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among islands and regions using nested, mixed-model ANOVA. We screened several potential estimators to find that the Chao 1 procedure provided the most stable values for local species richness. This estimator is the sum of the observed number of species and the quotient $a^2/2b$, where a and b equal the number of species represented by one and two colonies, respectively.

To analyse the local–regional species richness relationship in each habitat, we used a simple linear regression of the mean local richness per site in a region against habitat-specific regional richness. Linearity is supported by these and supplemental regressions using: (1) log-transformed richness data; (2) local richness standardized to 100 or more colonies per sample[18]; and (3) the two alternative measures of local species diversity, Fisher's alpha and the Chao 1 estimator of local richness.

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Global patterns in human consumption of net primary production

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The human population and its consumption profoundly affect the Earth's ecosystems[1,2]. A particularly compelling measure of humanity's cumulative impact is the fraction of the planet's net primary production that we appropriate for our own use[3,4]. Net primary production—the net amount of solar energy converted to plant organic matter through photosynthesis—can be measured in units of elemental carbon and represents the primary food energy source for the world's ecosystems. Human appropriation of net primary production, apart from leaving less for other species to use, alters the composition of the atmosphere[5], levels of biodiversity[6], energy flows within food webs[7] and the provision of important ecosystem services[8]. Here we present a global map showing the amount of net primary production required by humans and compare it to the total amount generated on the landscape. We then derive a spatial balance sheet of net primary production 'supply' and 'demand' for the world. We show that human appropriation of net primary production varies spatially from almost zero to many times the local primary production. These analyses reveal the uneven footprint of human consumption and related environmental impacts, indicate the degree to which human populations depend on net primary production 'imports' and suggest policy options for slowing future growth of human appropriation of net primary production.

An influential study[3] has estimated global human appropriation of terrestrial net primary production (HANPP) to be 31% of the total amount of net primary production (NPP) generated on land, with 'low' and 'high' estimates of 3% and 39%, respectively. A more recent study, using the same definition of appropriation, estimated a similar value for global HANPP (32%)[4], but high uncertainty was reported (10–55%; see ref. 7). This is a remarkable level of co-option for a species that represents roughly 0.5% of the total heterotroph biomass on Earth[9]. These previous estimates, however, were derived from global and biome averages, so that important spatial patterns in both NPP and HANPP remain hidden[7,10]. Understanding these patterns is critical for identifying areas experiencing severe human impacts on their ecosystems, for illuminating the effects of different consumption patterns among regions and cultures, and for indicating the directions of net energy flow due to regional and global trade.

To examine these issues we developed a global map of HANPP, which allows spatial comparison to NPP within the context of the global carbon cycle. We defined HANPP as the amount of terrestrial NPP required to derive food and fibre products consumed by

humans, including the organic matter that is lost during the harvesting and processing of whole plants into end products. We started with data from the Food and Agriculture Organization (FAO) on products consumed in 1995, for 230 countries in seven categories: vegetal foods, meat, milk, eggs, wood (for building and fuel), paper and fibre[11]. To these data we applied harvest, processing and efficiency multipliers, as well as estimates of below-ground production, to reconstruct the total amount of NPP required to derive the final products (Table 1, see Methods). We then calculated the per capita HANPP of each country and applied these values to a gridded database of the human population with a 0.25° spatial resolution[12] (this resolution was chosen to match that of the NPP data, see below). Our method assumes a homogeneous per capita consumption rate within each country, which, although unsupported in some cases, is a reasonable starting point[7,10]. In addition, terrestrial HANPP does not directly capture other important forms of environmental impact, including freshwater co-option, use of fossil fuels and appropriation of NPP from freshwater or marine systems[1].

The resulting map depicts the spatial pattern of HANPP, showing where the products of terrestrial photosynthesis are consumed (Fig. 1a). Summing for the globe, we estimated annual HANPP to

Table 1 **Product multipliers for estimation of HANPP**

Product/multiplier*	High estimate	Intermediate estimate	Low estimate
Vegetal food, fibre and grain fed to livestock†			
Post harvest losses[20,21]	0.4	0.10 (I) 0.40 (D)	0.1
Crop residue[22]	1.28	0.71	0.14
Milk efficiency factor[26,27] (kg grain/kg milk)	0.3	0.3 (I) 0.20 (D)	0.2
Eggs efficiency factor[26,27] (kg grain/kg eggs)	2.2	2.2 (I) 1.6 (D)	1.6
Wood and paper			
Milling loss[23]	0.34	0.07 (I) 0.34 (D)	0.07
Harvest loss[24]	0.54	0.22 (I) 0.54 (D)	0.22
Recycling (paper only)[25]	−0.20	−0.25 (I) −0.20 (D)	−0.25
Carbon/organic matter conversion[29]	0.50	0.475	0.45
Roots (short/tall vegetation)[13]	2.0/1.5	2.0/1.5	2.0/1.5

