Eating up the world's food web and the human trophic level

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Trophic levels are critical for synthesizing species' diets, depicting energy pathways, understanding food web dynamics and ecosystem functioning, and monitoring ecosystem health. Specifically, trophic levels describe the position of species in a food web, from primary producers to apex predators (range, 1–5). Small differences in trophic level can reflect large differences in diet. Although trophic levels are among the most basic information collected for animals in ecosystems, a human trophic level (HTL) has never been defined. Here, we find a global HTL of 2.21, i.e., the trophic level of anchoveta. This value has increased with time, consistent with the global trend toward diets higher in meat. National HTLs ranging between 2.04 and 2.57 reflect a broad diversity of diet, although cluster analysis of countries with similar dietary trends reveals only five major groups. We find significant links between socio-economic and environmental indicators and global dietary trends. We demonstrate that the HTL is a synthetic index to monitor human diets and provides a baseline to compare diets between countries.

human ecology | nutrition transition | trophic ecology

Trophic levels are a basic metric collected for ecological studies and have a wide range of applications (1). They describe the number of intermediaries between basal species and predators throughout the food web and help define species' roles in the ecosystem (2, 3). They represent a synthetic metric of species' diets, which describes the composition of food consumed and enables comparisons of diets between species.

Primary producers, such as plants or phytoplankton, are defined as trophic level 1 (1, 4). Subsequent trophic levels are then calculated as a mean of the trophic levels of food items in a species' diet, weighted by quantity, plus one. For example, herbivores such as cows feed on plants (trophic level 1); thus, their trophic level is 2. Similarly, a species whose diet is composed of half plant and half cow has a trophic level of 2.5 $\left(\frac{0.5*1+0.5*2}{1}+1\right)$. Therefore, a 0.5 difference in trophic level can reflect a completely different diet, e.g., from herbivory to omnivory. For carnivorous apex predators, such as polar bears or killer whales, trophic levels range up to 5.5 (5).

Between each trophic level, there is a loss of energy (3, 6), meaning that more primary production is required to sustain higher trophic levels (7). Assuming an energy transfer rate of 10%, it would require 100 kg C of primary production to produce 1 kg C of a species that has a trophic level of 3 (7). This energy transfer rate can vary significantly between ecosystems [3–20% (8)]. Net primary production (NPP) is the limited capacity of the globe to produce biomass. Humans currently appropriate 25% (8–14.8 Pg C) of the NPP through food production and land use (9, 10), and this human appropriation is approaching the planetary boundary (11, 12). Direct extraction of resources for food production represents 35–40% of human appropriation of NPP (10), relating both to the volume of food consumed and to diet composition. Therefore, for a fixed quantity of food consumed, it is more efficient for human populations to eat from lower trophic levels to reduce the extraction of resources.

There is currently no quantitative assessment of the human trophic level (HTL). Here, we calculate the HTL using the Food and Agricultural Organization (FAO) national data on the human food supply per food item per capita per year (1961–2009). Food supply data are available for 176 of 196 countries, i.e., 98.1% of the world population. We describe the temporal trends and regional variability of HTL. Using World Bank development indicators, we find significant links between HTL and important global socio-economic and environmental indicators. We find that HTL is a simple tool to quantify human diets, provide a baseline to compare diets between diverse countries, and facilitate the monitoring of global trends.

Results

We find the global median HTL in 2009 to be 2.21 (SD = 0.13). This represents a percentage increase of 3% since 1961 (Fig. 1*A*). The median HTL is weighted by the population size of each country, and thus this trend is mainly driven by China and India, whose median HTL has increased from 2.05 to 2.20 during this period (+7.4%; Fig. 1*A*). When these countries are removed from the analysis, the global HTL is stable over time at 2.31 (Fig. 1*A*).

