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12. Ectopic Upd was generated in GSCs and spermatogonia by expressing UAS-Upd (*4*) with a Nanos-Gal4 driver (*21*) (genotype *w/Y; P[w+, UAS Upd]/P[w+, Actin5c>y+ nGFP], P[w+, UAS nGFP]; P[w+; A4-1Nos-Gal4::VP16nos.UTR]/+*), or in SSCs and their progeny by inducing theActin5c promoter (*22*) according to (*23*). Males were heat-shocked twice at 37°C for 30 min, then aged 2 weeks at 25°C (genotype: *w/Y; P[w+, UAS Upd]/Actin5c>CD2>GAL4,UAS GFP; MKRS, P[ry+;hsp70 FLP]/+*), yielding indistinguishable results. Rabbit antibody to β-galactosidase (Abcam, diluted 1:2000), mouse monoclonal antibody 1B1 (DSHB, 1:50), mouse antibody to Eya (DSHB, 1:1000), and mouse antibody to BamC (1:2000) were used as described (*24*). Rabbit antibody to Anillin (1:1000) was used similarly, except that fixation was for 5 min; incubation in secondary antibody was followed by fixation for 30 min. DNA was counterstained with Oligreen (Molecular Probes, 1:4000) for 10 min, or with Toto-3 (Molecular Probes, 1:2000) for 20 min after treatment with ribonuclease A (0.04 mg/ml) for 30 min. Alexa 488– or Alexa 568–conjugated secondary antibodies were used (Molecular Probes, 1:400). Confocal images were obtained with Leica TCS NT and SP2 microscopes.
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Human Appropriation of Photosynthesis Products

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Previous global estimates of the human impact on terrestrial photosynthesis products depended heavily on extrapolation from plot-scale measurements. Here, we estimated this impact with the use of recent data, many of which were collected at global and continental scales. Monte Carlo techniques that incorporate known and estimated error in our parameters provided estimates of uncertainty. We estimate that humans appropriate 10 to 55% of terrestrial photosynthesis products. This broad range reflects uncertainty in key parameters and makes it difficult to ascertain whether we are approaching crisis levels in our use of the planet's resources. Improved estimates will require high-resolution global measures within agricultural lands and tropical forests.

Human use of photosynthesis products is pervasive, including direct use of plants for food and fiber as well as indirect use from grazing by domesticated animals. Population increases have led to speculation and estimates that the human footprint on the biosphere, in terms of the use of both plants and fresh water, is approaching the limit of planet sustainability (*1–5*). A key measure of human impact on the biosphere and hydrosphere is human use of terrestrial net primary production (TNPP), which represents the net energy (production minus respiration) created by carbon fixation on land. Previous estimates of global human appropriation of this biological resource (HTNPP)—which governs the total amount of food available on Earth—and its surrogates (*1, 6–8*) have used mean estimates of parameters that were made on the basis of limited, small-scale field studies. Here we incorporate contemporary data, many of which are satellite-based, to estimate HTNPP, and quantify the uncertainty in our knowledge of HTNPP.

HTNPP represents the combined effects of direct human use and use by human-altered ecosystems (*9*). We adopted the method of Vitousek *et al.* (*1*) to estimate HTNPP (Table 1 and Fig. 1), which uses global averages and sums the influences of agriculture, human-occupied lands, grazing, and forestry. To estimate HTNPP, we used available global-scale primary-source data in the literature (*10*). We did not include studies earlier than 1990 for parameters with large temporal variability (e.g., parameters dependent on areas or populations). We also removed estimates that appeared to be highly anomalous (more than two standard deviations from the other estimates). Reflecting the format of Vitousek *et al.* (*1*) and the majority of data sources, we present biomass and productivity values in terms of the weight of dry matter

(DM). Conversion of data from weight carbon (C) to DM included a 10% uncertainty in carbon content (0.45 to 0.50 g C per g DM), reflecting commonly cited carbon values (*11–16*).

