Human Appropriation of Net Primary Production: Patterns, Trends, and Planetary Boundaries

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Abstract

Economic and population growth result in increasing use of biophysical resources, including land and biomass. Human activities influence the biological productivity of land, altering material and energy flows in the biosphere. The human appropriation of net primary production (HANPP) is an integrated socioecological indicator quantifying effects of human-induced changes in productivity and harvest on ecological biomass flows. We discuss how HANPP is defined, measured, and interpreted. Two principal approaches for constructing HANPP assessments exist: (*a*) In an area-specific approach, HANPP serves as an indicator of land-use intensity, gauging impacts on terrestrial ecosystems in a defined area; and (*b*) the consumption-based "embodied HANPP" approach allows assessment of impacts related to individual products or the aggregate consumption of nation-states. The HANPP framework can help to estimate upper limits for the biosphere's capacity to provide humanity with biomass for food, fiber, and bioenergy and to analyze systemic feedbacks between the delivery of these resources. We outline HANPP's global patterns and trajectories and how HANPP relates to planetary boundaries, global resource use, and pressures on biodiversity.

Contents

INTRODUCTION

Biologically productive land is an indispensable resource for socioeconomic and ecological systems alike. The land surface area of the planet is the basis for all ecological processes, including plant growth, herbivory, predation, decay of litter, and soil formation. Humans harness these processes to provide food, feed, energy, and raw materials through hunting and gathering, agriculture (cropping, grazing, mowing, etc.), and forestry. Humans also need area as living- and workspace, for infrastructures and recreation, and for many other purposes. The notion of land-system change (1) recognizes how intricately entangled socioeconomic and ecological components of Earth's terrestrial systems are. Consequently, there is a need for a new, truly inter- and transdisciplinary research field of integrated land system science to analyze these complex interrelations (2).

Anthropocene: informal geological chronological term denoting the epoch characterized by global human impacts on biogeochemical patterns and processes

Human appropriation of net primary production (HANPP): a measure of human impacts on the flow of trophic energy in ecosystems

Trophic energy: chemical energy stored in biomass potentially available as food for heterotrophs in an ecosystem

Driven by the growth of the population and the economy, human demands on Earth's lands have increased dramatically in the past 50–100 years. Land-system change has been recognized as a pervasive driver of global environmental change (3), and the extent of the global human use of the land has contributed to new terms such as the Anthropocene (4) or the designation of Earth as a "cultivated planet" (5).

In this context, certain questions have received considerable attention (6–9): How much of Earth's productive capacity do humans use? What is the scale of human activity compared with natural processes on Earth? What is the extent and intensity of global land use, and how does it change? How large is the human domination of Earth's ecosystems? The concept of human appropriation of net primary production (HANPP) aims to help answer such questions. Broadly speaking, HANPP is an indicator that assesses the extent to which human activities affect flows of trophic energy (biomass) in ecosystems, namely net primary production (NPP), a key process in the Earth system. In the process of photosynthesis, plants use radiant energy from the sun to produce energy-rich organic compounds from inorganic compounds, chiefly CO_2 and H_2O. The total amount of

CO_2 fixed by autotrophs such as green plants is denoted as gross primary production (GPP). GPP minus plant respiration is denoted as NPP, which is the basis for plant growth as well as for the trophic energy supply of all heterotrophs (animals, fungi, many microorganisms). HANPP is an indicator of the extent to which humans interfere in these processes, thereby appropriating a fraction of NPP for their own use (7, 10–13). It is an integrated socioecological indicator that can be used to quantify human domination of ecosystems (9) and to understand and map important aspects of land-use intensity (13–15). HANPP has been used to analyze trajectories of socioecological systems consistently through time (16), to underpin sustainability in delta systems (17), and to study socioecological efficiencies [e.g., land-use efficiency (18) and resource intensity of consumption (19, 20)].

This article summarizes the history of the HANPP concept, discusses the different definitions of HANPP that can be found in the literature (in particular the distinction between area-specific and consumption-based approaches), reports what is known on patterns and trajectories of global and regional HANPP, and discusses implications of HANPP (in particular as related to planetary boundaries, analysis of systemic feedbacks in the land system, and biodiversity). So far, HANPP research has focused on terrestrial ecosystems, which is also the focus of this review. The penultimate section briefly summarizes studies related to aquatic systems.

CONCEPTS, DEFINITIONS, METHODS

A Plethora of Definitions Inside a Short History of HANPP Research

The first precursor of current HANPP research was presented in the article "Primary Production: The Biosphere and Man," by the ecologists Whittaker & Likens in the 1973 inaugural volume of *Human Ecology* (6). At that time, the International Biological Program, inspired by writings of systems ecologists such as Lotka (21), Lindeman (22), and the Odum brothers (23, 24), emphasized the importance of primary production and had inspired a wealth of empirical studies on energy flows and nutrient cycles in ecosystems (25). The article estimated global NPP and related it to the direct human consumption of biomass for food, timber, and other purposes, which the authors found to be on the order of a few percent of NPP—a result hardly raising concerns.

An article published over a decade later by Vitousek and colleagues in *BioScience* (7) received more attention. Calling their indicator the "human appropriation of the products of photosynthesis," they proposed three different estimates (or definitions) of what we here call HANPP: (*a*) a low estimate that included only the biomass consumed by humans and livestock (a similar approach as in Reference 6); (*b*) an intermediate estimate that also considered the entire NPP of human-dominated ecosystems (cropland, tree plantations) as appropriated; and (*c*) a high estimate that further included the human impacts on NPP (below denoted as $\text{HANPP}_{\text{luc}}$). They confirmed that the direct human biomass consumption (the lowest of their categories) indeed amounted to only a few percent of NPP, but their results based on the more inclusive intermediate and high definitions—27% and 39%, respectively, of potential terrestrial NPP—was widely discussed. For example, it was used as an indicator of the scale of human activities as a component of global ecosystems and its possible implications for limits to economic growth (8, 26). The argument boiled down to the idea that if humans already claimed $\sim$40% of global land-based NPP now, their future number and resource consumption could likely not be multiplied without breaching global ecological limits (27). However, that notion lost credit because it was argued that biomass harvest—and even more so, economic activity—can increase without commensurate increases in HANPP, a claim (28) that was supported by empirical long-term studies (29, 30; see below).

The seminal article by Vitousek and colleagues was soon followed by a paper by Wright (10) that used basically the same numbers but proposed still another definition of HANPP that emphasized

Biomass: the multitude of biochemical compounds making up the bodies of living organisms; it may be measured as fresh weight, dry matter, or carbon content

Net primary production (NPP): GPP minus plant respiration, i.e., the energy required by the plant for its own metabolism

Autotrophs: organisms capable of using solar energy (or other energy inputs) to synthesize organic materials from inorganic compounds, e.g., through photosynthesis

Gross primary production (GPP): the entire amount of CO_2 fixed by autotrophs, e.g., green plants capable of photosynthesis

Heterotrophs: organisms requiring uptake of organic material as a source of energy and chemical compounds for sustaining their metabolism

Socioecological systems: a term coined for the interdisciplinary analysis of the dynamic, systemic feedback and interaction processes involved in the interaction of human societies with ecosystems

THE DEFINITION OF HANPP IN THIS REVIEW

Based on Wright (10), Haberl and colleagues (11, 13, 16, 29, 37) defined HANPP as the sum of harvest and land use–related changes in NPP. In this work, HANPP is defined as the difference between the NPP of the natural vegetation thought to exist in the absence of land use [denoted as NPP_{pot}; i.e., the NPP of potential natural vegetation (152)] and the fraction of NPP remaining in the ecosystem after harvest under current conditions (denoted as NPP_{eco}; i.e., the NPP remaining in the ecosystem). That is, HANPP equals NPP_{pot} minus NPP_{eco}. This definition includes wood harvest and human-induced fires. NPP_{eco} is calculated by subtracting harvested NPP (denoted as $HANPP_{harv}$) from NPP_{act}, i.e., the NPP of the currently prevailing vegetation. Changes in NPP resulting from land conversion and land use—i.e., the difference between NPP_{pot} and NPP_{act}—are denoted as $HANPP_{luc}$. This notation is from Reference 16; different acronyms were used in the previous work, but the basic concept is the same. Unless explicitly stated otherwise, this is the definition of HANPP used in the present review.

the difference between potential and actual biomass availability in ecosystems. Wright's main intention was to use HANPP as an indicator for pressures on biodiversity, based on the so-called species–energy hypothesis (see below). He therefore considered as "appropriated" only that biomass actually lost as input to food webs; this definition included changes in NPP resulting from land use (denoted as $HANPP_{luc}$ below). Because of his less inclusive definition, Wright's estimate of global terrestrial HANPP was lower than that of Vitousek et al. (20–30% of potential NPP). DeFries (31) quantified human impacts on NPP but did not estimate harvest-related biomass flows. The definition of HANPP proposed by Haberl and colleagues, which is the basis for most of the following discussions, can be found in the sidebar.

