between people and biodiversity ($r_s$ = 0.361), measured as combined species richness of 10 analyzed groups are comparable to European-scale studies (Araújo, 2001). The highest association was found between HPD and the species richness of carabid ground beetles ($r_s$ = 0.430) (Figure 13) and plants ($r_s$ = 0.375) (see Tables 13, 14 and 15 for summary of results on the correlations between HPD and species richness and Fig. 12 for graphical presentation of the relationship based on combined species richness). When we calculated weighted species richness index, the correlation is slightly weaker for species richness combined ($r_s$ = 0.275).

For reptiles, spiders and birds, we didn´t found significant coincidence with people (Figure 14). Mammals are negatively correlated with human population density ($r_s$ = -0.126). When we assessed patterns of coincidence of combined invertebrate species richness and vertebrate species richness, these show weak correlation with human population densities and interdependencies are rather specific for taxonomic groups (Table 13). Similar patterns are found for correlations between landscape diversity index (SHLDI) and species richness. Majority of groups is positively correlated with landscape diversity, besides mammals and birds. Vertebrates in aggregate show no relationship with landscape diversity. Spiders and click beetles are most strongly related to the extent of protected areas. Reptiles, which distributions like spiders do not overlap with human population density, are also significantly correlated with protected areas.

Of special interest is also the spatial coincidence of different taxa among each other. Combined species richness and SRIndex perform equivalently in describing spatial congruence of species richness, but for reptiles, amphibians and longhorn bettles, SRIndex gives better spatial overlap. Mammals are not spatially related to any other group and birds doesn´t follow the distribution of some invertebrate groups. Plants coincide with majority of other species groups and with HPD as well (Figure 15).

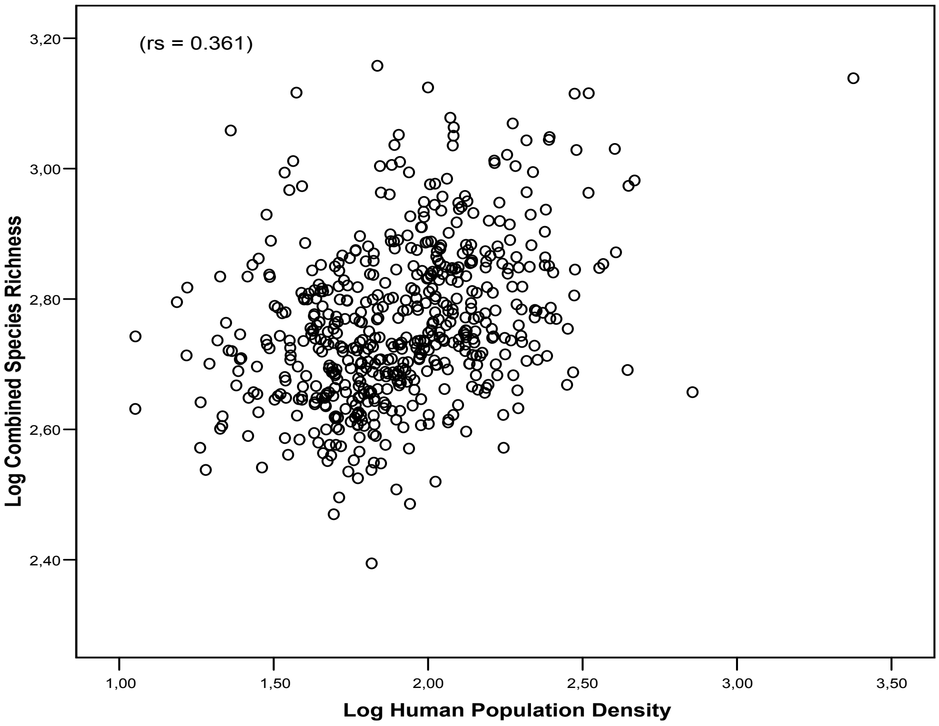

**Figure 12. The relationship between $\log_{10}$ Human Population Density and $\log_{10}$ Combined Species Richness. Results are reported for a sample of N=560 grid cells.**

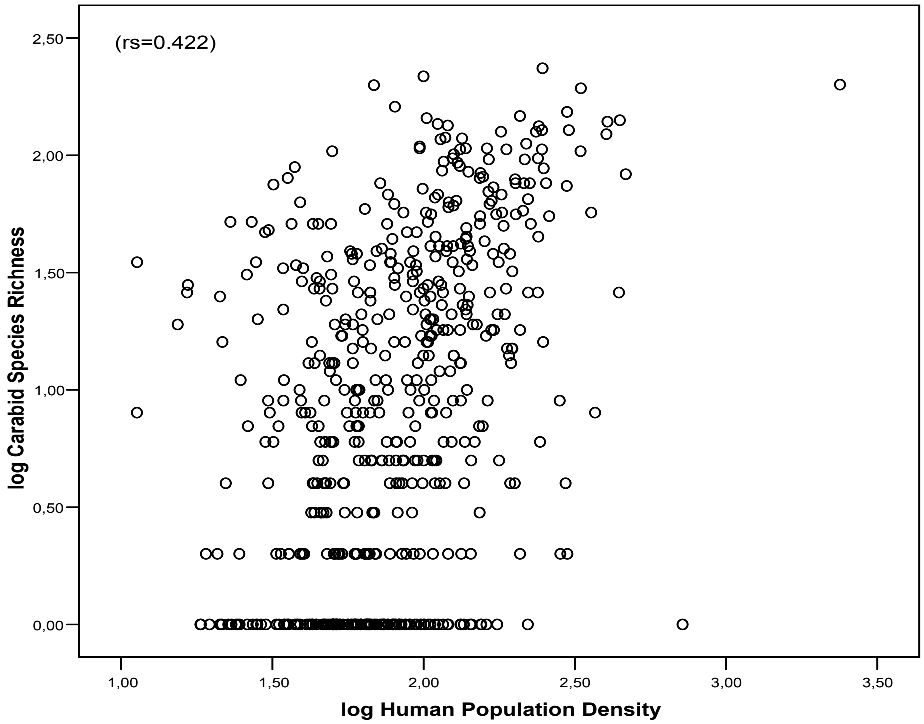

**Figure 13. Relationship between $\log_{10}$ Human Population Density and $\log_{10}$ Carabid (ground beetles) Species Richness. Results are reported for a sample of N=560 grid cells.**

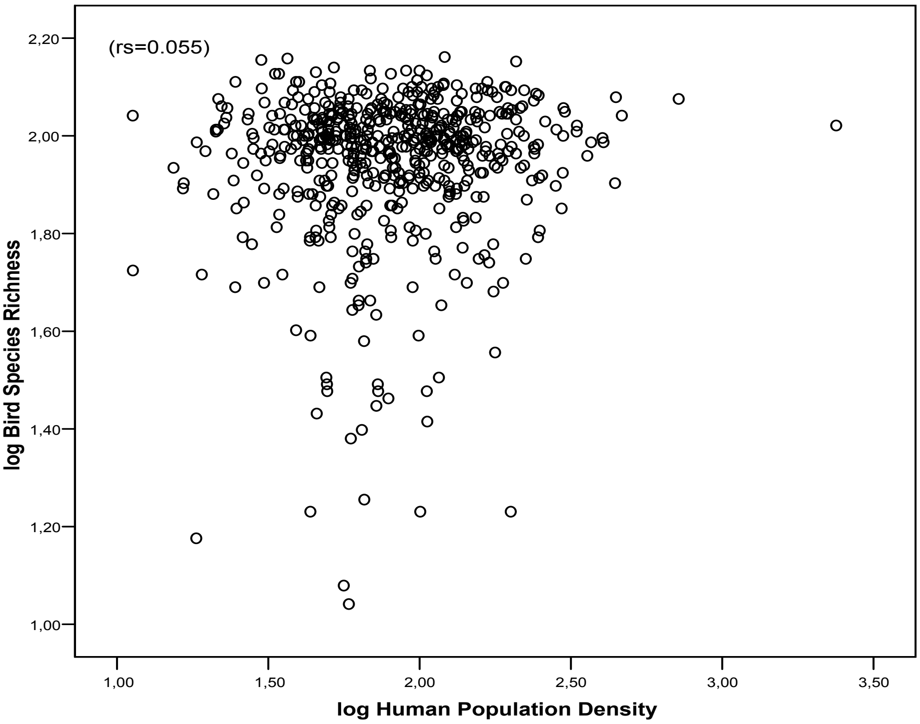

**Figure 14. Relationship between log$_{10}$ Human Population Density and log$_{10}$ Bird Species Richness. Results are reported for a sample of N=560 grid cells.**