HTL has a broad range of values that reflects large variations in diet between countries and over time (Fig. 1*B*). For example, in 2009, Burundi had an HTL of 2.04, representing a diet that is almost completely (96.7%) plant based. In contrast, Iceland had an HTL of 2.57 for the same year, representing a diet composed

Significance

Here we combine ecological theory, demography, and socio-economics to calculate the human trophic level (HTL) and position humans in the context of the food web. Trophic levels are a measure of diet composition and are a basic metric in ecology, but have never been calculated for humans. In the global food web, we discover that humans are similar to anchovy or pigs and cannot be considered apex predators. In addition, we show that, although countries have diverse diets, there are just five major groups of countries with similar dietary trends. We find significant links between HTL and important World Bank development indicators, giving insights into the relationship between socio-economic, environmental, and health conditions and changing dietary patterns.

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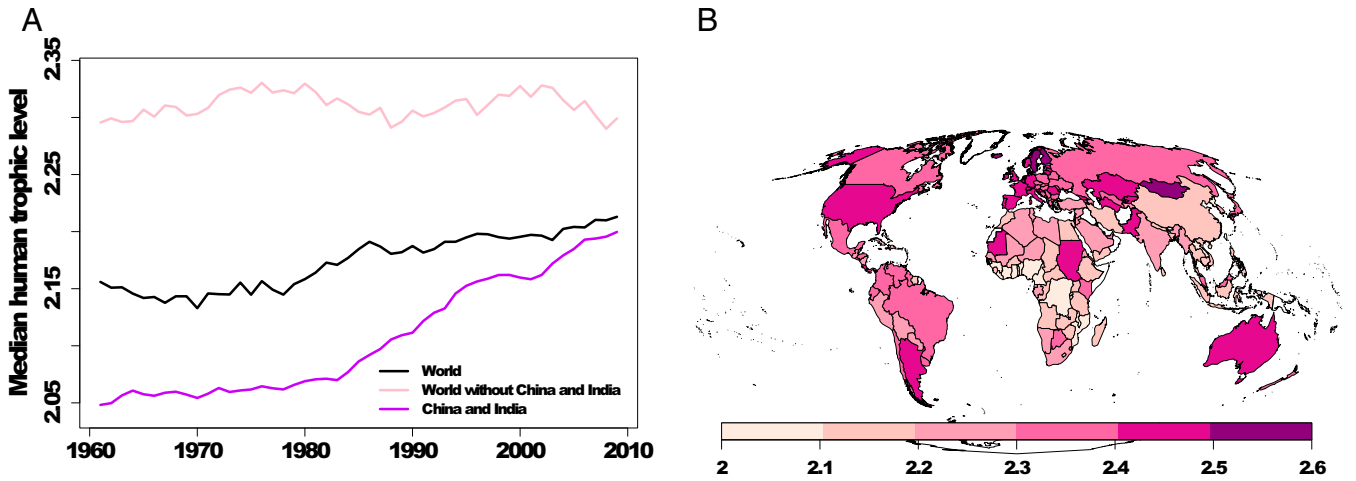

Fig. 1. (*A*) Trends in the human trophic level (1961–2009) and (*B*) map of the median human trophic level over 2005–2009.

of 50% meat and fish and 50% plants (*SI Appendix*, Fig. S5). Likewise, we find a wide range of values within countries over time, e.g., Iceland's HTL has decreased dramatically since 1974, when it was 2.76 (−7%).

Although there is remarkable diversity in diet between the 176 countries of this study, the cluster analysis unveils only five different groups of HTLs. Two groups have stable HTLs over the study period, two significantly increase, and one significantly decreases (Fig. 2). The majority of sub-Saharan countries and most of Southeast Asia have a pattern of low and stable HTL (group 1), reflecting diets that are primarily plant based (*SI Appendix*, Figs. S5–S8). Low and increasing HTLs are found for several countries throughout Asia, Africa, and South America, including China and India (group 2). Group 3, including Central America, Brazil, Chile, Southern Europe, several African countries, and Japan, has higher initial HTLs than group 2 and also shows an increasing trend. Increasing HTLs in groups 2 and 3 indicate diets that are shifting toward higher consumption of animals. Group 4, comprised of North America, Northern and Eastern Europe, Australia, and New Zealand, had high and stable HTLs until 1990, when they begin to decrease (*SI Appendix*, Fig. S9). Group 5 represents countries with the highest overall HTLs and decreasing trends, including Iceland, Scandinavia, Mongolia, and Mauritania. Traditional diets of this group were composed of meat, fish, or dairy products and low vegetable consumption.