Later work on global HANPP by Rojstaczer and colleagues (32), who used Vitousek et al.'s intermediate definition, claimed the existence of an enormous error range (10–55% of potential NPP) of global HANPP estimates. This study was based on global average factors and had not taken into account the wealth of spatially explicit data that had already been available at that time (33, 34). A recalculation of Vitousek et al.'s three definitions of HANPP using a highly resolved global database for the year 2000 confirmed Vitousek et al.'s original estimates, despite the much richer databases considered in that later study (13). As shown in a sensitivity analysis (16), robust estimates of HANPP trajectories can be derived despite substantial uncertainties such as the difficulties in estimating the effect of climate change on NPP. Apparently, the large range of HANPP results stems from the use of different definitions rather than from uncertainties in data. **Table 1** summarizes the different definitions used in the various studies and reports their respective estimates of global HANPP.

The abundance of different HANPP definitions and calculation details (**Table 1**) has been used as an argument against the HANPP concept altogether (35, 36). But the choice of definition depends on the context and aims of the respective study. For example, in HANPP studies aiming to measure human "colonization" or "domination" of ecosystems (11, 13, 16, 37) or to analyze pressures on biodiversity (38), an appropriate definition would include land use–related impacts on NPP and would count by-flows such as unused crop residues or roots as appropriated but would not include the entire NPP of human-dominated systems. In other contexts, such as in studies focused on human impacts on the land's carbon balance, a more suitable definition might exclude backflows to nature such as crop residues left on the field or manure dropped by grazing animals. Of course, any decision needs to be made explicit to allow correct interpretation of the results.

Biodiversity: diversity of life on all levels of organization, from genes to ecosystems

Table 1 Different definitions of HANPP, and related estimates of global HANPP

Study authors and reference	Definition (see text for details)	HANPP absolute (PgC/year)	HANPP relative (% of NPP_{pot})[a]	Year of reference
Whittaker & Likens (6)	Biomass directly used by humans for food, feed, timber, etc.	1.6	3%	1950s
Vitousek et al. low (7)	Biomass directly used by humans for food, feed, timber, etc.	2.6	3%	1970s
Vitousek et al. intermediate (7)	Direct human biomass consumption, wood harvest by-flows, NPP of "human-dominated ecosystems," land clearing, and human-induced fires	20.3	27%	1970s
Vitousek et al. high (7)	As "intermediate" plus NPP lost through land conversion (e.g., desertification, ecosystem degradation)	29.5	39%	1970s
Wright (10)	Difference between potential NPP and NPP remaining in the ecosystem after harvest; wood harvest and fires excluded	17.7	24% (20–30%)	1970s–1980s
Rojstaczer et al. (32)	Vitousek et al., intermediate	19.5 ± 14	32% (10–55%)	1980s–1990s
Imhoff et al. (12)	In terms of system boundaries like Vitousek et al., but using a consumption-based approach	11.5 (8.0–14.8)	20% (14–26%)	1995
Haberl et al. (13)	Difference between potential NPP and NPP remaining in the ecosystem after harvest; wood harvest, human-induced fires, and by-flows included	15.6	24%	2000
Krausmann et al. (16), year 1910	Same as Reference 13	6.9	13%	1910
Krausmann et al. (16), year 1950	Same as Reference 13	9.3	18%	1950
Krausmann et al. (16), year 2005	Same as Reference 13	14.8	25%	2005

[a] Estimates of potential NPP (NPP_{pot}) vary considerably between studies, amounting to 54 PgC/year (6), 66 PgC/year (13), or 75 PgC/year (7). (PgC, petagrams of carbon.)

Area-Specific Versus Consumption-Based HANPP Approaches

The first HANPP studies by Whittaker & Likens, Vitousek et al., and Wright were global and did not attempt to measure HANPP at any level below the global total. With the first studies applying HANPP to smaller spatial scales—e.g., to national (11, 29) or subnational (39) levels or in maps (13, 37, 40)—the question emerged whether HANPP relates to a spatially delineated land surface or to the consumption of the humans living within a defined region. Motivated by the idea that HANPP should be an indicator of land-use intensity and of the impacts of human activities on ecosystems and biodiversity, these first studies defined HANPP with reference to a spatially delineated land area (41), which is referred to in this article as the area-specific HANPP approach. The definition used in these studies is summarized in stylized form in **Figure 1**; for the notation see the sidebar on "The Definition of HANPP in This Review."

Such area-specific definitions of HANPP are useful to indicate the effects of land use on ecosystems on the land area within certain boundaries, but they ignore the effects of the production of imported products by the people living in a region on land outside the region's boundaries. If

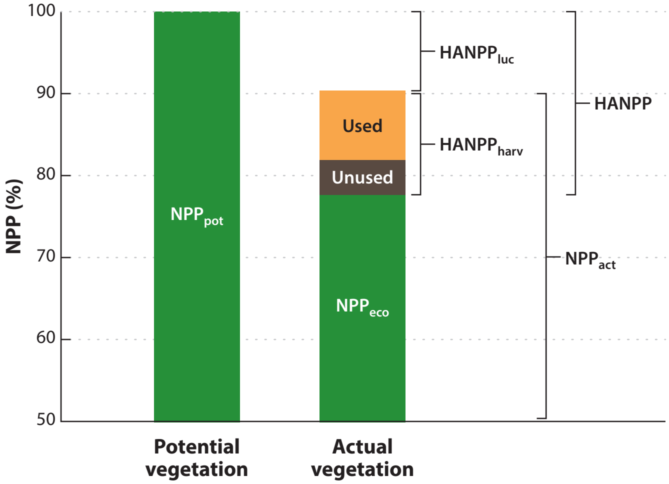


Figure 1

Definition of HANPP explained using global estimates for the year 2000. From a socioeconomic perspective, HANPP is the sum of productivity changes resulting from land conversion and land use ($HANPP_{luc}$) and harvest ($HANPP_{harv}$), and from an ecological perspective it is the difference between potential (NPP_{pot}) and current (NPP_{eco}) yearly biomass availability in ecosystems. The graph is stylized: NPP_{pot} may change over time, e.g., due to climate change; $HANPP_{luc}$ may also be negative, e.g., where the NPP_{act} of irrigated and fertilized agro-ecosystems exceeds NPP_{pot}. In the year 2000, $HANPP_{luc}$ accounted for 40% of global HANPP, and $HANPP_{harv}$ accounted for 60% (13). Two-thirds of $HANPP_{harv}$ was actually used for economic activities (used extraction, $HANPP_{ue}$), whereas unused fractions such as residues left on the field, roots of trees or crop plants, and human-induced fires amounted to one-third (52). Approximately 60% of the used extraction served as animal feed (grazing, fodder, etc.), whereas only 14% was directly used by humans as plant-based food; 16% of used extraction is wood harvest for fibers and fuel. (Source: redrawn after Reference 18, using the notation of Reference 16.)

land use within those boundaries serves to produce goods for export, its effect is counted, but the land requirements of imported products are not.

The study by Imhoff et al. (12) proposed an approach that allows including such flows by estimating HANPP from data on national-level biomass consumption. Using the intermediate definition of Vitousek et al., it used a set of literature-derived multipliers to account for biomass flows associated with the consumption of biomass products, such as losses in the production chain (felling losses, crop residues, etc.). This approach opened a new direction of HANPP research focused on resource consumption, akin to the ecological footprint approach (42, 43). This consumption approach later led to the development of the embodied HANPP (eHANPP) concept (19, 44, 45).

Embodied HANPP (eHANPP): HANPP resulting from the production of a defined good or service throughout its entire chain of production

The eHANPP method allows researchers to account for the HANPP resulting from the production chain of a product, or of the entire consumption within a defined entity, such as a national economy. First calculations differentiated only a few product groups and used a net trade approach to allocate global HANPP to the consumption of each nation. This approach can be used to calculate the average per capita HANPP embodied in each country's consumption and to map global patterns of eHANPP (44, 45). The analysis of trade between individual countries or the depiction of flows of individual products requires data from bilateral trade matrices; such databases (19) are powerful tools to analyze socioeconomic drivers of HANPP, including changes in consumption patterns, trade, and many other important socioeconomic factors. In the remainder of this article, the abbreviation HANPP denotes the area-specific approach, whereas eHANPP denotes the consumption-based approach. If not explicitly stated otherwise, the HANPP definition as explained in **Figure 1** and the sidebar is used.

An Overview of Methods and Data to Quantify HANPP

As shown in **Figure 1**, HANPP can be calculated using the following parameters: NPP_{pot}, NPP_{act}, NPP_{eco}, $HANPP_{harv}$, and $HANPP_{luc}$. HANPP can be calculated either as the sum total of $HANPP_{luc}$ and $HANPP_{harv}$ or as the difference between NPP_{pot} and NPP_{eco}, where NPP_{eco} is NPP_{act} minus $HANPP_{harv}$. Whereas some studies focus on estimating $HANPP_{luc}$ based on land-use data (7, 16), others use these data together with remotely sensed information to directly estimate NPP_{act} and calculate $HANPP_{luc}$ by subtracting NPP_{act} from NPP_{pot}. In both cases, an estimate of NPP_{pot} is required that can be derived by vegetation models of varying complexity: Empirical models (46–49) use correlations between climate and measured productivity at individual sites, using data sets collected during the International Biological Program (e.g., 50). Dynamic vegetation models are stock-flow models that simulate a plethora of ecological processes, including the exchanges between plants and atmosphere such as GPP and plant respiration, using spatially explicit climate data (51). $HANPP_{harv}$ is derived from agricultural and forestry statistics combined with material and energy flow methods (52, 53), land-use data, and simple models based on a large array of statistical data combined with basic physiological knowledge and thermodynamic considerations to close data gaps (for details, see the supporting online material in References 13, 16). Different approaches are used to estimate NPP_{act}. NPP_{act} on cropland can be extrapolated from data on crop harvest, using appropriate coefficients for the share of crop harvest in aboveground biomass (harvest indices) and ratios of aboveground to belowground biomass (54). NPP on forestland and grassland is usually derived with a vegetation model taking information on soil degradation and irrigation into account. Deriving land-use data sets suitable for robust HANPP calculations involves substantial efforts because a closed-budget approach is required to be able to consistently combine data from remote sensing, vegetation modeling, and statistical data sets in spatially explicit (geographic information systems, or GIS) databases (13, 55). Closed budget means that for each pixel, the sum of land-use classes (e.g., infrastructure, cropland, forestry, grazing, and wilderness) must total 100% and that national totals can be related to national totals of the respective land-use classes as reported in agriculture and forestry statistics (55).