*Multipliers were used to cumulatively add organic matter to the mass of FAO-reported products in a logical sequence (from top down in the table). Multipliers were either applied equally to all countries or were applied separately to industrialized (I) and developing countries (D). Development status was assigned according to ref. 22.
†For meat products, the only variable adjusted to derive high and low estimates is the efficiency with which grain feeds are produced.
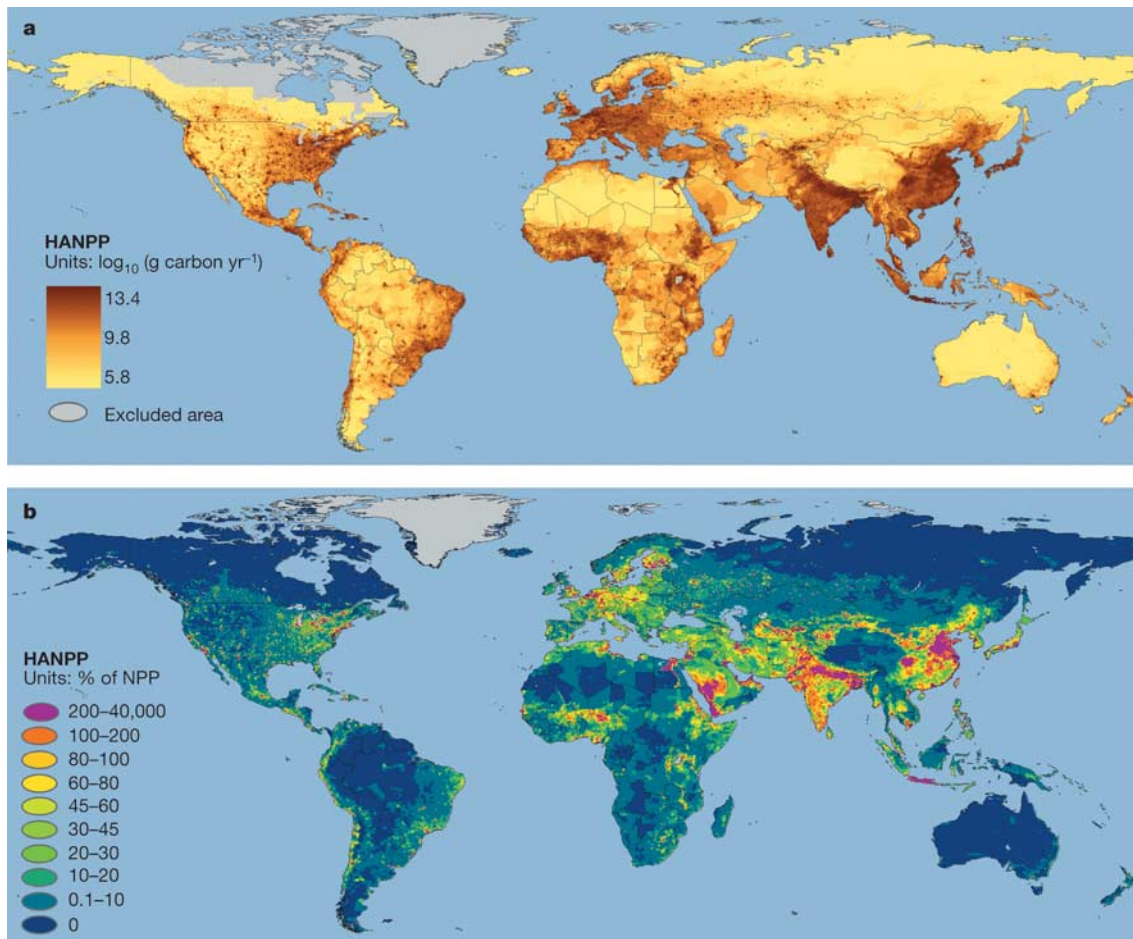

Figure 1 Spatial distribution of the annual NPP resources required by the human population. As measured by **a**, HANPP and **b**, HANPP as a percentage of local NPP. Both maps use the intermediate estimate for HANPP and are in units of carbon.