Over the 49 y of the dataset, HTL is significantly and consistently correlated to 18 essential indices of the 1,223 World Bank development indicators (Fig. 3 and *SI Appendix*, Fig. S11), reflecting complex associations between HTL and the socioeconomic, environmental, and cultural characteristics of countries. Large-scale patterns show that HTL is positively related to, for example, gross domestic product, life expectancy, CO_2 emissions, and urbanization rate until a point after which the relationships plateau and then turn negative (Fig. 3 and *SI Appendix*, Fig. S10). Further examination of these relationships shows that for groups 1–4, HTL and these development indicators increase over time; whereas for group 5, HTL decreases and indicators increase. It

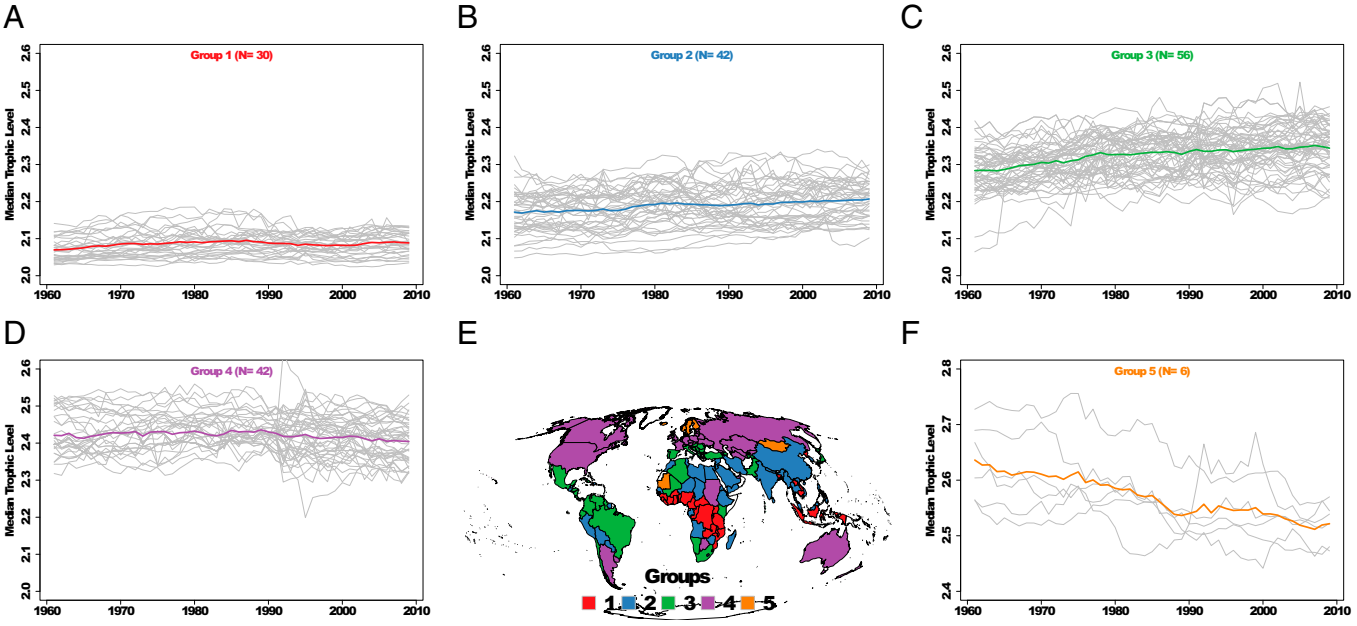

Fig. 2. (*A*, *B*, *C*, and *E*) Trends in HTL (1961–2009) for the five groups identified by the clustering method, and (*D*) the map of country groupings.