The estimation of NPP over larger areas or over time involves considerable uncertainties (47, 56) related to the used statistical data, to the assumptions underlying the applied estimation procedures, and to the NPP data derived from global vegetation models (57). Although such uncertainties in estimating NPP also affect HANPP calculations, careful estimation procedures can minimize the effect. For example, one may choose methods in which over- or underestimation of NPP_{pot} will result in a similar over- or underestimation of NPP_{act} such that the result for $HANPP_{luc}$ remains valid. Sensitivity analyses (16) suggest that these strategies to reduce uncertainty lead to reasonably robust estimates of HANPP even for long periods of time, e.g., the last century—meaning that although there is some uncertainty in terms of the absolute value of HANPP, the trends that are found when using substantially different assumptions on key factors are still similar (16).

An important question related to the calculation of harvested NPP ($HANPP_{harv}$) is how inclusive a definition is appropriate in the respective context. Biomass harvested for direct human use (food, raw materials) is included in all assessments; more encompassing notions of harvest also include biomass fed to livestock or plants killed by human activities or human-induced fires (7, 41). For many political units, from districts to nations, data on biomass flows such as crop or timber harvest are available in agricultural and forestry statistics, but biomass grazed by livestock or crop

NPP_{pot}: NPP of the potential natural vegetation, i.e., the vegetation assumed to exist in the absence of human land use under given climatic conditions

NPP_{act}: NPP of the currently prevailing vegetation

NPP_{eco}: fraction of NPP_{act} remaining in the ecosystem after harvest

$HANPP_{harv}$: harvested biomass, including biomass destroyed during harvest (e.g., roots of plants killed, biomass burned in human-induced fires)

$HANPP_{luc}$: HANPP resulting from land conversion and land use; it includes changes in NPP resulting from conversion of native vegetation to agro-ecosystems or infrastructure

HANPP EFFICIENCY

The ratio of harvested biomass to total HANPP is a measure of the efficiency of land use. The higher the HANPP efficiency, the larger the fraction of biomass that can be used for human purposes, compared with the total human impact on ecological energy flows. Depending on research question and data availability, HANPP efficiency may be calculated as the ratio of used biomass extraction (HANPP$_{ue}$) to HANPP or as the ratio of HANPP$_{harv}$ to HANPP. Although the second definition requires less data, the first is often more useful because it also considers that not all biomass affected by harvest activities (and included in HANPP$_{harv}$) is actually used, e.g., forest slash or some crop residues. HANPP intensity is the inverse of HANPP efficiency; it represents the HANPP related to a defined amount of biomass used by humans or to a biomass-derived product.

residues is usually not reported. Standardized estimation procedures have been developed to close these data gaps. Unused fractions of crop and wood harvest (unused crop residues, forest slash, and belowground compartments) are often extrapolated from harvested fractions using standard coefficients (52, 58, 59).

Regular burning of grasslands (such as to prevent reestablishment of woody plants) was also included in some HANPP assessments (13, 16, 60). However, it is conceptually intricate to assess biomass burned in human-induced open vegetation fires because humans often also inhibit the outbreak of natural fires and thereby potentially decrease the amount of biomass burned compared with the potential vegetation (41, 60).

The definition of different components of HANPP allows for the generation of intensive variables and indicators. One particularly interesting ratio is the so-called HANPP efficiency ratio, which can be assessed as the share of harvested biomass (either used extraction, abbreviated HANPP$_{ue}$, or HANPP$_{harv}$) in total HANPP, e.g., as HANPP$_{ue}$/HANPP (see sidebar on "HANPP Efficiency") (61, 62). Land-use systems with low HANPP$_{luc}$ are characterized by a higher HANPP efficiency than are those with large productivity losses. A high HANPP efficiency is related to a high share of harvest in total HANPP because the bulk of the appropriated biomass enters the socioeconomic system. The calculation of HANPP efficiency provides additional information, in particular in time series analysis, as it allows the analysis of mechanisms underlying land-use transitions (63).

The reciprocal term to HANPP efficiency (e.g., HANPP/HANPP$_{ue}$) can be interpreted as HANPP intensity, providing information on the amount of HANPP associated with each unit of biomass harvest (64). Such indicators are used in consumption-based approaches to extrapolate HANPP flows from the amount of consumed biomass products (12). At the national and subnational scales, simple approaches have been proposed that use only a limited number of product aggregates and world-average multipliers to estimate the HANPP associated with imported goods (44). More sophisticated approaches are based on bilateral trade matrices and highly detailed trade statistics to account for differences in upstream requirements at the product-group level as geographic differences in land-based production (19).

HANPP$_{ue}$: used extraction of biomass refers to the fraction of HANPP$_{harv}$ that is used in socioeconomic processes (e.g., feed for domesticated animals or food for humans)