We estimated uncertainty for parameters with only one or two literature references using either literature-cited values or an ad hoc estimate that the standard deviation was one-half of the mean (*17, 18*). Although 8 of 34 parameters are estimated with a single measurement, the median number of measurements per parameter is 5.5, indicating that half of the parameters have enough independent measurements to provide at least rudimentary evaluation of their uncertainty. Only nine parameters have normalized 2σ error bounds less than unity, indicating that most parameters are not well known. Uncertainty in our parameters, however, does not significantly increase and correlate with sample size ($r^2 = 0.10$ for estimates using three or more samples), which reflects the fact that the literature-based estimates we used are derived, either directly or indirectly, from physical measurements. Differences between our mean estimates and those of Vitousek *et al.* (*1*) represent updates using newer literature. Coincidentally, the median difference for all 34 of the parameters is negligible, −1.2%.

In addition to using more contemporary and larger scale measurements, we explicitly incorporated uncertainty in our estimate of HTNPP through stochastic simulations. Monte Carlo techniques allow each parameter to randomly vary constrained by its mean and estimated variance. We derived an estimate of variability in our knowledge of HTNPP by repeating these calculations 1 million times (*19*).
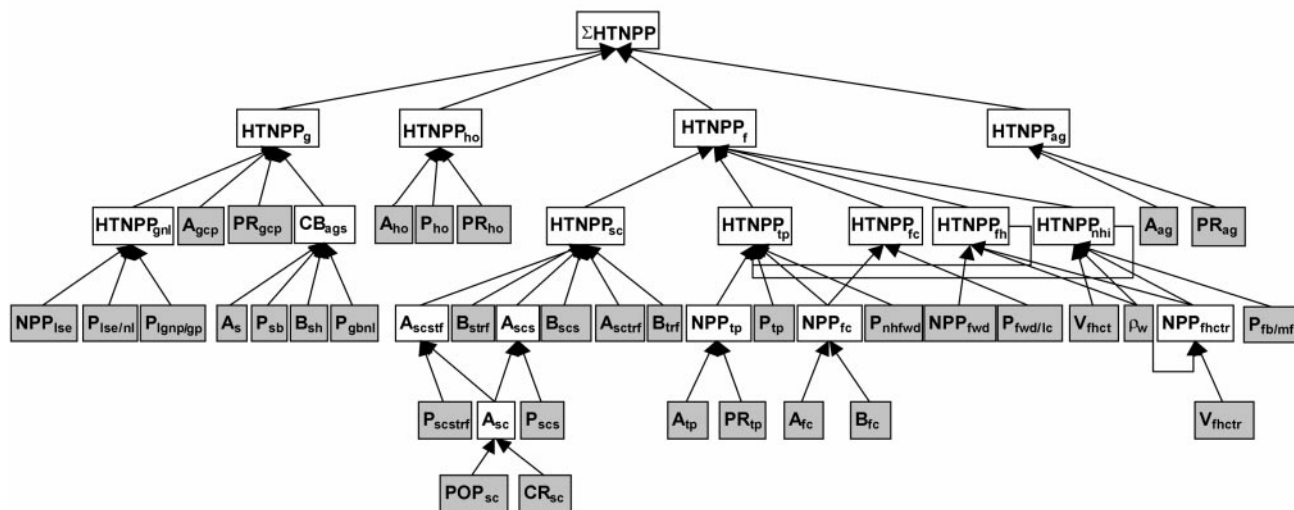
Our mean estimate of HTNPP is 39 Pg DM (20 Pg C, where we assume carbon is 50% of dry matter) (Fig. 2) or 32% of TNPP (*20*), which almost precisely matches that of Vitousek *et al.* (*1*). This agreement is coincidental because our newer estimates of the parameters are considerably different from those of Vitousek *et al.* The mean absolute difference between our estimate of the contributing parameters and those of Vitousek *et al.* is, excluding the values for four