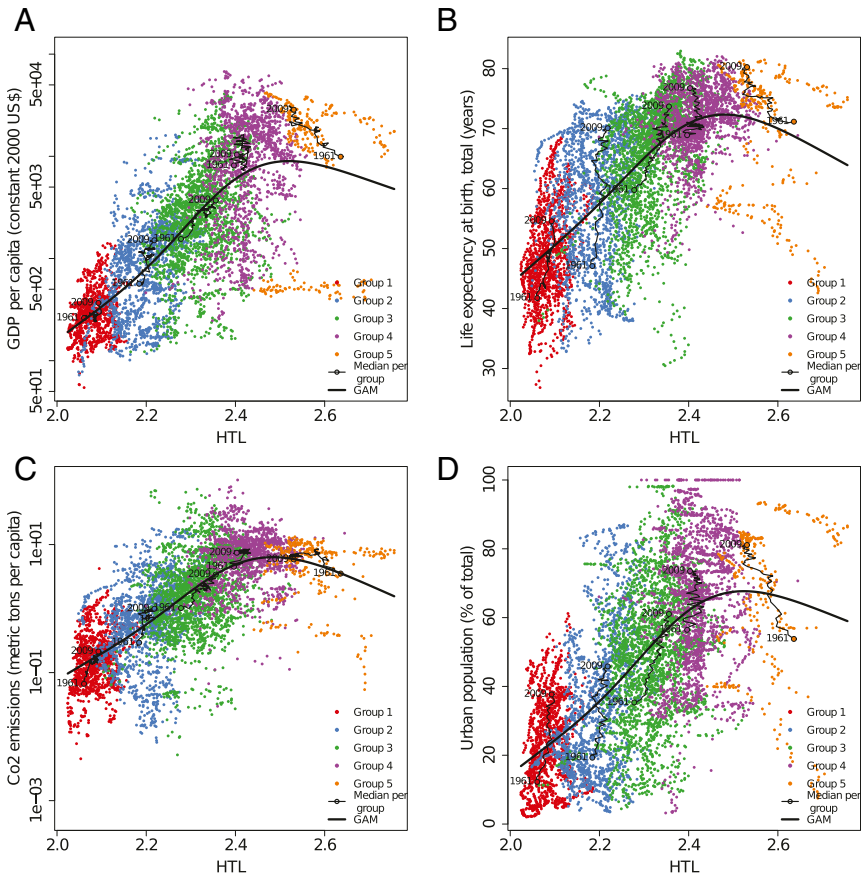

Fig. 3. Relationships between the human trophic level and (*A*) Gross Domestic Product, (*B*) life expectancy at birth, (*C*) CO_2 emissions, and (*D*) urban population over 1961–2009 for the 176 countries analyzed. The median for each group is represented by the thin black line. To examine the global pattern of the relationships, a generalized additive model is fit to the data (black thick line, see *SI Appendix*).

seems that over time there is a convergence of HTL at ~2.4 in relation to development indicators.

Discussion

Positioning Humans in the Food Web. This first estimate of HTL at 2.21, i.e., a trophic level similar to anchoveta and pigs, quantifies the position of humans in the food web and challenges the perception of humans as top predators (2). Humans dominate ecosystems through changes in land use, biogeochemical cycling, biodiversity, and climate (11, 13, 14). It is not sufficient to separate humans from analyses of ecosystem processes, because there are no remaining ecosystems outside of human influence (15). Thus, investigations of ecosystems, without accounting for the presence of humans, are incomplete (13). There is a variety of other ecological indicators based on trophic ecology theory or diets, e.g., the omnivory index, that may also prove useful in assessing the impact of humans in the functioning of ecosystems. However, a first estimate of an HTL gives us a basic tool that places humans as components of the ecosystem and assists in further comprehending energy pathways, the impact of human resource use, and the structure and functioning of ecosystems.