PATTERNS OF GLOBAL HANPP

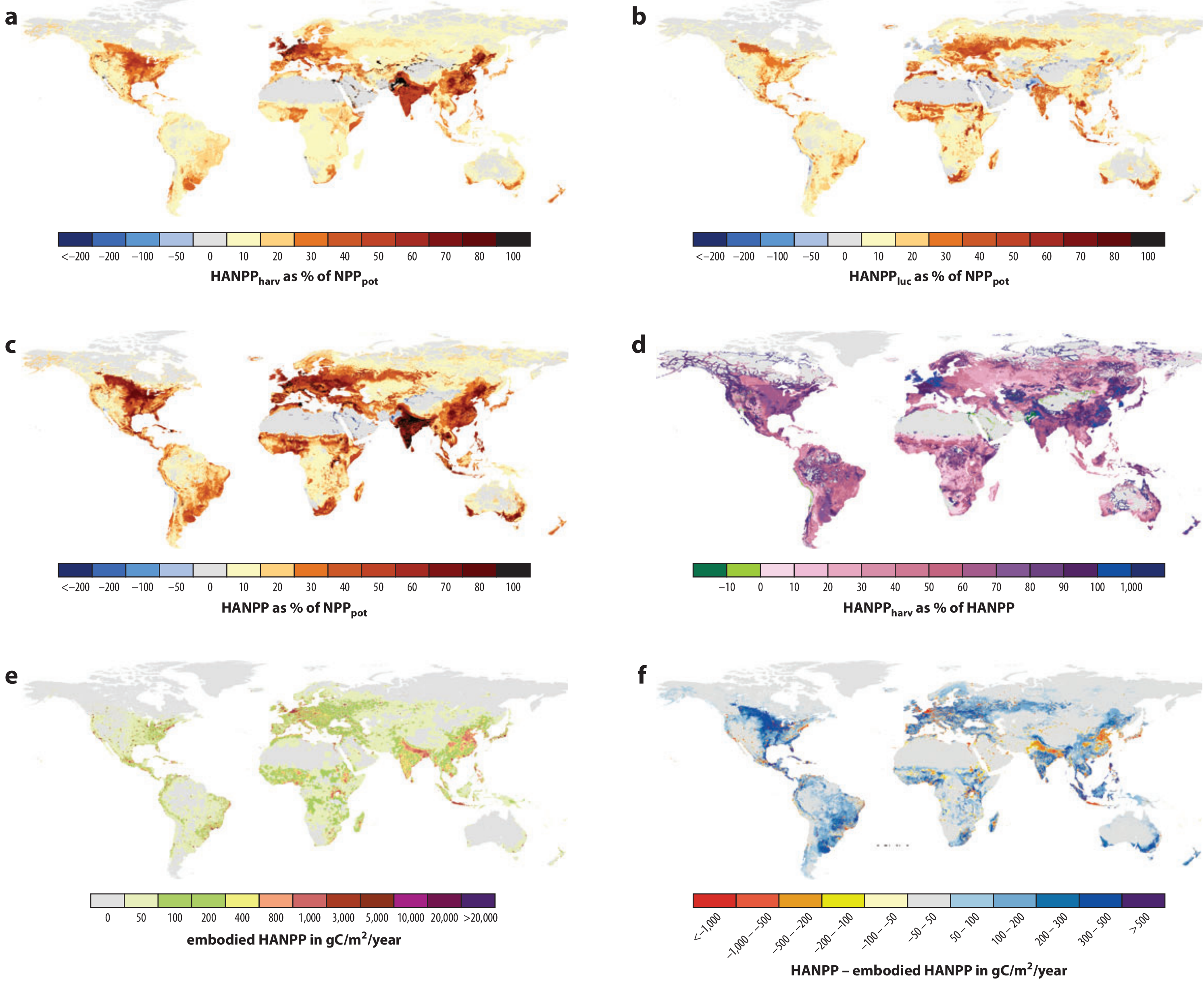
Global Patterns of Area-Specific HANPP

Area-specific assessments of HANPP allow researchers to localize the impact of human activities on ecosystems. These assessments consistently show that cropland and infrastructure/settlement areas are characterized by the highest HANPP per unit area values (70–85% of NPP_{pot}; 13). Grazing and forestry are associated with lower HANPP values in the global average (19% and 7% of NPP_{pot}, respectively; 13), with notable regional exceptions (e.g., extremely high values of HANPP are found on grazing lands in India). Infrastructure area is mostly situated in regions that are the most productive (65), but its contribution to overall HANPP is small owing to the small extent of this land-use type. Cropland, in contrast, contributed around 50% to the global HANPP in 2000, despite its relatively confined extent (12% of the terrestrial ice-free surface), due to its high HANPP per unit area (13). Consequently, at the global scale, areas dominated by cropland and infrastructure are characterized by high $HANPP_{harv}$ and HANPP values (**Figure 2*a*** and ***c***). Lower overall HANPP values can be found in regions dominated by forestry and grazing, and little or no HANPP prevails in regions dominated by wilderness or very low land-use intensity. In regions where land-use intensification techniques boost plant productivity, particularly on croplands in industrialized agriculture or in arid areas with high irrigation potential (e.g., near streams), $HANPP_{luc}$ can be negative (**Figure 2*b***). This can result in low or even negative HANPP, albeit with confined regional extent, because enhanced plant growth is usually associated with large harvests (**Figure 2*a*** and ***c***). As shown in **Figure 2*c***, aggregate HANPP (as a percentage of NPP_{pot}) in 2000 is comparably low in Central Asia, the Russian Federation, and Oceania (including Australia). The highest HANPP values are found in South and Southeast Asia as well as in Europe. When measured in annual carbon flows, a somewhat different picture of HANPP patterns emerges, as the amount of HANPP correlates to certain degrees with the NPP_{pot}. For instance, HANPP measured as carbon flow per unit area may be low in a region because of low intensity of land use compared with the productive potential but also because of a low productive potential of the land due to aridity or low temperatures (18).

Human-induced fires, often counted as a component of $HANPP_{harv}$ (13), contributed ~12% to overall HANPP in 2000 and are particularly important in sub-Saharan Africa, Latin America, and Southeast and Central Asia, whereas in regions dominated by industrialized countries, anthropogenic vegetation fires play a minor role. One-third of this biomass flow is consumed in shifting cultivation, with a high concentration in Latin America and sub-Saharan Africa (60).

The contribution of $HANPP_{harv}$ (**Figure 2*a***) and $HANPP_{luc}$ (**Figure 2*b***) to overall HANPP differs between regions. HANPP efficiency ($HANPP_{harv}$/HANPP, **Figure 2*d***) is high in areas with low $HANPP_{luc}$, which are mostly areas with industrialized agriculture that leads to relatively high NPP_{act} values (situated primarily in regions of the temperate zone, e.g., northern Europe, China). In areas with negative $HANPP_{luc}$, HANPP efficiency ratios are larger than 1. Some areas with high population densities in nonindustrialized regions that are characterized by lower NPP_{act} also show high HANPP efficiencies, such as in southern Asia (66). A low HANPP efficiency is found in regions with low population densities, such as in parts of Central Asia and eastern and southeastern Europe, but also in parts of sub-Saharan Africa, Latin America, and Southeast Asia (**Figures 2*d*** and **3*b***).

One reason for a high $HANPP_{luc}$ is the agricultural yield gap prevailing in many regions of the world, particularly sub-Saharan Africa (67). Yield gap denotes the difference between current agricultural yields in a farm or region and the maximum yields achievable under similar production conditions, either in the same region or globally (see the sidebar on "Yield Gap") (67–69). The concept is constructed along a similar line of reasoning as the HANPP concept, as it contrasts the actual state in productivity with a hypothetical reference measure, which is technology-dependent, in contrast to NPP_{pot}. Another mechanism that leads to substantial levels of $HANPP_{luc}$ is human-induced soil degradation, particularly relevant in global dry lands. According to a recent study (70), 2% of the global terrestrial NPP are lost each year due to dryland degradation, which is 4–10%


a
<−200 −200 −100 −50 0 10 20 30 40 50 60 70 80 100
HANPP$_{harv}$ as % of NPP$_{pot}$
b
<−200 −200 −100 −50 0 10 20 30 40 50 60 70 80 100
HANPP$_{luc}$ as % of NPP$_{pot}$
c
<−200 −200 −100 −50 0 10 20 30 40 50 60 70 80 100
HANPP as % of NPP$_{pot}$
d
−10 0 10 20 30 40 50 60 70 80 90 100 1,000
HANPP$_{harv}$ as % of HANPP
e
0 50 100 200 400 800 1,000 3,000 5,000 10,000 20,000 >20,000
embodied HANPP in gC/m^2/year
f
<−1,000 −1,000 – −500 −500 – −200 −200 – −100 −100 – −50 −50 – 50 50 – 100 100 – 200 200 – 300 300 – 500 >500
HANPP – embodied HANPP in gC/m^2/year

YIELD GAP

The yield gap is defined as the difference between potential yields of a crop and the yields of the same crop actually achieved by farmers (67–69). In most definitions, yield potentials are determined by the yields that can be achieved in the absence of water or nutrient limitations as well as pests and diseases, i.e., under ideal conditions, with the best available technologies. Yield potentials can be estimated based on simulations with crop models, experimental fields, or maximum yields achieved by farmers under defined soil and climate conditions; these approaches also lead to different results (68).

of NPP_{pot} in dry lands, or 20–40% (in extreme cases 55%) of NPP_{pot} on degraded agricultural areas in the global average. This effect of degradation on NPP in dry lands is of similar scale as the overall annual socioeconomic biomass harvest on these lands.

Determinants of the pattern of global HANPP were analyzed with national-level data (18), revealing a strong positive correlation between the suitability of land (approximated by NPP_{pot}) and HANPP per unit area. Obviously, low initial productivity constrains land use and thus also HANPP per unit area, but with higher NPP_{pot}, HANPP can increase. Although no correlation was found between NPP_{pot} and population density, HANPP per unit area and population density were strongly positively correlated at the national level. This is plausible because HANPP per unit area and year is, by definition, the product of population density and HANPP per capita and per year. Population density varies between countries by a factor of over 700, whereas per capita HANPP is much less variable (factor of 40). At the subnational level, HANPP does not strictly follow gridded population density maps: For instance, although population density is highest in urban areas and much lower in intensively managed rural agricultural areas, HANPP is often lower in urban and semiurban environments than on croplands. The relationship between HANPP per capita and population density is strongly negative. This can be explained as a legacy of the historically evolved regional differences in production and consumption patterns determined by land availability and resource endowment (18): In regions with high population densities (low per capita land availability), diet patterns with a comparatively low share of animal protein evolved (e.g., Korea, Japan), associated with much lower level of $HANPP_{harv}$ than is required in the meat-rich diet of sparsely populated regions (e.g., in the Americas).

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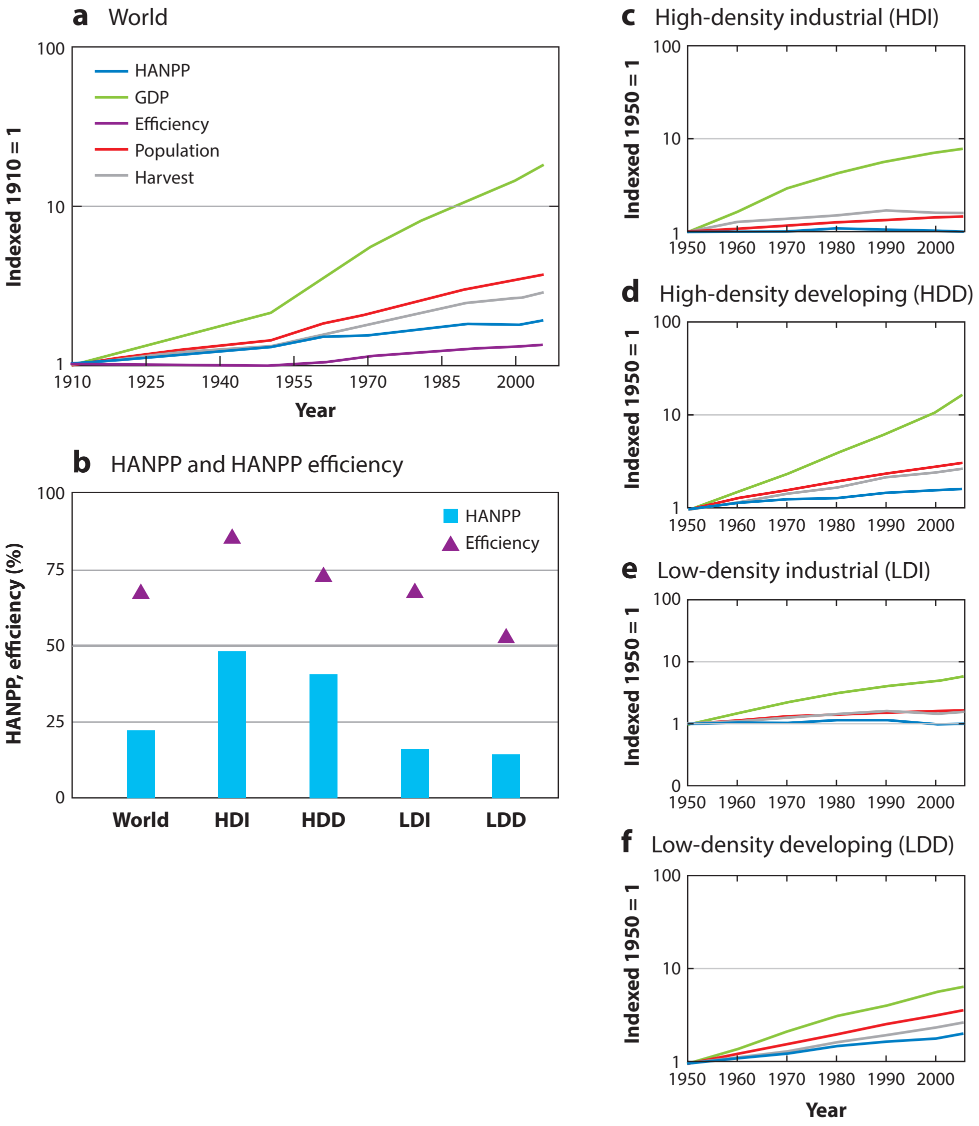
Figure 2