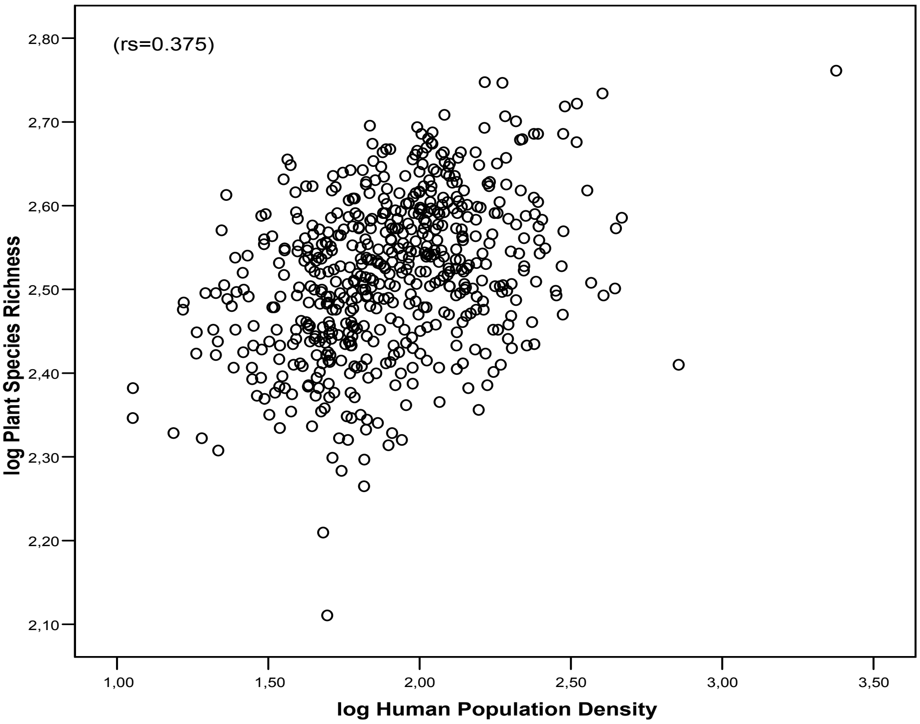

**Figure 15. Relationship between log$_{10}$ Human Population Density and log$_{10}$ Plant Species Richness. Results are reported for a sample of N=560 grid cells.**

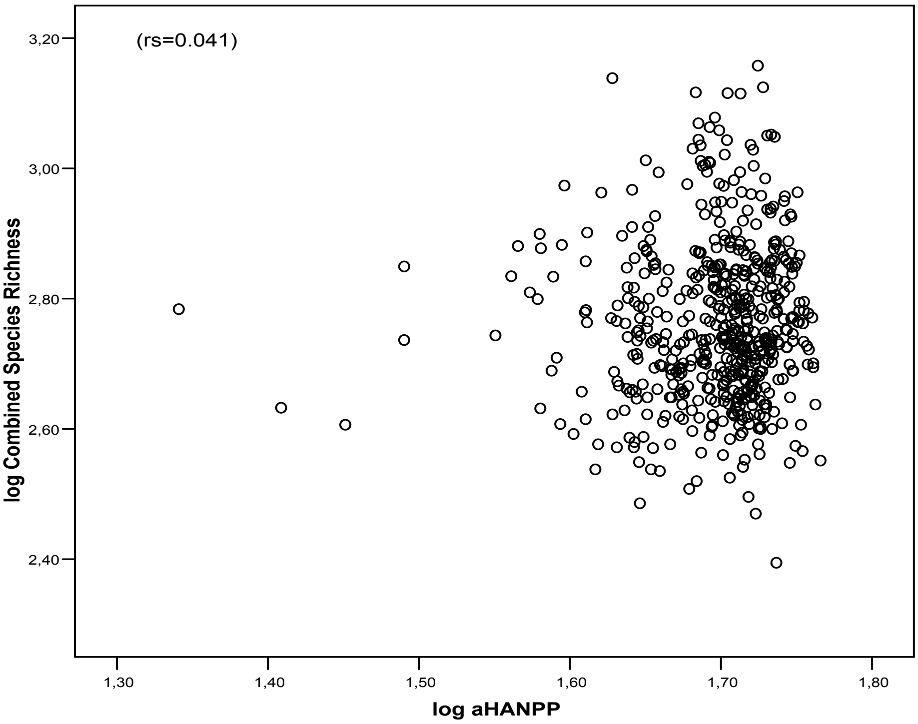

**Figure 16. Relationship between $\log_{10}$ aHANPP (Human Appropriation of Aboveground Net Primary Production) and $\log_{10}$ Combined Species Richness. Results are reported for a sample of N=560 grid cells.**

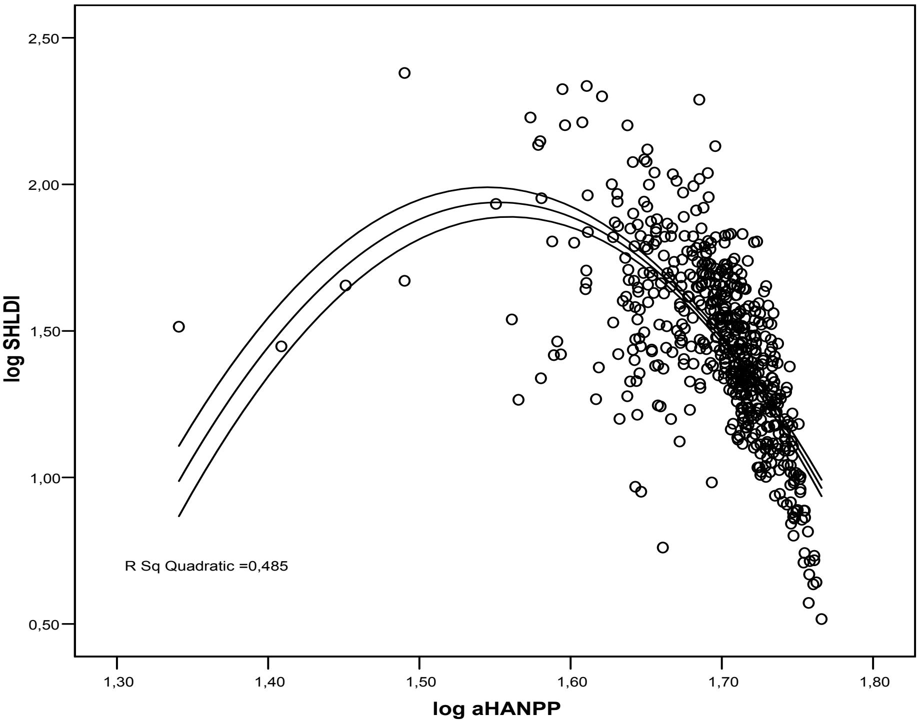

**Figure 17. Relationship between $\log_{10}$ aHANPP (Human Appropriation of Aboveground Net Primary Production) and $\log_{10}$ Shannon Landscape Diversity Index (SHLDI). $R^2$ and 95% confidence intervals are based on a sample of N=560 grid squares.**