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Fig. 1. Template used to estimate HTNPP. The formula on which the template is based is the intermediate calculation of Vitousek *et al.* (*1, 9*). Gray boxes represent independent parameters and are defined in Table 1. White boxes represent dependent parameters and are intermediate or final calculations. Abbreviations: HTNPP, co-opted terrestrial NPP; A, area; CB, co-opted biomass. Subscripts: g, livestock grazing; ho, human-occupied lands; f, forests; ag, agriculture; gnl, livestock grazing on natural lands; ags, burning in savannas; sc, shifting cultivation; tp, tree plantation; fc, forest clearing (land use change); fh, industrial forest harvesting; nhi, not harvested but affected industrial forest; scstrf, shifting cultivation in secondary tropical forests; scs, shifting cultivation in savannas; fhctr, industrial forest harvesting in tropical forests.

parameters (*17*) directly assumed from (*1*), 37%; positive differences in some parameters are fortuitously canceled by negative differences in others.

Five parameters (Table 1), two of which are area calculations, have updated estimates with standard error bounds below or above the estimates of Vitousek *et al.* (*1*): area of forest converted to grazing (A_{gcp}), area of tree plantations (A_{tp}), clearing rate of shifting cultivation (CR_{sc}), population that uses shifting agriculture (POP_{sc}), and volume of forest harvest for wood used for construction and fiber in temperate areas (V_{fhct}). With the exception of CR_{sc}, each estimate is based on limited updated data and relies heavily on recent compilations from the Food and Agriculture Organization (FAO) of the United Nations (*21–27*). It is debatable whether updated estimates for these parameters are more valid than those obtained earlier, but in any case, these five parameters have little bearing on our results. Our mean estimate of HTNPP is unchanged at 39 Pg if we use the earlier estimates (*1*) for these parameters. However, the variance in our estimates of parameters does influence uncertainty in our estimate of HTNPP significantly. The 95% confidence intervals in our estimates of HTNPP are ±27 Pg DM (14 Pg C) (*28*). These error bounds are so wide that mean estimates of HTNPP like that obtained here and earlier have limited utility.

Although there is a large degree of uncertainty, it is clear that human impact on TNPP is significant. The lower bound on our estimate (12 Pg DM, 6.0 Pg C), although nowhere near total TNPP, indicates that humans have had more impact on biological resources than any single species of megafauna known over the history of Earth.
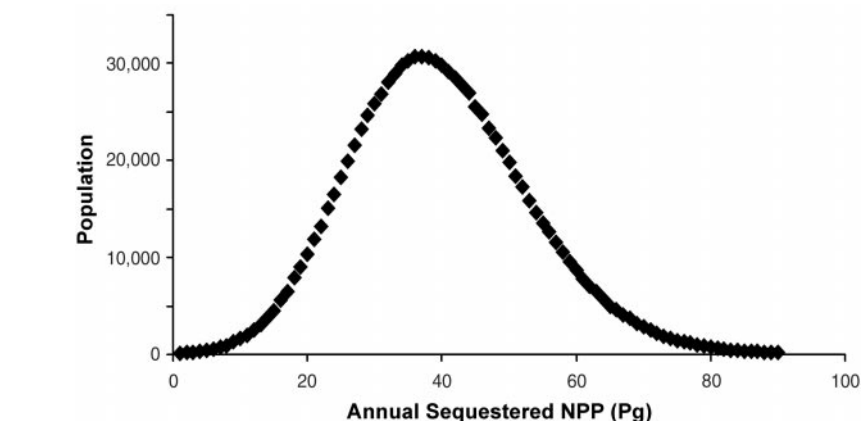
Fig. 2. Histogram of estimate of HTNPP allowing all parameters in the formula to vary with limits set by their estimated uncertainty. Histogram represents 1 million simulations. All independent parameters were constrained to be greater than zero. "Population" refers to the number of estimates represented by each data point on the plot.