Global patterns of HANPP in 2000. (*a*) $HANPP_{harv}$, (*b*) $HANPP_{luc}$, and (*c*) HANPP as a percentage of potential productivity (NPP_{pot}). In *b* and *c*, negative values (*blue color gradient*) indicate areas in which current productivity (NPP_{act} in *b*) and the remaining NPP after harvest (NPP_{eco} in *c*) exceed NPP_{pot} owing to high inputs, particularly irrigation in arid environments. $HANPP_{harv}$ resulting from human-induced fires is not included in *a* or *c*. (*d*) HANPP efficiency, expressed as the ratio of $HANPP_{harv}$ to HANPP. The map shows the fraction of HANPP that can potentially serve as a socioeconomic resource. If HANPP is negative, so is HANPP efficiency ($HANPP_{harv}$ is always ≥ 0). In areas where NPP_{act} exceeds NPP_{pot} and NPP_{eco} is smaller than NPP_{pot} (areas of intensive agriculture with high fertilizer use or irrigation), HANPP efficiency exceeds 1 (*blue colors*). (*e*) Map of embodied HANPP associated with the consumption of biomass-derived products of the humans living in each grid cell. The map refers to HANPP equivalents of the apparent consumption of biomass products (domestic extraction plus imports minus exports). (*f*) The difference between HANPP and embodied HANPP of consumption in each grid cell, expressed in gC/m^2/year, showing areas where HANPP exceeds the consumption of embodied HANPP (positive values indicate net-producing areas; *blue color gradient*), and the opposite pattern (net-consuming areas; *yellow-red color gradient*). All maps are available at **http://www.uni-klu.ac.at/socec/inhalt/1088.htm**. Data sources: Reference 13 for *a–d*; Reference 44 for *e*, *f*. (*a–c*) Reprinted in modified form from Reference 13 according to the copyright policy of the *Proceedings of the National Academy of Sciences USA*. (*e*, *f*) Reprinted in modified form from Reference 44 (Erb et al. 2009, *Ecological Economics*, Vol. 69, pp. 328–34), with permission from Elsevier.

In per capita terms, $\mathrm{HANPP_{harv}}$ and HANPP are strongly correlated (18), although the relationship between final biomass consumption—i.e., the biomass contained in products purchased by final consumers—and $\mathrm{HANPP_{harv}}$ is much weaker. Biomass consumption is closely correlated with affluence and development, but the efficiency with which biomass is used increases, in general terms, with affluence. This compensates for the richer diets and other consumption patterns in affluent regions that tend to drive up HANPP. Furthermore, economic growth is also associated with growing biomass trade as well as with technological innovations that can help reduce a nation's HANPP per unit of biomass consumption (20).

Gridded population density information can be used to allocate per capita biomass flow data and therefore to map the spatial patterns of eHANPP (**Figure 2*e***; 12, 44). These maps reveal consumption hotspots in densely populated areas (e.g., in urban regions), as well as in areas with



comparatively high biomass consumption (e.g., in industrialized countries). Rural, intensively managed areas with low population density are characterized by low eHANPP consumption. National-level eHANPP is correlated neither with other resource-use indicators nor with GDP, owing to the differences in land-use efficiency mentioned above (20). However, only about half of the variation in national eHANPP can be explained by differences in national land-use systems because trade with biomass products plays a significant role.

Gross domestic product (GDP): the market value of all goods and services produced within a national economy in one year

PgC: petagrams of carbon, 1 Pg = 10^{15} g = 10^{9} t = 1 billion metric tons

Teleconnections in the Global Land System

The eHANPP concept can be used to analyze global teleconnections in the land system (19, 44, 71). Trade balances the difference between area-specific HANPP and consumption-related eHANPP. Contrasting imbalances between HANPP on a region's land and the eHANPP related to the consumption of its inhabitants allows a display of the spatial disconnect between biomass production and consumption (**Figure 2*f***). On almost half of Earth's surface (42% or 56 million km^2), production and consumption are unbalanced (44), with the remaining areas situated primarily in unfavorable climate with almost no land use (55). Net-consuming areas (eHANPP $>$ HANPP) are by a factor of four smaller than net-producing areas (eHANPP $<$ HANPP), and the "virtual" flow of eHANPP associated with international trade is found to be as large as 1.7 PgC/year, with a dominant flow direction from sparsely populated regions (e.g., the Americas, Oceania, Kazakhstan) to densely populated regions (e.g., China, Japan, the Netherlands), seemingly independent of development status. However, in 2000, only a few countries participated to a large extent in this international exchange: Ten countries, principally located in the Americas and Oceania, supply 86%, and ten countries, located in East Asia and Europe, consume 59% of the total HANPP embodied in global biomass exports. This is expected to change in the near to mid-term future, however, as trade volumes surge (72).

GLOBAL AND REGIONAL HANPP TRAJECTORIES

Changes in HANPP over time have been a major focus of HANPP research for more than a decade. Major factors that are known to codetermine HANPP—e.g., population density, food consumption, livestock husbandry, agricultural intensity, and deforestation and forest management—have changed since humans began managing terrestrial ecosystems through agriculture and forestry (36, 73). In the past 300 years, human population has increased by a factor

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Figure 3

Long-term development of HANPP, biomass harvest, HANPP efficiency (share of harvest in HANPP), population, and GDP (*a*) for the world 1910 to 2005 and (*c*–*f*) for specific country groups (low-density industrial/developing; high-density industrial/developing; see definitions just below) from 1950 to 2005. (*b*) HANPP as a percentage of NPP$_{pot}$ and HANPP efficiency in 2005. In *c*–*f*, countries are grouped according to a population density threshold of 50 cap/km^2 in 2005 and development status. The "industrial" groups include the developed regions according to a UN classification (see **http://unstats.un.org/unsd/methods/m49/m49regin.htm#developed**) and the former Soviet Union. All other countries are subsumed under "developing." During the past 100 years, global HANPP has been growing, but at a much slower pace than GDP, population, and harvest. The decoupling of HANPP from population occurred only since 1950 (as shown in *a*) in all country groupings, although biomass harvest has been largely growing with population in that period (*c*–*f*). In the industrial countries, HANPP has been remarkably stable, but it has been growing considerably in the developing countries. The decoupling of HANPP from population growth has been largest in the fast-growing high-density developing countries. Densely populated countries have a much higher HANPP than sparsely populated countries and also a higher HANPP efficiency; HANPP grew fastest in the low-density developing countries. Human-induced fires are excluded. (Data source: Reference 16.)

of 10, with the concomitant expansion of agriculture resulting in a loss of 8–13 million km^2 of forest area (74) and with an expanding amount of biomass extracted by humans directly or through livestock grazing (36, 75). These developments had major implications for the NPP of land ecosystems, helped drive global HANPP to its current global average level of ∼25%, and shaped the patterns of HANPP discussed above. In this context, researchers ask two key questions: What factors determine changes in HANPP over time and how is HANPP related to the growth of human population and economic activity, in particular agriculture, energy use, and food consumption.

Regional Trajectories

Empirical evidence for the development of HANPP over time became available only in the past 20 years. The first national case study that analyzed the development of aboveground HANPP in a centennial time series yielded estimates of aboveground HANPP for Austria for 1830 to 1995 (29). Contrary to widespread assumptions that HANPP would grow in parallel with population and affluence (8, 27), it turned out that HANPP declined from ∼60% to ∼50% during industrialization, while population doubled and biomass harvest increased by ∼70%. A number of national-level case studies corroborated these general findings: In the United Kingdom, aboveground HANPP fluctuated between 60% and 70% without a clear trend throughout the period from 1800 to 2000, while biomass harvest doubled (76). A similar decoupling of biomass harvest and HANPP was observed in Spain (77), Italy (62), Hungary (78), and the Czech Republic (79). In these European countries, HANPP efficiency ($HANPP_{harv}$/HANPP) increased over time (18, 20). In the second half of the twentieth century, HANPP efficiency grew more strongly than harvest in all countries, resulting in a stable or declining HANPP. The country-specific cases identified two important factors behind this decoupling: (*a*) an increase in forest area at the expense of agricultural area and (*b*) an increase in the NPP of agricultural land, in particular cropland. Both trends drive increases in average national NPP_{act} and consequently contribute to a decline in $HANPP_{luc}$. The reductions in $HANPP_{luc}$ overcompensate for the growth of $HANPP_{harv}$ and the expansion of built-up land with a high $HANPP_{luc}$—two factors that would otherwise drive up HANPP.