Human appropriation of aboveground net primary production (aHANPP) was negatively correlated (weakly but significantly) with weighted species richness index ($r_s = -0.146$) but not with CSR (Figure 16). Concerning the relationships with particular groups, aHANPP was negatively correlated especially with the species richness of reptiles and spiders. Positive correlation was achieved for plants, birds, and amphibians (Table 14). Distribution of other groups was not related to land and ecosystem use intensity. However, the pattern most pronounced in the results is a negative correlation between aHANPP and landscape diversity index (SHLDI) ($r_s = -0.7$). Therefore, I fitted a regression model describing relationship between aHANPP and landscape diversity (Figure 17). While linear model gives relatively sufficient fit, I estimated also quadratic (curvilinear) model which gives better estimation of the pattern. Comparison of linear and quadratic model parameters is given in Table 11. The quadratic model better corresponds to underlying hypothesis about human use and biodiversity (see Chapter 5 for discussion). I didn´t find appropriate strong and unbiased model describing the relationship between combined species richness and aHANPP (Figures 18, 19).

The linear relationship between aHANPP and SHLDI can be expressed by an equation ($R^2 = 0.327$):
$SHLDI = 7.930 – (3.819 * aHANPP)$.

Quadratic equation gives better estimate than linear model ($R^2=0.485$) and can be expressed as:
$SHLDI = - 49.427 + (66.185 * aHANPP) – (21.32 * aHANPP^2)$.

Statistical tests (ANOVA $F$ test and $t$ test) cause us to reject the null hypothesis that coefficient $\beta$ equals zero. The relationship between $F$ (270.57) and t (-16.449) in a linear model is $F = t^2$. The $r^2$ value of 0.327 in a linear model and 0.485 in a quadratic model denotes the amount of variance explained by the model (Quinn & Keough, 2002). To test results we ran ordinary least square regression (OLS) in ArcGIS environment (ESRI ArcInfo 9.3) and compared outputs to geographically weighted regression (GWR). The OLS results are same as in linear regression model. However, GWR results are biased due to spatial autocorrelation of geographic data, i.e. output feature class residuals are not randomly distributed (Figure 20).

**Table 11. Comparison of linear and quadratic regression model for aHANPP as independent variable and SHLDI as dependent variable. Quadratic model provides better fit as measured by R squared. Quadratic model also corresponds to underlying intermediate disturbance hypotheses.**

```
LINEAR model
Multiple R         0.57145
R Square           0.32655
Adjusted R Square    0.32535
Standard Error       0.25093

Analysis of Variance:
             DF   Sum of Squares      Mean Square
Regression       1       17.037099       17.037099
Residuals      558       35.135353         0.062967

F =     270.57366      Signif F =  0.00001

 Variables in the Equation:

Variable               B               SE B       Beta        T        Sig T
aHANPP          -3.819044     0.232173   -0.571449 -16.449  0.00001
(Constant)        7.929869     0.393924                     20.130    0.00001

QUADRATIC model
Multiple R          0.69646
R Square            0.48505
Adjusted R Square    0.48320
Standard Error       0.21962

Analysis of Variance:

             DF   Sum of Squares      Mean Square
Regression       2       25.306263       12.653131
Residuals      557       26.866190         0.048234

F =     262.32950      Signif F =  0.00001

Variables in the Equation:

Variable               B                SE B      Beta              T       Sig T
aHANPP           66.185701    5.350392   9.903453     12.370  0.00001
aHANPP**     -21.320427    1.628323 -10.482465   -13.093  0.00001
(Constant)     -49.427136    4.394122                     - 11.248 0.00001
```

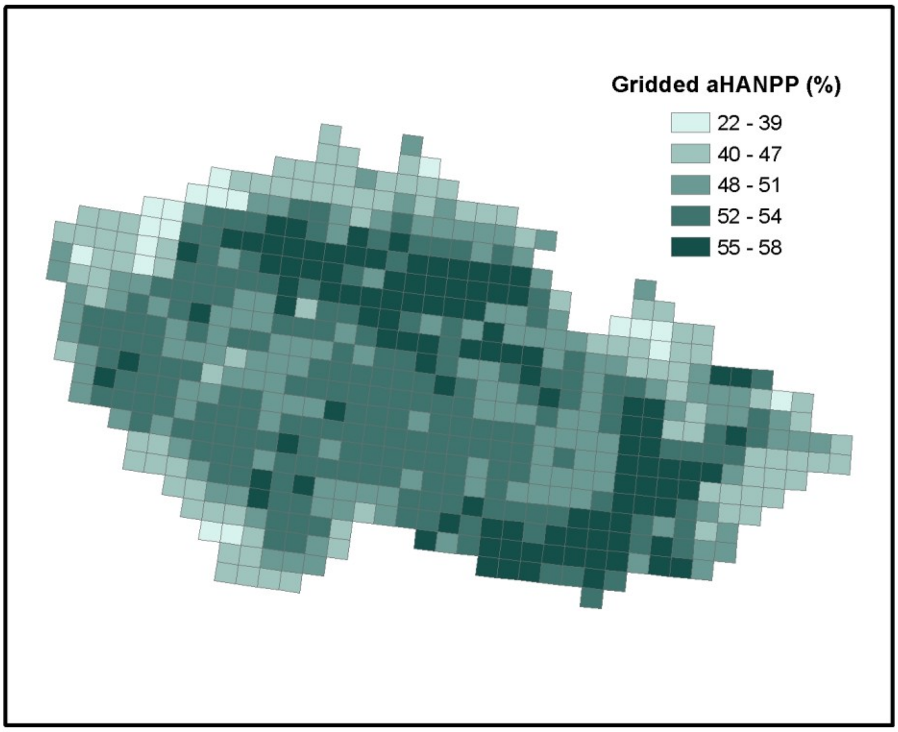

Figure 18. Gridded values of Human Appropriation of Aboveground Net Primary Production (aHANPP in %). Values show clustering according to prevailing land cover/land use in a grid.