Monitoring Human Diets. The global increase in HTL is consistent with the nutrition transition that is expected to continue for several decades (16, 17) from plant-based diets toward diets higher in meat and dairy consumption (18–22). This 0.15 increase in HTL from 1961 to 2009 is mainly due to the increased consumption of fat and meat (*SI Appendix*, Figs. S5–S8), as opposed to a shift toward the consumption of species with higher trophic levels. In fact, we find that the mean trophic level of terrestrial animals that are consumed by humans has only slightly increased (by 0.01 or 0.5%) due to the higher proportion of pork and poultry in the diet (*SI Appendix*, Fig. S11*A*), whereas that of marine animals has decreased markedly from 2.88 in 1961 to 2.69 in 2009 (*SI Appendix*, Fig. S11*B*). This decline in the trophic levels of marine food items in human diets is consistent with the global decline in the mean trophic level of marine fisheries catches. This decline has been related to the consequences of fishing pressures on marine predators (23), although changes in the characteristics of fisheries over time may also influence this trend (24).

The global convergence in HTL is consistent with the convergence in diet structure between countries with diverse levels of development (18, 19), and in agreement with previous studies of the FAO (17, 25). Globalization and economic development facilitate the access to diverse foodstuffs and can enhance the rate of this convergence (18, 26). For India, China, and countries in groups 1–3, HTLs are low and rising. With economic growth, these countries are gaining the ability to support the human preference for high meat diets (18, 19, 26). For countries in group 4, the nutrition transition has reached a point where health problems associated with high fat and meat diets (i.e., high HTLs) have led to changes in policy and government-run education programs that encourage these populations to shift to more plant-based diets [i.e., lower their HTL; *SI Appendix*, Figs. S4–S8 (18, 20, 22)]. Similarly, countries with high initial HTLs (i.e., group 5) show decreasing trends with time (Fig. 3). For Scandinavian countries, this decline is due to government policies promoting healthier diets (18, 22). For example, in 2011,

Sweden consumed historically high levels of meat due to low market prices, leading the Swedish government into discussions of a Pigovian tax to reduce this consumption (27). Changes in diet in Mauritania (decreased meat and dairy consumption) and Mongolia (increased proportion of vegetables) are linked to increased urbanization and economic development and decreased nomadism.

HTL is a composite metric that reflects what is known about global patterns of diet in a simple and synthetic way. As with trophic levels in ecology, the HTL has wide applications. HTL can be used by educators to illustrate the ecological position of humans in the food web, by policy makers to monitor the nutrition transition at global and national scales and to analyze the effects of development on dietary trends, and by resource managers to assess the impacts of human diets on resource use.

Materials and Methods

Data. The HTL is a mean of the trophic level of food items in the diet, weighted by quantity. It is calculated as $\mathrm{HTL} = 1 + \frac{\sum_i Q_i * TL_i}{\sum_i Q_i}$, where Q_i is the quantity (in kilograms) of the food item i consumed, and TL_i is the trophic level of the food item. We use the FAO national data on the human food supply per food item per capita per year (1961–2009). The FAO human food supply data represent each country's production of foodstuffs for human consumption, accounting for imports, exports, and food used for livestock (*SI Appendix*). Food supply data are available for 176 of 196 countries. We assume that food supply is a good proxy for food consumption, although it includes waste (21). The trophic level of each food item is gathered from the literature (*SI Appendix*, Table S1). We assume that the trophic level for animals was constant between countries, although there is likely to be variability due to differences in feed and production methods of the lower trophic levels.

Statistical Analyses. First, we analyze the temporal trends and spatial variability in HTL globally and between countries. Analysis of each country's HTL is beyond the scope of this paper, as individual values and trends are linked to national histories, culture, and geopolitics (18). Thus, we instead examine common patterns of the HTL time series between countries using a hierarchical clustering method based on a dynamic time warping algorithm (*SI Appendix*). Finally, we use these country groupings to analyze the relationships between the HTL and the 1,223 World Bank development indicators that describe demography, economy, environment, and health (*SI Appendix*). These relationships are investigated using the maximal information coefficient (28) (range: 0, no relationship to 1, strong linear or nonlinear relationship; P value corrected for multiple testing).

HTL is calculated using freely available FAO data, and we encourage its use by providing open source code. The code reported in this paper is available at http://datadryad.org and has been developed using the R software (29).

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