In contrast to these European countries, in the Philippines HANPP doubled from 1910 to 2005 (80). HANPP growth resulted from massive deforestation and large increases in biomass harvest. After 1970, however, HANPP stabilized at the high level of 60%, as deforestation ground to a halt and agricultural productivity increased with the introduction of green revolution technologies. Kastner (80) has argued that European countries had experienced large-scale deforestation earlier, whereas in the Philippines this process began only in the twentieth century; in that island nation, rapid deforestation and slash-and-burn agriculture resulted in steep growth of HANPP in the first part of the twentieth century. After 1970, similar mechanisms as those observed in Europe resulted in a decoupling of HANPP from biomass harvest and helped to stabilize HANPP. A study for South Africa (81) found low and stable HANPP in the period 1961–2005 owing to a remarkably stable land-cover pattern and increasing HANPP efficiency. In New Zealand, a decrease of HANPP occurred after 1980, before which the HANPP trajectory showed alternating phases of increase and stagnation, while HANPP efficiency steadily increased (61).

A study by Krausmann et al. (63) compared six long-term national HANPP studies for Austria, the United Kingdom, Hungary, Spain, the Philippines, and South Africa and pointed to remarkable similarities among these HANPP trajectories, despite considerable biogeographic and socioeconomic differences. Based on these cases and on cross-country analyses (18, 20), a general model for changes in HANPP during agrarian-industrial transitions was proposed (82, 83), according to which HANPP increases during early periods of industrialization (albeit usually more slowly than population), when growing demand for agricultural produce is met by expanding agricultural land. In this phase, population growth is usually stronger than the growth of yields, and HANPP can reach high levels that may exceed 70% of $\mathrm{NPP}_{\mathrm{pot}}$. Agricultural intensification, in particular the green revolution (84, 85), helps to reverse this trend: Increases in land-use intensity can lead to increasing harvests without increasing HANPP. In combination with the reforestation of marginal land within the so-called forest transition (86, 87), these trends can reduce HANPP by reducing $\mathrm{HANPP}_{\mathrm{luc}}$, even while $\mathrm{HANPP}_{\mathrm{harv}}$ is growing. The Krausmann et al. (63) study emphasized that trade can weaken the link between population growth, domestic biomass demand, and HANPP. For example, both the United Kingdom and the Philippines import large amounts of their food and biomass demands, which contributes to keeping domestic HANPP low but results in higher HANPP elsewhere on the planet (19, 44). Hence, increasing trade volumes may influence national HANPP trajectories.

Bioenergy: energy derived from living or recently living organisms; includes solid, liquid, and gaseous energy carriers

Global Changes in HANPP

A first assessment of the global long-term HANPP trajectory (16) quantified HANPP for six world regions, showing that global HANPP increased from 6.9 gigatons of carbon (GtC)/year in 1910 to 14.8 GtC/year in 2005, or from 13% to 25% of $\mathrm{NPP}_{\mathrm{pot}}$. This growth was much slower than that of population, GDP, or biomass harvest (**Figure 3**). Measured as a percentage of $\mathrm{NPP}_{\mathrm{pot}}$, HANPP increased most strongly in Asia, Latin America, and Africa and was stable or even declined in the industrial countries and the former Soviet Union. In all regions, HANPP grew at a smaller rate than population size; hence, HANPP per capita declined by 28–56% during the twentieth century. Although harvest and biomass use increased roughly threefold at the global scale and by and large as rapidly as population numbers, $\mathrm{HANPP}_{\mathrm{luc}}$ declined and helped to slow HANPP growth. HANPP efficiency (i.e., the ratio $\mathrm{HANPP}_{\mathrm{harv}}$/HANPP) improved from 0.48 to 0.63. Based on past trends and the forecasts for population and the economy, as well as on different assumptions regarding future bioenergy use, the study also presented scenarios for future HANPP. Assuming that past improvements in HANPP efficiency will continue, the calculations indicate that it might be possible to meet global biomass demand in 2050 with comparatively modest increases in HANPP of 7–17% over the present HANPP value. However, the expansion of biomass for bioenergy toward potential deployment levels identified by the Intergovernmental Panel on Climate Change's *Special Report on Renewable Energy Sources and Climate Change Mitigation* (88) (an additional 50–250 exajoules/year) could increase global HANPP by up to 80% to perhaps 44% of $\mathrm{NPP}_{\mathrm{pot}}$. A major and perhaps bold assumption underlying these scenarios is that further improvements in HANPP efficiency can be achieved through sustainable intensification (89, 90).

Decoupling of Population, GDP, and HANPP

This research demonstrates that, due to increases in efficiency, HANPP can decline even if population, the economy, and biomass consumption rise. However, in the past, such decoupling of HANPP from socioeconomic growth came at considerable ecological costs (16, 63). Increases in the NPP of agro-ecosystems were achieved by expanding irrigation, applying massive amounts of fertilizers and pesticides, and reducing the diversity of agricultural landscapes with ensuing negative consequences for soils, groundwater, and biodiversity (5, 91). Improvements in HANPP efficiency were also often related to a deterioration in agriculture's energy efficiency, measured as energy return on investment, or EROI (see sidebar) (92, 93). These aspects clearly suggest that HANPP is not an all-encompassing indicator of ecological pressures resulting from land use (63) and cannot detect all relevant problem shifts. It has a narrow focus on energy flows in terrestrial ecosystems and indicates negative environmental consequences of land use (intensification) only

ENERGY RETURN ON INVESTMENT (EROI)

Humans need to invest energy to extract energy from their environment. For example, hunter-gatherers need muscle power to collect edible plants and kill their prey, agriculturalists expend work and draught power of animals to secure their harvest, oil exploration and drilling as well as coal mining require energy, etc. The ratio of energy gained for human use to energy invested by humans is denoted as energy return on investment, or EROI (92, 93). Agricultural EROI refers to the energy content of agricultural produce per unit of energy invested in agricultural activities. Biomass extracted from agro-ecosystems is the dominant energy source of agrarian societies, and hence these societies vitally depend on a positive EROI of agriculture (usually at or above 5:1). In contrast, industrial societies can afford to subsidize agriculture with energy based on fossil fuel–driven technologies, and these societies' agricultural EROI declines and may even drop below 1:1 (64).

if human activities reduce NPP. By focusing on NPP, HANPP also excludes issues related to the quality of this NPP with respect to ecosystem services and human needs (35). The long-term studies underscore the importance of combining HANPP with other suitable indicators in order to draw robust conclusions for sustainability of land use.

Long-term HANPP studies also point to the need for further NPP research. Estimates of NPP derived from remote sensing differ considerably from model outputs in terms of long-term trends. Global NPP derived from satellite data using the Moderate Resolution Imaging Spectroradiometer (MODIS) NPP algorithm for the period from 1982 to 2009 (94, 95) was almost perfectly stable at 53.6 PgC/year, with less than 2% year-to-year variation (96). Drawing heavily on remotely sensed data, e.g., on indicators such as the leaf area index (LAI), the fraction of photosynthetically active radiation (FPAR), and climate and land-cover data, this algorithm is still no direct measurement of NPP, but it is perhaps the closest currently available proxy. In contrast, however, dynamic global vegetation models, which calculate NPP based on climate, soil, and land-use data, typically indicate long-term increases in global NPP attributed to climate change, in particular CO_2 fertilization (97). For example, LPJmL, a vegetation model used in many HANPP studies, indicates an increase of global NPP from 55 to 59 PgC/year between 1980 and 2005 and of 15% between 1910 and 2005 (16), driven by CO_2 fertilization and climate change. Although currently used methods to estimate HANPP are capable of dealing with uncertainties in NPP_{pot} (16), this discrepancy needs to be considered in interpreting observed changes in NPP_{act} and NPP_{eco}.

ECOLOGICAL IMPACTS RELATED TO HANPP

Human Impacts on Biogeochemical Cycles

HANPP quantifies the extent to which human activities alter biomass flows in ecosystems, i.e., how biomass availability in an ecosystem differs between a hypothetical natural state and the current situation. Because biomass is the trophic energy potentially available to all heterotrophic organisms in an ecosystem, HANPP directly measures human impacts on trophic, i.e., nutritional, energy availability (7, 10). Given that dry-matter biomass consists of carbon (45–50%) and plant nutrients, HANPP is directly related to human impacts on the flows of carbon and nutrients in ecosystems. Because HANPP is also associated with a replacement of original vegetation, e.g., forests, with agro-ecosystems with different hydrological characteristics (evaporation, water retention capacity, etc.), HANPP is expected to be directly related to changes in the water cycle (9, 98). Fundamental ecological principles, above all those related to trophic-dynamic aspects of ecology (21, 22) and ecological energetics (23, 24, 99), suggest that HANPP is connected to changes in patterns, processes, and functions of ecosystems. This is to some extent self-evident, because many of these changes—e.g., prevalence or absence of certain species, maximization of the production of specific plant parts, or the maintenance of defined structures such as buildings and roads—are intended outcomes of the human activities (agriculture, forestry, etc.) accounted for in HANPP.