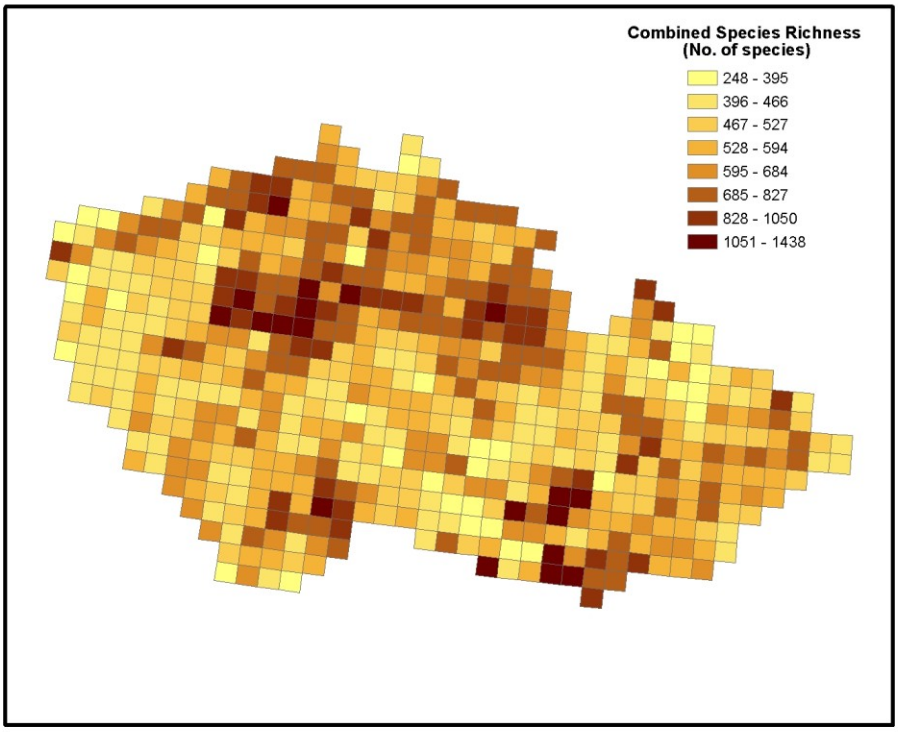

Figure 19. Gridded Combined Species Richness for 10 taxonomic groups analyzed in this study. All data are spatially autocorrelated due to spatial contiguity of biodiversity data.

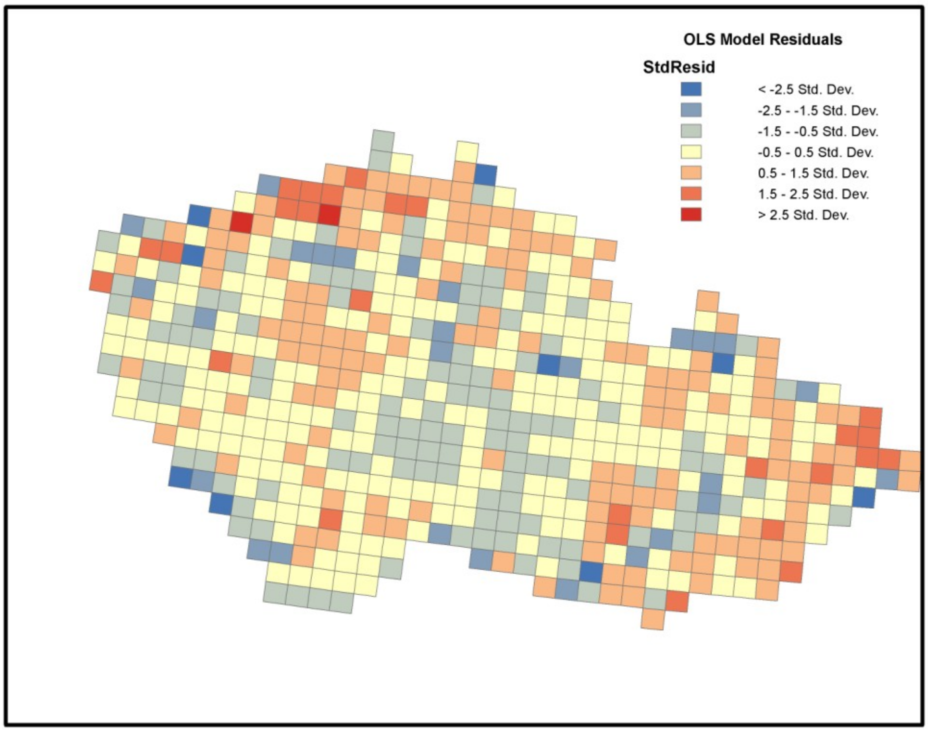

**Figure 20. Geographically distributed residuals of the OLS model describing the relationship between aHANPP and Shannon Landscape Diversity Index. Red areas indicate over-predictions, while blue areas indicate under-predictions, measured as standard deviations from the estimated value of predictor variable (aHANPP in this case). Additional analyses indicate spatial clustering and residual deviations from a normal distribution.**

**Table 12. Results of spatial autocorrelation analysis of main indicators used in a study. All partial data (species richnes of taxonomic groups, land cover and land use) tend to be also spatially autocorrelated.**

| Indicator | Moran's I Index | Z-score | Significance level p-value | Pattern |
|---|---|---|---|---|
| **CSR** | 0.49 | 11.59 SD | 0.01 | Clustered |
| **SRIndex** | 0.46 | 10.95 SD | 0.01 | Clustered |
| **aHANPP** | 0.63 | 15.26 SD | 0.01 | Clustered |
| **SHLDI** | 0.53 | 12.69 SD | 0.01 | Clustered |
| **HPD** | 0.58 | 13.87 SD | 0.01 | Clustered |

As grid cells are contiguous, data are probably spatially autocorrelated (Luck, 2006). Spatial autocorrelation was calculated using the Moran spatial statistics which evaluates whether the pattern expressed is clustered, dispersed, or random (Table 12). Z score and p-value evaluate the significance of the index. Z score indicates how many standard deviations (SD) is the result above or below a mean. P-values express the likelihood that the pattern could be a result of random chance. All main parameters are spatially clustered (autocorrelated) ($P<0.01$). Therefore, the null hypothesis about the spatially random distribution of indicators can be rejected. Our results indicate the presence of spatial hotspots and coldspots, i.e. unequal and spatially clustered distribution of studied phenomena.

Besides the aggregate measures of human pressures and biodiversity, we were interested in patterns of coincidence of species richness and land cover/land use (Table 15). Urban areas highly correlate with human population densities ($r_s=0.724$). Therefore, patterns of urban areas coincidence with species richness are equivalent to coincidence with HPD. Coincidence of urban areas and plants was more pronounced in comparison with HPD and plants congruence ($r_s=0.518$). However, birds and spiders were significantly correlated with urban areas rather than with HPD. Concerning agricultural land use, invertebrates were rather negatively spatially correlated, while vertebrates rather positively correlated (especially bird species). Surprisingly, majority of species groups was negatively or neutrally related to forest land cover. Only reptiles positively spatially overlapped with forest area, as well as with meadows and pastures.

All invertebrate taxa were related to natural grassland and heathland. On the contrary, no species richness associate with bare area and open spaces. While birds spatially coincide with both wetland and water habitats, amphibians are spatially congruent with water areas only. Besides mammals and reptiles, all other species groups performed positively with regard to coincidence with water areas. However, several species groups show sensitivity to land use intensity rather than to the area of land cover (Table 14). Carabids are negatively related to harvest intensity ($r_s=-0.302$) and reptiles seems to be sensitive to the overall aHANPP, while amphibians are related to aHANPP positively. Majority of groups is also positively related to the amount of protected areas available, besides the mammals.