The uncertainty in our estimates also has implications for assessing the state of human use of fresh water. Postel *et al.* (*2*) used mean estimates of HTNPP obtained from Vitousek *et al.* (*1*) to estimate that 26% of all terrestrial evapotranspiration is appropriated by humans. The high degree of uncertainty in our understanding of HTNPP means that Postel *et al.*'s estimate may significantly overestimate or underestimate human appropriation of evapotranspiration. Given our relatively poor knowledge of HTNPP, we cannot know whether human impact on our plant and water resources is in a state of crisis.

We reran our Monte Carlo simulations and systematically held every variable constant except one to determine the influence of variability of each parameter on our estimate of HTNPP

(Fig. 3). The most significant variables are agricultural productivity (PR_{ag}) and biomass of secondary tropical forest (B_{strf}). Estimates of PR_{ag} and B_{strf} are extensive in the literature, but they vary widely. It is not surprising that there would be a high degree of variability in these parameters. PR_{ag} and B_{strf} can be expected to be highly heterogeneous. Depending on fertilizer, irrigation, and crop type, PR_{ag} can vary by as much as a factor of 5 from field to field (*14, 29–31*).

Uncertainty in three other parameters—area of agricultural lands (A_{ag}), biomass of forest areas permanently cleared for population increase and colonization (B_{fc}), and proportion of shifting cultivation in secondary tropical forest (P_{scstrf})—contributes significantly to our uncertainty in HTNPP (greater than 6 Pg DM varia-

Table 1. Description of variables in the formula used (see Fig. 1) with updated estimates. Weights are in units dry matter. For source values and references beyond (31), see *Science* Online (www.sciencemag.org/cgi/content/full/294/5551/2549/DC1).