Land-related activities represented in HANPP also affect biomass (and hence carbon) stocks in ecosystems (37, 100). However, the relationship between stocks and flows of carbon in ecosystems is complex, and HANPP and human impacts on biomass stocks are far from perfectly correlated. The reason is that across ecosystems the range of carbon stocks is much larger than the range of NPP, and land use affects stocks and flows differently. For instance, if forests are replaced by croplands, large carbon stocks are depleted, but NPP may be similar or even higher (when $\text{HANPP}_{\text{luc}}$ is small or negative), although there are also instances when replacement of forests with agro-ecosystems results in significant $\text{HANPP}_{\text{luc}}$. Hence, losses of carbon stocks may be associated with NPP losses, but this is not always the case, and the NPP loss is often smaller than that of the carbon stock.

The Austrian case, for which consistent long-term data sets of HANPP and human impacts on the terrestrial carbon balance exist (29, 101–104), can be used to illustrate the complex interrelationship between land use, HANPP, and carbon stocks. The reduction of HANPP in Austria from 1830 to 1995 (see above) resulted from increases in crop yields by factors of 4–7, which allowed for a substantial reduction of cropland, meadow, and pasture areas as well as significant increases in forested area (from ∼37% to >45%). Carbon stocks in biota and soils increased substantially, which resulted about equally from increased forest area and from the growth of forest carbon stocks per unit area (103). This carbon sink can be largely attributed to the cessation of land-use practices such as forest grazing or litter raking that became obsolete with industrial production techniques in agriculture (105). Agricultural intensification helped to increase NPP_{act} even more than $\text{HANPP}_{\text{harv}}$, thereby allowing increases in forest area and stocking density to happen, despite increased biomass harvest. This increase in carbon stocks was related to direct and indirect inputs of fossil fuels in agriculture and has been denoted as "fossil-fuel powered carbon sink" (102). On the global level, however, carbon depletion due to expansion of agriculture into pristine ecosystem is not compensated for by the carbon sink in returning forests, leading to considerable net carbon emissions from land-use change (106, 107).

HANPP and Biodiversity

From the start of HANPP research, the suspected relevance of HANPP for biodiversity was an important research motivation. As early as 1986, Vitousek and colleagues (7, p. 368) wrote:

> *Homo sapiens* is only one of perhaps 5–30 million animal species on Earth . . . , yet it controls a disproportionate share of the planet's resources. . . . NPP provides the basis for maintenance, growth, and reproduction of all heterotrophs (consumers and decomposers); it is the total food resource on Earth. We are interested in human use of this resource . . . for what it implies for other species, which must use the leftovers . . . . The co-option, diversion, and destruction of these terrestrial resources clearly contributes to human-caused extinctions of species and genetically distinct populations.

Wright (108) had initially been interested in the species–energy hypothesis, primarily because of his interest in the determinants of biodiversity, following earlier work by Hutchinson (109) and Brown (110). The species–energy hypothesis claims that energy availability, in particular the availability of trophic energy, is an important factor determining large-scale patterns of biodiversity (111). It may also play a role in explaining the large gradient of species richness from the equator to the poles, although other factors may be even more important in that respect (112). Vitousek et al.'s (7) seminal HANPP study motivated Wright to take the species–energy hypothesis further by estimating the expected level of global species endangerment resulting from humanity's withdrawal of trophic energy from ecosystems. He performed a HANPP calculation based on a definition he believed to be best suited to estimate global species endangerment resulting from human withdrawal of energy from ecosystems (see above). The global HANPP level he found (20–30%) was consistent with estimates of global species endangerment and loss prevalent at that time (10).

Although popular among macroecologists and biogeographers (e.g., 110, 111, 113), the species–energy hypothesis is criticized by other ecologists. In particular, the idea that the interrelation between energy flow and species richness was monotonous (i.e., species richness should universally increase with energy flow) is contested. Other ecologists proposed a unimodal (hump-shaped) pattern in which species richness was expected to be highest at intermediate levels of energy availability and lower at low and high levels (114). It was argued that the monotonous pattern may prevail at larger scales but that the species–energy relationship was unimodal at smaller scales (115). A meta-analysis of empirical studies of the productivity–species richness relation published in 1999 suggested that monotonous and unimodal relationships were about equally frequent (116). However, a 2012 meta-analysis (117) concluded that earlier studies had misclassified many case studies as unimodal and suggested that if correct attribution methods were used and only robust studies were included, monotonous productivity–species richness relationships prevail at all scales.

Even if it were possible to demonstrate unequivocally that energy and species richness are positively related in more or less undisturbed ecosystems, it would not be self-evident that this relationship also holds in strongly human-dominated systems. Empirical tests are difficult for several reasons, most importantly because, according to the species–energy hypothesis, HANPP (i.e., the reduction of energy availability) should be correlated with species loss (i.e., the reduction of species richness). But although sufficiently detailed data on current species richness are becoming available, spatially explicit data on species loss or species endangerment compared with a hypothetical undisturbed level of species richness do not exist. So far, few studies have tested the relationship between energy availability in the ecosystem (NPP_{eco}) and species richness. Those that did (38, 118, 119) found that, consistent with the species–energy hypothesis, NPP_{eco} is monotonously correlated with species richness. These statistical tests provide indirect evidence that HANPP is correlated with species loss, but a direct test of the claim that HANPP results in species loss due to a reduction of trophic energy flows so far remains elusive and deserves more research in the future.

PLANETARY BOUNDARIES RELATED TO HANPP

Since HANPP's inception, one of the main motivations for its study has been to analyze biospheric limits to human activities on Earth (6, 7). Early attempts to directly interpret HANPP as an indicator of ecological limits to growth (8, 26, 27) lost credit due to the above-discussed decoupling of HANPP, population, and GDP. Recently, however, the publication of a widely discussed paper on planetary boundaries (120) triggered a new debate on the significance of primary production in terms of limiting human activities on Earth (96, 121, 122). In particular, the latter papers argued that NPP and HANPP were better suited as indicators of land-related planetary boundaries than the land-use indicator (a fixed percentage of cropland) used in the original publication (120).

Briefly, the argument is the following: Although it is very difficult to derive a meaningful estimate of the upper limit of the fraction of Earth's lands that can be sustainably used as cropland (or for livestock husbandry), humans can certainly not harvest more than is growing, at least not over longer periods of time (in forests, harvest can exceed increment, but this depletes the stock of standing timber and is hence unsustainable; 123). By intersecting NPP maps with GIS data on land use, land cover, HANPP, and ancillary data, one can estimate the upper limits of the yearly biomass production that might become available for human use in the future (96). Even if reconstructions of the past suggest that humans can increase the fraction of NPP that can be used as commercial product (e.g., the harvest index) as well as the efficiency with which biomass is used (e.g., the feeding efficiency of livestock or the amount of food losses), NPP remains an important limiting factor (121). Furthermore, increasing HANPP might result in negative climate feedbacks that negatively influence plant growth, as a systematic analysis based on a dynamic vegetation-climate system model suggests (124).

One can estimate the upper limits for the yearly flow of biomass that could be harvested without converting forests to herbaceous vegetation (crop fields, grazing lands). This is especially relevant in discussions on planetary boundaries related to bioenergy (122). Models that consistently account for competing demands for biomass within a conceptual framework derived from HANPP enable the exploration of the systemic interdependencies between food consumption, agricultural technology (in particular crop yields and feeding efficiencies), and area demand. Such models have been applied to estimate global bioenergy supply potentials under different assumptions about future food demand and agricultural technology (125–128). This work suggests that previous estimates of future global bioenergy potentials had most likely been too high, motivating a downward revision of bioenergy potentials in recent assessment reports (e.g., 129). It also helped researchers to better understand trade-offs (e.g., food-energy competition) and synergies (e.g., residue potentials) in the global land-use system (130).

One key question in that debate is the extent to which NPP can be increased through human activities, either purposively, through intensification, or inadvertently, through climate change, and at what cost. Regional studies (63; see above) as well as global maps (**Figure 2**) suggest that the NPP of intensively cultivated regions may exceed $\mathrm{NPP_{pot}}$ on regional levels. Nevertheless, the challenge of increasing $\mathrm{NPP_{act}}$ above $\mathrm{NPP_{pot}}$ over larger areas must not be underestimated. As discussed above, MODIS data indicate that global terrestrial NPP was constant in the last three decades, despite considerable land-use intensification (96, 122).