**Table 13. Cross-correlations between main parameters constructed in the analysis and components of species richness. The most pronounced relationships are positive spatial correlation between Human Population Density (HPD) and Combined Species Richness (CSR), and negative spatial correlation for Human Appropriation of Aboveground NPP (aHANPP) and Landscape Diversity Index (SHLDI). Results are reported for a sample of N=560 grid cells.**

| | HPD | CSR | aHANPP | SHLDI | SRIndex | PAAREA | Inverteb | Verteb | Plants | REPT | AMPHI | CARAB | BUTTER | MAMM | SPIDER | ELATERID | CERAMB | BIRD |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **HPD** | 1.000 | 0.361 | 0.039 | 0.309 | 0.263 | 0.069 | 0.267 | 0.077 | 0.375 | 0.079 | 0.162 | 0.422 | 0.181 | -0.126 | 0.073 | 0.158 | 0.241 | 0.055 |
| **CSR** | | 1.000 | 0.041 | 0.280 | 0.736 | 0.392 | 0.856 | 0.426 | 0.763 | 0.311 | 0.464 | 0.613 | 0.530 | -0.006 | 0.644 | 0.607 | 0.588 | 0.358 |
| **aHANPP** | | | 1.000 | -0.699 | -0.146 | -0.129 | -0.118 | 0.124 | 0.179 | -0.364 | 0.133 | -0.056 | -0.075 | 0.012 | -0.150 | -0.082 | -0.057 | 0.131 |
| **SHLDI** | | | | 1.000 | 0.351 | 0.155 | 0.301 | 0.049 | 0.209 | 0.379 | 0.094 | 0.255 | 0.255 | -0.080 | 0.210 | 0.184 | 0.242 | 0.014 |
| **SRIndex** | | | | | 1.000 | 0.381 | 0.698 | 0.376 | 0.503 | 0.652 | 0.712 | 0.511 | 0.470 | -0.017 | 0.505 | 0.624 | 0.536 | 0.250 |
| **PAAREA** | | | | | | 1.000 | 0.409 | 0.200 | 0.252 | 0.216 | 0.191 | 0.254 | 0.259 | -0.010 | 0.377 | 0.379 | 0.278 | 0.166 |
| **Inverteb** | | | | | | | 1.000 | 0.215 | 0.403 | 0.298 | 0.341 | 0.661 | 0.637 | 0.046 | 0.778 | 0.596 | 0.644 | 0.152 |
| **Verteb** | | | | | | | | 1.000 | 0.262 | 0.102 | 0.437 | 0.098 | 0.163 | 0.144 | 0.146 | 0.133 | 0.187 | 0.984 |
| **Plants** | | | | | | | | | 1.000 | 0.236 | 0.393 | 0.382 | 0.238 | -0.135 | 0.265 | 0.444 | 0.344 | 0.205 |
| **REPT** | | | | | | | | | | 1.000 | 0.196 | 0.166 | 0.215 | -0.004 | 0.294 | 0.238 | 0.166 | 0.021 |
| **AMPHI** | | | | | | | | | | | 1.000 | 0.236 | 0.145 | -0.034 | 0.264 | 0.351 | 0.288 | 0.298 |
| **CARAB** | | | | | | | | | | | | 1.000 | 0.333 | -0.055 | 0.359 | 0.481 | 0.444 | 0.058 |
| **BUTTER** | | | | | | | | | | | | | 1.000 | 0.064 | 0.274 | 0.266 | 0.383 | 0.136 |
| **MAMM** | | | | | | | | | | | | | | 1.000 | 0.096 | -0.081 | -0.005 | 0.133 |
| **SPIDER** | | | | | | | | | | | | | | | 1.000 | 0.408 | 0.356 | 0.091 |
| **ELATERID** | | | | | | | | | | | | | | | | 1.000 | 0.552 | 0.070 |
| **CERAMB** | | | | | | | | | | | | | | | | | 1.000 | 0.143 |
| **BIRD** | | | | | | | | | | | | | | | | | | 1.000 |

**Table 14. Cross-correlations between aHANPP parameters and species richness parameters. There is no consistent relationship between aHANPP and species richness. However, plants and amphibian richness is positively related to aHANPP, while spider and reptile richness is negatively related to aHANPP. Actual NPP is rather negatively related to species richness, as high $NPP_{ACT}$ is usually associated with higher harvest intensity $NPP_{H}$. Results are reported for a sample of N=560 grid cells.**

| | aHANPP | NPP0 | NPPACT | NPPH | NPPT | dNPPLC | Inverteb | Verteb | Plants | REPT | AMPHI | CARAB | BUTTER | MAMM | SPIDER | ELATERID | CERAMB | BIRD |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **aHANPP** | 1.000 | -0.257 | -0.276 | 0.643 | -0.808 | 0.032 | -0.118 | 0.124 | 0.179 | -0.364 | 0.133 | -0.056 | -0.075 | 0.012 | -0.150 | -0.082 | -0.057 | 0.131 |
| **NPP0** | | 1.000 | 0.329 | -0.039 | 0.379 | 0.474 | -0.157 | -0.067 | -0.171 | 0.048 | -0.196 | -0.165 | -0.068 | 0.061 | -0.088 | -0.204 | -0.228 | -0.042 |
| **NPPACT** | | | 1.000 | 0.449 | 0.719 | -0.605 | -0.106 | -0.127 | -0.235 | 0.095 | -0.153 | -0.260 | -0.006 | 0.038 | -0.029 | -0.084 | -0.036 | -0.118 |
| **NPPH** | | | | 1.000 | -0.181 | -0.447 | -0.209 | -0.008 | -0.026 | -0.233 | 0.029 | -0.302 | -0.095 | 0.019 | -0.161 | -0.154 | -0.089 | -0.005 |
| **NPPT** | | | | | 1.000 | -0.343 | 0.005 | -0.165 | -0.248 | 0.307 | -0.168 | -0.131 | 0.042 | -0.007 | 0.069 | 0.003 | 0.005 | -0.165 |
| **dNPPLC** | | | | | | 1.000 | -0.035 | 0.036 | 0.071 | 0.004 | -0.054 | 0.113 | -0.052 | 0.002 | -0.042 | -0.080 | -0.164 | 0.050 |
| **Inverteb** | | | | | | | 1.000 | 0.215 | 0.403 | 0.298 | 0.341 | 0.661 | 0.637 | 0.046 | 0.778 | 0.596 | 0.644 | 0.152 |
| **Verteb** | | | | | | | | 1.000 | 0.262 | 0.102 | 0.437 | 0.098 | 0.163 | 0.144 | 0.146 | 0.133 | 0.187 | 0.984 |
| **Plants** | | | | | | | | | 1.000 | 0.236 | 0.393 | 0.382 | 0.238 | -0.135 | 0.265 | 0.444 | 0.344 | 0.205 |
| **REPT** | | | | | | | | | | 1.000 | 0.196 | 0.166 | 0.215 | -0.004 | 0.294 | 0.238 | 0.166 | 0.021 |
| **AMPHI** | | | | | | | | | | | 1.000 | 0.236 | 0.145 | -0.034 | 0.264 | 0.351 | 0.288 | 0.298 |
| **CARAB** | | | | | | | | | | | | 1.000 | 0.333 | -0.055 | 0.359 | 0.481 | 0.444 | 0.058 |
| **BUTTER** | | | | | | | | | | | | | 1.000 | 0.064 | 0.274 | 0.266 | 0.383 | 0.136 |
| **MAMM** | | | | | | | | | | | | | | 1.000 | 0.096 | -0.081 | -0.005 | 0.133 |
| **SPIDER** | | | | | | | | | | | | | | | 1.000 | 0.408 | 0.356 | 0.091 |
| **ELATERID** | | | | | | | | | | | | | | | | 1.000 | 0.552 | 0.070 |
| **CERAMB** | | | | | | | | | | | | | | | | | 1.000 | 0.143 |
| **BIRD** | | | | | | | | | | | | | | | | | | 1.000 |