Table 2 **Annual global HANPP estimates**

Product	Low estimate (Pg C)	Intermediate estimate (Pg C)	High estimate (Pg C)
Vegetal food	0.90	1.73	2.95
Meat	1.69	1.92	2.22
Milk	0.15	0.27	0.43
Eggs	0.09	0.17	0.26
Food (subtotal)	2.83	4.09	5.86
Paper	0.20	0.28	0.38
Fibre	0.32	0.36	0.42
Wood (fuel)	2.68	4.31	4.71
Wood (construction)	1.97	2.50	3.44
Wood and fibre (subtotal)	5.17	7.45	8.95
Total	8.00	11.54	14.81
% of annual NPP (56.8 Pg)	14.10	20.32	26.07

be 11.5 Pg carbon (24.2 Pg organic matter; $1Pg = 10^{15}$ g) (Table 2). This value is lower than the intermediate estimates of earlier studies[3,4] (40.6 and 39 Pg organic matter, respectively), but the difference is largely due to items we have omitted. First, we included only the NPP required to produce consumed goods, not the components of NPP that are lost to land transformation (for example, 'shifting cultivation' and 'land clearing'[3]). Second, we do not treat below-ground biomass in grazed lands as being appropriated by humans because we assume that most of it survives grazing. If we include these components in our analysis, our global estimate increases to 20.8 Pg carbon (43.8 Pg organic matter), a value remarkably close to those reported in the previous studies[3,4], despite differences in method.

To address uncertainties we bracketed our estimate of HANPP with low and high calculations using the range of efficiency, loss and residue multipliers reported in the literature (Table 1). For the intermediate estimate we applied these multipliers according to each country's development status[11]. For low and high estimates we applied to all countries the multipliers that produce minimum and maximum values. Our low and high estimates for HANPP are 8.0 and 14.8 Pg carbon, respectively (Table 2).

To compare HANPP to the global pattern of NPP, we mapped terrestrial NPP using a carbon model driven by global satellite-derived vegetation index and climate data obtained between 1982 and 1998 (refs 13, 14). The use of data collected over such a long baseline reduces short-term variations in NPP while incorporating the cumulative and more recent effects of human influence on the land surface. The resulting global map of NPP matches both the spatial resolution and the time interval of our HANPP data. We estimate global annual NPP to be 56.8 Pg carbon (119.6 Pg organic matter); a value that is close to the average of previous estimates[15].

Expressing HANPP as a percentage of NPP reveals a spatially explicit balance sheet of NPP 'supply' and 'demand' (Fig. 1b), revealing a level of spatial heterogeneity not seen in earlier studies. Globally, we found that humans appropriate approximately 20% of terrestrial NPP, with low and high estimates of 14 and 26%, respectively (Table 2). Some regions, however, such as western Europe and south central Asia, consume more than 70% of their regional NPP (Table 3). Conversely, HANPP in other regions is less

than 15% of NPP, with the lowest value (about 6%) found in South America. At local scales the spatial variation in HANPP is even more striking, varying from nearly 0% of local NPP in sparsely populated areas to over 30,000% in large urban centres (Fig. 1b).

Human populations clearly are not limited to consuming the products of local photosynthesis. Regional and global trade transports these products widely, such that the environmental impacts of human consumption are partly realized far from where products are actually consumed. International trade may also affect HANPP because imported goods are often produced using different efficiencies than those in the consuming country (Table 1). Our high and low estimates set upper and lower boundaries for this latter uncertainty, but our analyses do not explicitly consider transportation issues. Nevertheless, the maps (Fig. 1) identify areas that clearly require net imports of NPP, and they depict the distribution of local impacts accompanying population and consumption (such as waste production, pollution and urbanization). Measuring the global flows of NPP-based goods is a significant future challenge to understanding the environmental impacts of human populations[16,17].

The equation $I = PAT$ (ref. 18) describes the overall ecological impact (I) of human activities, which involves the product of population size (P), per capita consumption (A, for 'affluence') and the technologies employed (T). Our results illustrate the importance of each of these factors. The role of population is clear from Fig. 1, despite vast differences in consumption among nations. For example, east and south central Asia, with almost a half of the world's population (Table 3), appropriates 72% of its regional NPP despite having the lowest per capita consumption of any region (1.29 tonnes (t; $1t = 10^6$ g) yr^{-1}). Affluence also plays an important part. Average annual per capita HANPP for industrialized countries (3.2 t) is almost double that of developing nations (1.8 t), which host 83% of the global population[19]. If the per capita HANPP of developing nations increased to match that of industrialized countries, global HANPP would increase by 75% to 20.2 Pg carbon (that is, 35% of the current global NPP). Finally, technologies strongly determine the efficiency with which NPP is appropriated. In industrialized countries, for example, 1 t of milled lumber requires approximately 1.3 t of harvestable above-ground tree biomass, whereas in developing countries over 2 t is required (Table 1).