In principle, planetary boundaries related to NPP can be pushed. One option is to aim to increase NPP through, for example, irrigation, fertilization, soil management, and optimized crop rotation or intercropping schemes that use the vegetation period fully. This strategy requires substantial capital investments, energy, and know-how, sometimes at prohibitively high costs. A second option is for NPP to be used more efficiently, either by increasing the usable fraction (e.g., the crop-to-shoot ratio or harvest index), by minimizing losses to other organisms (e.g., insects, rodents or fungi), or by reducing wastes and losses in the chains of production. With either option, trade-offs with other environmental goals are possible. Agricultural intensification may have substantial adverse effects, such as nutrient leaching, soil degradation, use of toxic chemicals, or negative impacts on biodiversity (91). The extent to which such impacts can be mitigated while yields continue to increase (sustainable intensification; 89) is contested. Organic agriculture can help to increase yields over those reached in many traditional systems, but compared with the yields of intensive, industrialized agriculture, organic yields are lower, particularly due to the need for intercrops and fallow periods (126, 131–133). Moreover, in the past, improvements of yields per unit area and year were associated with a considerable reduction of the agricultural EROI, i.e., the ratio of socioeconomic energy inputs to the energy content of agricultural produce (92, 93). The impressive yield gains in Austria during the last two centuries discussed above were associated with a deterioration of the agricultural EROI from about 6:1 to about 1:1 (64). Higher livestock feeding efficiencies may result in trade-offs with animal well-being, such as if animals are kept in stables instead of being allowed to roam in order to reduce energy losses or if herd management is optimized purely in terms of feed-to-product ratios (134). The efficiency of biomass use chains can be increased through a strategy of cascade utilization that aims to use all residues and by-products and to reuse wastes (135). But there are trade-offs with soil conservation if agricultural residues are used that are required as input of organic material to the soil to maintain soil fertility (136).

Natural capital: an extension of the economic term of capital to natural assets; it denotes the stock of ecosystems that can generate a flow of services from which humans benefit

RELATED CONCEPTS: THE FAMILY OF FOOTPRINT INDICATORS

HANPP is one of several concepts for measuring different aspects of a phenomenon that has been denoted the "human appropriation of natural capital" (137), although this notion is somewhat misleading because many concepts subsumed in that notion measure human appropriation of resource flows, whereas capital usually denotes a stock that produces a flow of services (138). Indicators in this family include the ecological footprint (42), the water footprint (139), the human appropriation of renewable freshwater (140, 141), the land footprint of human activities (142), and indicators of actual land demand (72, 143, 144). These indicators aim to measure the extent to which humans appropriate a limited biospheric resource such as land, water or biomass production. Another family of indicators is somewhat related, although with important differences: the "carbon footprint" (145) and the "material footprint" (146). Both indicators aim at allocating to each nation the global impact of national-level consumption, in the case of the carbon footprint in terms of CO_2 or greenhouse gas emissions and in the case of the material footprint in terms of material flows. Both are less directly related to the human appropriation of ecological assets than are the other indicators discussed here, but they are related to biospheric processes such as climate change (carbon footprint) or resource use (material footprint).

Perhaps the most prominent indicator in this family is the ecological footprint. It accounts for the area of biologically productive land required to sustain human consumption of biophysical resources. It is measured in global hectares, i.e., hectares of globally average productivity (42, 147). The ecological footprint accounts for three functions of ecosystems used by humans: resource supply, waste absorption, and space occupied by infrastructure. Both HANPP and the ecological footprint refer to biological productivity as a key measure of natural resources appropriated by humans (43). When applied to national economies, the ecological footprint refers to the national apparent consumption of biophysical resources, just like eHANPP (44).

Differences between HANPP and the ecological footprint include the following (43):

1. The ecological footprint considers all resource flows that require biologically productive land for their production or for the absorption of wastes or emissions, including fossil energy. In contrast, HANPP relates only to biomass use, except for area demand of infrastructure, which is included in both indicators. When interpreting HANPP results in the context of sustainability, it is thus important to use complementary resource-use indicators (e.g., on fossil energy) to obtain a comprehensive picture.
2. Ecological footprints can be directly contrasted to an indicator of global resource availability that is denoted as biocapacity. Because of the virtual area that would be required to absorb CO_2 emitted during fossil fuel combustion, the ecological footprint can detect overshoot, i.e., a situation in which humanity's resource demand exceeds the planet's capacity to supply humans with those resources. According to empirical estimates, humanity's footprint exceeds biocapacity by 20–30% (147). The identification of limits related to HANPP is less straightforward (see above).
3. Whereas the ecological footprint methods use a plethora of weighting factors aiming to standardize different aspects of resource use or land of different qualities to global hectares

(137, 147), HANPP methods do not include weighting of biomass flows or land areas, akin to the water footprint approach that also does not use weighting (137).

Explicitly in relation to Vitousek et al.'s (7) work on HANPP, Postel et al. (140) quantified the global human appropriation of renewable freshwater. They estimated that 30% of all freshwater accessible to humanity is appropriated by humans either by direct use (e.g., as drinking water, for irrigation, or in industrial processes) or through indirect effects (e.g., reservoir loss). A similar study estimated that human appropriation of renewable freshwater in Africa was 17% in the year 2000 (141).

Vitousek et al. (7) had already discussed another important aspect, the human appropriation of aquatic NPP. Using assumptions on ecological efficiencies and the trophic level of fish caught, they estimated the global amount of NPP required to support yearly fish catches to be approximately 2.2% of total aquatic NPP. A later study split global annual fish catches into species groups and assigned them to these fractional trophic levels (148). According to this study, the total primary production required to support global fisheries was ~8% of total yearly aquatic NPP in the late 1980s and early 1990s. A global, spatially explicit study (149) used a NPP approach to analyze the geographic expansion of global marine fisheries from 1950 to 2005. It showed that the expansion of marine fisheries in the past five decades appropriated more than 10% of total annual oceanic NPP, one-third in the open oceans and two-thirds on the continental shelves. It is important to note, however, that humans use terrestrial and aquatic systems in very different ways: Biomass gained on land is mostly extracted from managed systems, whereas capture fisheries extract fish from unmanaged ecosystems. The meaning of the indicator "primary production required to support fisheries" differs considerably from the HANPP concepts discussed above (150).

CONCLUSIONS

In ecology, the invasion of new habitats by plant or animal species is usually denoted as colonization (151). In this sense, *Homo sapiens* is among the most successful species on Earth, having colonized almost all terrestrial habitats. Evaluating the scope of the ecological effects of human colonization of land and the scale of human activities on Earth (8) is one of the major objectives of HANPP research. In the past four decades, HANPP has proven to be fruitful in analyzing many aspects of human colonization of the land, which far exceeds the mere invasion of new areas. Understanding this process requires the quantification and mapping of, among other things, (*a*) human impacts on biogeochemical flows of carbon, water, or plant nutrients; (*b*) land-use intensity; and (*c*) pressures on biodiversity. HANPP can help us understand planetary boundaries related to land or biomass availability that are highly relevant for climate-change mitigation (130) and global bioenergy potentials (98, 122). HANPP allows the extension of the socioeconomic metabolism approach (53) to a socioecological metabolism approach, which aids our understanding of humans' role in shaping global land systems (1, 2, 5) in the Anthropocene (4). HANPP is a research framework, allowing the construction of multiple indicators that have been proven useful in different contexts. Although HANPP cannot detect all negative effects associated with land-use intensification and hence needs to be complemented by other indicators, the reductionism of the HANPP framework also has advantages, e.g., that consistent data sets of production and consumption can be derived without the need for arbitrary weighting factors. One of its strengths is that a consistent application of thermodynamic principles, such as the law of energy conservation, as adopted in comprehensive HANPP studies, reduces the risk of double counting and clarifies systemic biophysical feedbacks that result in synergies and trade-offs in the land system (130). Recognition is growing among researchers of the importance of such feedbacks and hence is motivating future efforts to embark on the laborious and time-consuming process of empirically assessing the human appropriation of NPP on global and other scales for the past, present, and future.

SUMMARY POINTS

1. The human appropriation of net primary production (HANPP) is an integrated socioecological indicator of the magnitude of human colonization of global ecosystems.
2. By consistently quantifying and mapping effects of human-induced changes in productivity and harvest on biomass flows in ecosystems, HANPP provides a measurable metric of land-use intensity.
3. In the past century, global HANPP grew from 13% to 25% of the NPP of potential natural vegetation.
4. The growth of HANPP was much slower than that of economic activity, population, or biomass harvest.
5. HANPP efficiency can be increased through land-use intensification, but this may involve high costs in terms of energy inputs and ecological pressures such as nutrient leaching or soil degradation.
6. Biomass trade results in a growing spatial disconnect between where NPP is appropriated and where the products are consumed, as evidenced by analyses of embodied HANPP.
7. According to the species–energy hypothesis, HANPP contributes to species loss through a reduction of trophic energy in ecosystems, a conjecture supported by macroecological theory and indirect empirical evidence.
8. HANPP can help us understand planetary boundaries related to land and biomass availability, which is relevant for climate-change mitigation and estimation of global bioenergy potentials.

FUTURE ISSUES

1. Although HANPP is a useful indicator of land-use intensity, it remains unclear which level of HANPP can be considered sustainable at which spatial scale.
2. Planetary boundaries related to HANPP need to be better understood.
3. Estimates of terrestrial NPP derived from remote sensing differ considerably from model outputs in terms of long-term trends, calling for a better understanding of the effects of global change on NPP.
4. More research is needed on how HANPP efficiency can be increased without commensurate increases in ecological costs such as soil degradation, biodiversity loss, nutrient leaching, or a deterioration of the energy return on investment.
5. The embodied HANPP concept opens a plethora of options for analyzing ecological effects related to trade, particularly the trade of biomass-based products.
6. The relation between HANPP, consumption, and economic activity should be further studied to better understand options for increasing efficiency and decoupling resource use from socioeconomic well-being.

7. The HANPP framework offers a range of promising options for analyzing trade-offs and synergies in the global land system, particularly those related to land-use competition.
8. More research and empirical evidence on various spatial and temporal scales could help us better understand the impacts of changes in NPP and HANPP on biodiversity.

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