**Table 15. Cross-correlations between land cover and land use classes and species richness. Association between urban areas and plant and carabid richness can indicate sampling effect for these groups. Several other interesting patterns is evident from the analysis. For example, reptiles doesn´t associate with agricultural areas, plants are negatively correlated with forests, butterflies have strongest association with natural grasslands and heathlands, and amphibians positively relate to water availability. Results are reported for a sample of N=560 grid cells.**

| | URBAN | AGRI | PAST | FOREST | GRASS | BARE | WET | WATER | Inverte | Verteb | Plants | REPT | AMPHI | CARAB | BUTTER | MAMM | SPIDER | ELATERI | CERAM | BIRD |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **URBAN** | 1.000 | 0.306 | -0.249 | -0.470 | -0.060 | 0.018 | -0.090 | 0.134 | 0.310 | 0.159 | 0.518 | 0.055 | 0.270 | 0.433 | 0.198 | -0.098 | 0.110 | 0.226 | 0.287 | 0.125 |
| **AGRI** | | 1.000 | -0.614 | -0.846 | -0.224 | -0.012 | -0.215 | 0.076 | -0.154 | 0.127 | 0.164 | -0.347 | 0.124 | -0.082 | -0.099 | 0.011 | -0.164 | -0.123 | -0.125 | 0.135 |
| **PAST** | | | 1.000 | 0.304 | 0.017 | 0.024 | 0.129 | -0.091 | -0.056 | -0.072 | -0.179 | 0.246 | -0.166 | -0.051 | -0.037 | 0.088 | 0.011 | -0.101 | -0.157 | -0.063 |
| **FOREST** | | | | 1.000 | 0.186 | 0.002 | 0.150 | -0.159 | 0.053 | -0.178 | -0.247 | 0.265 | -0.164 | -0.084 | 0.045 | -0.024 | 0.092 | 0.073 | 0.106 | -0.178 |
| **GRASS** | | | | | 1.000 | -0.020 | 0.184 | -0.063 | 0.151 | 0.042 | -0.019 | 0.039 | 0.016 | 0.118 | 0.155 | -0.011 | 0.103 | 0.131 | 0.157 | 0.044 |
| **BARE** | | | | | | 1.000 | -0.014 | -0.041 | 0.055 | -0.038 | 0.026 | 0.013 | -0.006 | 0.048 | 0.022 | -0.023 | 0.052 | 0.061 | 0.039 | -0.038 |
| **WET** | | | | | | | 1.000 | 0.184 | 0.186 | 0.120 | -0.071 | -0.011 | 0.070 | 0.106 | 0.103 | 0.108 | 0.138 | 0.182 | 0.166 | 0.120 |
| **WATER** | | | | | | | | 1.000 | 0.196 | 0.321 | 0.152 | 0.062 | 0.248 | 0.152 | 0.143 | 0.049 | 0.154 | 0.133 | 0.150 | 0.297 |
| **Inverte** | | | | | | | | | 1.000 | 0.215 | 0.403 | 0.298 | 0.341 | 0.661 | 0.637 | 0.046 | 0.778 | 0.596 | 0.644 | 0.152 |
| **Verteb** | | | | | | | | | | 1.000 | 0.262 | 0.102 | 0.437 | 0.098 | 0.163 | 0.144 | 0.146 | 0.133 | 0.187 | 0.984 |
| **Plants** | | | | | | | | | | | 1.000 | 0.236 | 0.393 | 0.382 | 0.238 | -0.135 | 0.265 | 0.444 | 0.344 | 0.205 |
| **REPT** | | | | | | | | | | | | 1.000 | 0.196 | 0.166 | 0.215 | -0.004 | 0.294 | 0.238 | 0.166 | 0.021 |
| **AMPHI** | | | | | | | | | | | | | 1.000 | 0.236 | 0.145 | -0.034 | 0.264 | 0.351 | 0.288 | 0.298 |
| **CARAB** | | | | | | | | | | | | | | 1.000 | 0.333 | -0.055 | 0.359 | 0.481 | 0.444 | 0.058 |
| **BUTTER** | | | | | | | | | | | | | | | 1.000 | 0.064 | 0.274 | 0.266 | 0.383 | 0.136 |
| **MAMM** | | | | | | | | | | | | | | | | 1.000 | 0.096 | -0.081 | -0.005 | 0.133 |
| **SPIDER** | | | | | | | | | | | | | | | | | 1.000 | 0.408 | 0.356 | 0.091 |
| **ELATERI** | | | | | | | | | | | | | | | | | | 1.000 | 0.552 | 0.070 |
| **CERAM** | | | | | | | | | | | | | | | | | | | 1.000 | 0.143 |
| **BIRD** | | | | | | | | | | | | | | | | | | | | 1.000 |

# 5. Discussion

## 5.1. Human appropriation of aboveground net primary production

The concept of human appropriation of net primary production was proposed as an indicator measuring the environmental sustainability of human society (Imhoff et al. 2004a; Haberl, 1997; Haberl et al., 2007; Rojstazcer et al., 2001; Vitousek et al., 1986). Humans are motivated to harness ecosystems for marketed production and disregard the overall ecosystem carbon balance. However, this notion can be changed with regard to carbon trading and payment schemes in the context of climate change mitigation. Therefore, HANPP indicator can contribute to complex carbon accounting. Human appropriation of net primary production can be regarded as a biophysical measure of sustainability as there is no weighting of the social importance of NPP. On the other hand, NPP is often used as a proxy for other ecosystem services, including carbon storage, climate regulation or biodiversity provision (MA, 2005). We found that the indicator is sensitive to detect changes in time and enables spatial disaggregation and regional comparison of aHANPP patterns.

Our results contribute to discussions about human environmental impacts in a cultural landscape (Haberl et al., 2001; Krausmann, 2001). Results for the Czech Republic are consistent with estimates of HANPP for Eastern Europe region (52%) (Haberl et al., 2007), Austria (51%) (Haberl et al., 2001) or Hungary (49%) (Kohlheb & Krausmann, 2009). HANPP in the Czech Republic is considerably higher than the global averages (Imhoff et al., 2004; Haberl et al., 2007; Vitousek et al. 1986) but could also correspond to higher bounds of global estimates (Rojstaczer et al., 2001). The area of the Czech Republic is intensely managed with the arable land occupying 39% of the territory and the managed forests occupying 25% of the total area. Provided the agricultural, managed forest and urban land is taken into account, then the proportion of human-dominated land amounts to 90%, which should hypothetically translate into considerable impacts on ecosystems.

Of special concern is the uncertainty of the NPP data. As revealed by the comparison of the global models, the range of terrestrial net primary production estimates is relatively broad (Cramer et al., 1999). For some land cover types, the NPP data are rather scarce and gained with differing methodologies. However, the data assembled in this study represent a broad array of ecosystem types. The highest uncertainty in estimates can be found in alluvial forests, wetlands and urban habitats. This may reflect the variability of habitat types dependent on the actual natural conditions. The main reason for this uncertainty lies in a small sample size of these NPP values. The estimates of the productivity of artificial surfaces have to be considered rather rough as they are approximated from an insufficient number of studies on the productivity in urban areas. However, urban heat islands and urban land management could affect productivity in urban areas and relatively high values thus can be reasonable. With regard to the small area of urban fabric and wetlands, changes in NPP values would not translate into changes in overall results.

Another source of uncertainty can be the use of harvest indices. However, this is a relatively common approach for estimating NPP on agricultural land (Lobell et al., 2002; Prince et al., 2001) and our sample of harvest indices is relatively extensive (Chapter 3.1.4). Our average aNPP for agricultural land (412 g C $m^{-2}$) closely matches other studies and corresponds to values reported from field studies (Lobell et al., 2002). Concerning the estimates of livestock dry matter intake, pasture quality or pasture allowance are factors influencing overall dry matter intake and substitution rates (Bargo et al., 2003). However, we treated pastures in the Czech Republic uniformly and did not differentiate between pasture types. Pasture aHANPP increased during the period 1990-2006 despite the decreasing overall feed demand of livestock. This trend is caused by decreased supply of feedstuffs from agricultural land and industrial feedstuffs.