Changing patterns of HANPP will have important consequences for human welfare and global biodiversity. Further growth and development in areas of high HANPP is likely to impoverish local ecosystems and diminish the vital services they provide[8]. These areas will also require increased NPP imports, alterations to flows of NPP-based products and exertions of greater pressure on ecosystems elsewhere[16,17]. Improved technologies, meanwhile, may help to reduce HANPP through better efficiencies and product substitutions. These changes will be complex, interacting and difficult to predict. Spatially explicit measures of HANPP, however, will help to illuminate current human impacts on the biosphere, monitor changes in these impacts over time and explore the potential of various policies for alleviating them. □

Table 3 **HANPP for selected regions of the world (intermediate estimate)**

Region*	Area (10^6 km^2)	Population (10^6)	Per capita HANPP (t)	NPP (Pg)	HANPP (Pg)	HANPP (% of NPP)
Africa	31.1	742	2.08	12.50	1.55	12.40
East Asia	11.9	1,400	1.37	3.02	1.91	63.25
South central Asia	10.9	1,360	1.21	2.04	1.64	80.39
Western Europe	1.20	181	2.86	0.72	0.52	72.22
North America	19.7	293	5.40	6.67	1.58	23.69
South America	18.4	316	3.11	16.10	0.98	6.09

*Definitions of regions were taken from ref. 22.

Methods

FAO data

We scanned the country-level FAO data for 1995 for internal consistency, missing data and reporting errors. Missing data were assigned values using the average per capita consumption of countries in the same development category. Over-reporting because of multiple entries for the same country was corrected. For national entities or territories reporting under another administrative country, their populations were added to that of the reporting country to compute the per capita consumption. We defined consumed products as the domestic supply (that is, production plus imports minus exports) to constrain the country totals to products consumed *in situ*.

HANPP calculations

For vegetal foods and fibre, mass was successively added to account for post-harvest processing, transport losses[20,21] and crop residue[22]. Crop residue is the residue to product ratio. For the intermediate estimate we used the weighted mean for major world crops whereas high and low estimates are ± 1 s.d. (Table 1). For wood, fuel wood and paper products, organic matter was added to account for processing[23] and harvest losses[24]. For paper, recycling was also considered[25]. If the individual plant is killed (all cases except pasture) we included the biomass of the root system using the values in Table 1 (ref. 13).

Meat consumption was based on wet carcass weight and it combined all meat types. The meat component of the total HANPP was estimated by summing the NPP required for grain and pasture-based feed, assuming a global average of 62% grain and 38% forage[26]. We estimated the amount of organic matter used as feed by applying efficiency values for grain (an average of 2.3:1 kg grain/kg carcass for all meat types) and for pasture (21.46:1 for ruminants) using data from previous studies[27,28]. The total NPP required for grain feed was then calculated in the same way as for vegetal foods, adding residue and loss factors appropriate to each country's development status. Because grazing occurs *in situ*, no loss or residue factors were added to pasturage. Efficiency factors for milk and eggs are for the grain component only. Carbon/organic matter ratios used for the high, intermediate and low estimates span the range (intermediate estimate uses average value) of reported values for various plants[29].

NPP model

We used the Carnegie Ames Stanford Approach carbon model to estimate NPP. The model incorporates satellite and climate data to estimate the fixation and release of carbon based on a spatially and temporally resolved prediction of NPP in a steady state. The performance of this model is evaluated in ref. 15.

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A proteoglycan mediates inductive interaction during plant vascular development

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Inductive cell–cell interactions are essential for controlling cell fate determination in both plants and animals[1]; however, the chemical basis of inductive signals in plants remains little understood. A proteoglycan-like factor named xylogen mediates local and inductive cell–cell interactions required for xylem differentiation in *Zinnia* cells cultured *in vitro*[2,3]. Here we describe the purification of xylogen and cloning of its complementary DNA, and present evidence for its role *in planta*. The polypeptide backbone of xylogen is a hybrid-type molecule with properties of both arabinogalactan proteins and nonspecific lipid-transfer proteins. Xylogen predominantly accumulates in the meristem, procambium and xylem. In the xylem, xylogen has a polar localization in the cell walls of differentiating tracheary elements. Double knockouts of *Arabidopsis* lacking both genes that encode xylogen proteins show defects in vascular development: discontinuous veins, improperly interconnected vessel elements and simplified venation. Our results suggest that the polar secretion of xylogen draws neighbouring cells into the pathway of vascular differentiation to direct continuous vascular development, thereby identifying a molecule that mediates an inductive cell–cell interaction involved in plant tissue differentiation.

The plant vascular system, comprised of xylem and phloem, forms a continuous network throughout the plant body to transport water, nutrients and signalling molecules. Vascular cells differentiate