Our estimates of NPP values for coniferous forests are corresponding to the estimates of Mellilo et al. (1993) and Schulze et al. (2000a), as well as estimates from other studies. Given the incompleteness and uncertainty of the forest NPP estimates (Clark et al., 2001), our sample estimates of average forest aNPP is probably rather conservative. As noted by Reich and Bolstad (2001), the variation within each forest type is much larger than their average differences. The highest NPP values of coniferous forests are comparable with the highest values found in broadleaved forests. The highest NPP value in our sample belongs to the alluvial forest (849 g C m$^{-2}$), followed by beech (793 g C m$^{-2}$), oak (773 g C m$^{-2}$), spruce (736 g C m$^{-2}$) and pine (688 g C m$^{-2}$). Forest aHANPP data show relatively uniform human impact on forests between forest types, indicating that forests in the Czech Republic are intensively managed plantations rather than semi-natural forests (i.e. human impacts are similar in coniferous, mixed and broadleaved forests).

Humans alter ecosystems in the way that benefits their well-being (MA, 2005). These changes result in a net NPP changes as compared to the natural potential productivity. The majority of productivity changes occurred at the expense of the productivity of beech forests in the Czech Republic. The agricultural land replaced mainly the beech, hornbeam and oak vegetation ranges. Managed forests are distributed primarily in the area occupied by the beech and oak woodlands. These represent climatically and pedologically suitable land for agricultural and forestry production. Artificial surfaces are spread relatively equitably across the broadleaved biomes. Natural pine, spruce and mires represent predominantly marginal land with regard to the natural productivity. The dominating activities responsible for the productivity losses of these naturally marginal habitat types are the mineral extraction sites and dump sites. As documented by our results, the net primary productivity of green urban surfaces, managed forests and wetlands can exceed the natural potential productivity.

In some cases, negative changes in NPP can translate into positive changes for other ecosystem services. According to our calculations, the NPP of potential natural vegetation replaced by semi-natural grasslands was reduced by some 54%. However, this fact cannot be interpreted in the way that maintaining grasslands is environmentally unsustainable. Semi-natural grasslands have a social importance with regard to biodiversity and landscape character (Isselstein et al., 2005). They are usually protected by the law and managed (grazed or mowed) to prevent natural succession, which would restore the forest. Equivalently, the urban fabric provides no primary productivity (humans appropriated 100% of NPP). However, it accommodates socioeconomic production, which can promote the sustainability of job and income generation.

Future strategies of NPP management have to take into consideration the globally-reaching transformations of regional ecosystems. Increasing the share of the “planetary pie” appropriated by humans (Foley et al., 2007) reduces the space available for biodiversity and natural processes. Although the artificial surfaces completely seal the available land, the urban green areas can even enhance the natural productivity levels and can host considerable biodiversity (Milesi et al., 2005; Shochat et al., 2006). Some managed ecosystems can reach higher levels of biodiversity than natural ecosystems. In Central Europe, there is a long-term record of positive impacts of aNPP appropriation on biodiversity in grasslands (Isselstein et al., 2005) and in forests (Bengtsson et al., 2000). A range of practices have been identified, which enhance biodiversity and simultaneously contribute to the carbon storage in ecosystems and other vital ecosystem services. This has important implications for example on climate change mitigation strategies (Lal, 2004; Schulze et al., 2000b) or water footprints on agricultural land (Hoesktra & Chapagain, 2007).

## 5.2. Human pressures and biodiversity

Maintenance of the positive spatial relationship between human population density (HPD) and species richness can be considered as an established hypothesis in a field of macroecology (Araújo, 2003; Balmford et al., 2001; Chown et al., 2003; Evans & Gaston, 2005; Hugo & van Rensburg, 2008; Luck, 2007; McKinney, 2002; Pautasso, 2007). The hypothesis proposes a positive spatial relationship between human population density and species richness (i.e. null hypothesis states that the relationship between human population density and biodiversity is neutral). Our results contribute to previous studies which showed positive spatial correlation between human population density and species richness (Araújo, 2003; Luck, 2006; Luck et al., 2004; Hugo & van Rensburg, 2008). Human population density has been introduced as a proxy for environmental pressures (Luck, 2006; Spangenberg, 2007), including for example land conversion, invasions of introduced species, or environmental degradation. As shown in our results, extent of urban areas is also a good correlate of species richness. These results correspond to increasing recognition, however counterintuitive, that urbanized landscapes can host diverse ecological elements.

Several mechanisms have been suggested to be responsible for positive population-biodiversity relationship. Urbanization plays a considerable role in hypothesis aimed to explain positive spatial relationship between biodiversity and human population density (McKinney, 2002). These include especially four hypothesis closely related to urban areas:

- Habitat heterogeneity. Although urban areas are usually not dominating land use type (which is agriculture), artificial areas considerably contribute to novel habitats and increase habitat heterogeneity (Hobbs et al., 2006). Urban nature reserves, parks and other urban green surfaces can provide refuges for endangered species. Anthropogenic habitats can provide environments for introduced or expanding species. Thus, anthropogenic landscapes contribute to the establishment of new ecological equilibriums of biotic dynamics.
- Urban climate and productivity. Urban areas are responsible for urban heat islands, which can lead to favourable climates and increased productivity (Shochat et al., 2006). Urban productivity can be further increased by irrigation

and deposition of nutrients, for example the fertilization effects of carbon dioxide and nitrogen.

- Conservation in urban areas. Natural patches in urban areas have been traditionally well-conserved. Therefore, it is possible that at finer spatial scales biological diversity in protected areas can persists in isolated islands of nature. This urban biodiversity associate with urban ecosystem services (Colding et al., 2003).
- Sampling effect. Intensive sampling in areas adjacent to urban areas can artificially increase species richness of urbanized regions (Evans et al., 2007). Therefore, data samples especially for some species groups could be biased toward greater species richness.

Patterns of species richness have been already tested for the area of the Czech Republic (Krojerová-Prokešová et al., 2008; Konvička et al., 2003;  Pyšek et al., 2002; Storch et al., 2003). However, no study tested explicitly the relationship between the HPD and biodiversity. Moreover, we included aHANPP as an indicators of the intensity of land and ecosystem use by humans. Our analysis also introduces novel datasets not analyzed previously in the Czech Republic, especially concerning invertebrates datasets. However, several potentially useful indicator data were not available at the national level (e.g. Boháč, 1999). Krojerová-Prokešová et al. (2008) analyze patterns and predictors of vertebrate species richness in the Czech Republic. They identified two main gradients by using Principal Component Analysis (PCA). The first one represents a gradient from urban habitats at lower altitudes to more homogenous habitats with dominant coniferous forests and meadows situated at higher altitudes. The second gradient shows the importance of natural habitats (represented by broad-leaved and mixed forests, and protected areas) and landscape heterogeneity. These environmental gradients (variation in altitude and urbanisation) represent two important drivers of spatial distribution of species richness in the Czech Republic.

Possible uncertainties and artifacts in our data are related to sampling bias which has been often detected in biodiversity data (Evans et al., 2007). Sites closer to urban areas has been suggested to be sampled more intensively than remote places, especially when monitoring program is not thoroughly designed and sampling proceeds rather haphazardly (Yoccoz et al., 2003). For the sample size concerned (i.e. 10 broader taxonomic groups), we were not able to standardize sampling effort due to limited data availability. Protected areas could be also suggested to be sampled more intensively. As indicated by our results, spatial correlation of protected areas (PA) and combined species richness (CSR) is equivalent ($r_s$=0.361 for HPD vs. $r_s$=0.392 for PA). However, HPD and PA are not spatially related ($r_s$= 0.069). Therefore, spatial correlation between HPD and biodiversity is probably not a sampling artifact. As shown by Evans et al. (2007), sampling effort only slightly influences the form of species richness–human population density relationships. The positive correlation between species richness and human population are thus not artefactual patterns generated by confounding human density and sampling effort.

The relationship between Human appropriation of aboveground net primary production (aHANPP) and Shannon Landscape Diversity Index (SHLDI) was described by a quadratic regression model which performed best with regard to explained amount of variance. The curvilinear model is in accord with intermediate disturbance hypotheses (IDH) which states that highest biodiversity is achieved at intermediate levels of disturbance (Connel, 1978). IDH arises from a set of factors influencing species coexistence (Roxburgh et al., 2004). The basic mechanism behind the IDH is probably an enabling environment for the coexistence of species with different traits. Our results are completely consistent and similar in strength with results for Austria (Wrbka et al., 2004), where hump-shapes curvilinear relationship was detected for aHANPP nad landscape diversity measures ($r^2$=0.43). This correspondence could indicate general widespread patterns of land and ecosystem use intensity impacts on higher hierarchical biodiversity levels, that is landscape diversity in this case, in human dominated or cultural landscapes.

Disturbance mechanisms are responsible also for the spread of introduced species. At global scales, land conversionn and the introduction of exotic species are the main factors contributing to declines in species diversity. At regional and local scales, evidence for biodiversity declines is mixed, and recent work suggests that diversity might commonly be increasing (Sax & Gaines, 2003). This effect can be ascribed to the biotic homogenization at the regional scale, where introduced species are enriching local fauna and flora and occasionally also create new emerging ecosystems. Olden et al. (2006) report biotic homogenization showing a statistically significant relationship with human population geography for all major taxonomic groups. However, results from this and similar studies suggest that despite the significance of the impact of human population on biotic homogenisation, approximately two thirds of variance remain unexplained and further research is needed to account for this residual variation.

Correlation which we selected as a main methodological approach is measuring the amount of association between two variables (Quinn & Keough, 2002). Therefore, we were interested to determine whether and to what extent human population density and species richness are interdependent or covary. This approach is consistent with several recent studies (e.g. Araújo, 2003; Luck et al., 2004). Correlation coefficient detects possible linearity between examined variables. In other words, correlation analysis tests monotonic relationship between variables. Correlation analysis is related to regression in such a way that population slope of the linear regression is related to the correlation by the ratio of the standard deviations between analyzed variables (Quinn & Keough, 2002). Therefore, established correlation indicates an existence of functional relationship between variables, i.e. we are able to identify response (Y) and predictor (X) variable. We established a regression model of the relationship between aHANPP and SHLDI as we were interested in constructing a model explaining the strong relationship evident from correlation analysis.

Data from contiguous grid cells are often spatially autocorrelated, which violates the assumptions of independent errors on which many classical statistical tests are based (Hugo & van Rensburg, 2008). Although we combined a HPD, aHANPP and SHLDI as potential predictor variables in a model explaining combined species richness (CSR), despite the high negative AIC (Akaike Information Criterion, a measure of goodness of fit of a model), general assumptions for OLS or GWR were not met in this case. According to the Jarque-Bera statistic which indicates whether or not the residuals (the observed/known dependent variable values minus the predicted/estimated values) are normally distributed, our results couldn´t be considered normally distributed. Additional spatial autocorrelation tests (Moran I statistics) revealed significant spatial autocorrelation in our data. Therefore, the null hypothesis about the spatially random distribution of residuals could be rejected.

Potential conflicts can arise from the spatial coincidence of people and biodiversity (Luck et al., 2004). People tend to inhabit areas with high energy availability, i.e. high net primary production, where biodiversity should be also highest (Evans & Gaston, 2005). Our results indicate that urban areas coincide with the $\Delta aNPP_{LC}$ term expressing the changes in productivity induced by land conversion ($r_s$=0.301). However, we did not find spatial relationships between primary productivity and species richness. This relationship can be distorted in a cultural landscape, as intensively used ecosystems don´t associate with high species richness. The HPD-species richness relationship is also scale-dependent. Our data doesn´t enable testing of this scale dependency. However, Pautasso (2007) found that the correlation turns from positive to negative bellow the grain of 1 km$^2$ and study extent of 10,000 km$^2$. At broader scale, people and biodiversity are allowed to coexist. At smaller scales, urban surfaces and sealed land outcompete biodiversity and urbanization leads to biodiversity loss (Hahs et al., 2009). The relationship between HPD and biodiversity is therefore important to consider in conservation and urban planning (Ricketts & Imhoff, 2003), given the urban land use development trends in Europe (Reginster & Rounsevell, 2006).

# 6. Summary and conclusions

I found that human appropriation of aboveground net primary production (aHANPP) amounts to 56 percent of potential aboveground net primary production in the Czech Republic. Aboveground HANPP is composed of aNPP changes induced by land conversion ($\Delta aNPP_{LC}$) which was determined at 11% of $aNPP_0$, and socioeconomic harvest forming 45% of $aNPP_0$. People harvested 16.9 Tg C from ecosystems annually in 2000 and this amount of harvest declined from 18.5 Tg C harvested in 1990s and increased again to 17.3 Tg C in 2006. Decline of production on arable land has been partially counterbalanced by increasing pastures and forest harvest. Dominant contribution to aHANPP in the Czech Republic is made by agriculture (49.98%), followed by forestry (25%) and pastures (15%). The increasing impact of urbanization cannot be neglected with 7.4% contribution to overall aHANPP.

The analysis aimed to quantitatively estimate human impacts on ecosystems while taking into account natural limits represented by the potential natural vegetation. The changes in the net primary productivity induced by human activities can be considered as one of the robust leading indicators of human footprint on ecosystems (Haberl et al., 2004). Our main assumption was that human economic activities are manifested by land conversion and ecosystem use and thus change the amount of organic material available for natural processes. We choose the aboveground net primary production as a common unit for the comparison of human impacts with the potential natural state. As evinced in our results, humans have considerable impact on ecosystems and flows of carbon.

Hypothesis about spatial coincidence of people (measured by human population density - HPD) and biodiversity (measured by combined species richness CSR of 10 taxonomic groups of vertebrates, invertebrates, and plants) was tested for the area of the Czech Republic. I found significant spatial congruence between HPD and species richness of majority of groups. While Human appropriation of aboveground net primary production (aHANPP) wasn´t related to species richness,  I found a statistically significant relationship between aHANPP and landscape diversity (measured by Shannon Landscape Diversity Index – SHLDI) as a measure of biodiversity at higher (habitat, ecosystem an landscape) hierarchical levels. The relationship between aHANPP and

SHLDI was best described by a quadratic regression equation (*F* (2, 557) = 262.330, $p<0.01$) and the curvilinear model explained 48.5% of variance. The quadratic model is consistent with the intermediate disturbance hypothesis, where highest biodiversity is achieved at intermediate levels of human impacts. However, the lower intensity end is almost missing in the human dominate landscape of a Central European country.

Our analysis contributes to the discussion about the extent of human dominance and the relationship between human activity and biodiversity in urbanized and managed landscapes. As evinced in the results, intermediate levels of land and ecosystem use can maintain considerable biodiversity at species and habitat levels. Biodiversity of cultural landscapes can be even higher than biodiversity of natural communities. Human introduce novel land cover types and habitats associated with ecosystem use through appropriation of net primary production and other processes. There is some indication that humans and biodiversity can coexist, given that land and ecosystem use is accounted in societal indicators and frameworks. Biodiversity boosts in conservation areas as well as urbanized landscapes. Therefore, strategies for biodiversity conservation and management should aim not only at the traditionally protected areas, but also on novel land and ecosystem types which can host significant fraction of species richness.

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