Source variable	Description	Prior estimate (1)	Contemporary mean	SD mean	Number of samples
A_{ag} (m²)	Area of agricultural land (21, 33–43)	1.6×10^{13}	1.3×10^{13}	0.33	11
A_{fc} (m²)	Area permanently cleared for population increase and colonization (26, 43–48)	1.2×10^{11}	1.3×10^{11}	0.23	7
A_{gcp} (m²)	Area of forest converted to grazing for all time (21)	7×10^{12}	3.3×10^{12}	0.50	1
A_{ho} (m²)	Area of human-occupied lands (38–40, 49)	2×10^{12}	1.8×10^{12}	1.2	4
A_s (m²)	Area of savanna (39–40, 42, 44, 50–52, 215)	1.5×10^{13}	1.7×10^{13}	0.46	8
A_{sctrf} (m²/year)	Area cleared in tropical virgin forests by shifting cultivation (1, 53, 54)	1.0×10^{10}	3.8×10^{10}	0.79	3
A_{tp} (m²)	Area of tree plantations (12, 22–24, 47, 55–57)	1.5×10^{12}	1.2×10^{12}	0.18	6
B_{fc} (Pg/m²)	Biomass of forest areas permanently cleared for population increase and colonization (1, 11–14, 27, 47, 48, 50, 58–109, 111–116, 214)	2.2×10^{13}	3.3×10^{13}	0.91	61
B_{scs} (Pg/m²)	Biomass of savanna in shifting cultivation (including below-ground) (13, 39, 48–50, 54, 98, 109, 110, 113–129)	8.5×10^{12}	5.6×10^{12}	1.1	23
B_{sh} (Pg/m²)	Biomass of above-ground grasses in burned savanna (1, 103, 104, 109, 130–141)	3.9×10^{11}	6.7×10^{11}	0.60	14
B_{strf} (Pg/m²)	Biomass of secondary tropical forest (including below-ground) (11, 12, 48, 72–89, 109, 115, 116, 142, 143)	1.8×10^{13}	1.7×10^{13}	0.65	20
B_{trf} (Pg/m²)	Biomass of tropical forests (including below-ground) (11, 13, 16, 27, 47, 48, 50, 84–103, 107–114, 143–150)	3.9×10^{13}	3.6×10^{13}	0.58	43
CR_{sc} (m² person⁻¹ year⁻¹)	Clearing rate of shifting cultivation (1, 53, 102, 151, 152)	2.0×10^{3}	1.7×10^{3}	0.16	5
NPP_{fwd} (Pg/year)	NPP of firewood (27, 44, 54, 55, 152–159)	1.0	0.90	0.80	10
NPP_{lse} (Pg/year)	NPP eaten by livestock (1, 8, 109, 160–164)	2.2	3.6	0.53	5
$P_{fb/mf}$	Proportion of forest biomass relative to merchantable fraction (1, 15, 16, 68–72, 89, 90, 104, 107, 115, 158, 166–171)	2.1	2.7	1.2	21
$P_{fwd/lc}$	Proportion of firewood that is met by land clearing and cultivation (102, 104)	0.30	0.65	0.75	2
P_{gbnl}	Proportion of burning on natural grazing lands (1)	0.43	0.43	0.50	1
P_{ho}	Proportion of productive human-occupied lands (13)	0.40	0.40	0.50	1
$P_{lgnp/gp}$	Proportion of natural pasture grazed by livestock relative to all grazed pasture lands (1)	0.50	0.50	0.50	1
$P_{lse/nl}$	Proportion of NPP eaten by livestock that comes from natural lands (172)	0.68	0.87	0.50	1
P_{nhfwd}	Proportion of firewood harvested but not used every year (1)	0.50	0.50	0.50	1
POP_{sc}	Population that uses shifting agriculture (25, 173)	2.0×10^{8}	4.5×10^{8}	0.15	2
PR_{ag} (Pg m⁻² year⁻¹)	Productivity of agricultural lands (1, 13, 14, 30, 31, 39, 42, 48, 91, 98, 105, 109–112, 116, 129, 174–178)	9.4×10^{13}	9.0×10^{13}	0.55	16
PR_{gcp} (Pg m⁻² year⁻¹)	Productivity of lands converted to pasture (1, 13, 14, 30, 31, 39, 48, 50, 101, 105, 109–112, 116, 129–132, 154, 178–196)	1.4×10^{12}	1.1×10^{12}	0.82	37
PR_{ho} (Pg m⁻² year⁻¹)	Productivity of human-occupied lands (39, 197)	5.0×10^{13}	3.5×10^{13}	0.60	2
PR_{tp} (Pg m⁻² year⁻¹)	Productivity of tree plantations (12, 13, 39, 55, 95, 96, 109, 198)	1.75×10^{12}	1.60×10^{12}	0.81	8
P_{sb}	Proportion of savanna burned annually (44, 54, 125, 157, 179, 199–202)	0.40	0.40	0.75	9
P_{scs}	Proportion of shifting cultivation in savannas (1, 72, 152, 203, 204)	0.43	0.46	0.41	5
P_{scstrf}	Proportion of shifting cultivation in secondary tropical forest (44, 53, 72, 87, 109, 152, 204)	0.57	0.64	0.42	6
P_{tp}	Proportion of wood that humans use of tree plantation origin (22, 55)	0.25	0.22	0.50	1
ρ_w (Pg/m³)	Density of fiber/construction wood (1, 12, 15, 16, 89, 99, 106, 107, 115, 170, 205–213)	6.0×10^{-10}	5.6×10^{-10}	0.55	17
V_{fhct} (m³/year)	Volume of forest harvest for wood used for construction and fiber in temperate areas (26, 27, 36)	1.65×10^{9}	1.1×10^{9}	0.1	52
V_{fhctr} (m³/year)	Volume of forest harvest for wood used for construction and fiber in tropical areas (27)	4.0×10^{8}	3.9×10^{8}	0.50	1

tion). Two of these parameters are area calculations and indicate that our lack of knowledge extends to what should be relatively simple parameters to measure precisely.

Our analysis indicates that the assessment of human limits to plant and water use will require better estimation of some highly heterogeneous parameters, including global productivity of agricultural, grazed, and human-occupied lands. Reduction in the uncertainty of these parameters will likely demand detailed worldwide assessment through a combination of many pieces of information, including satellite data, national crop figures, and patterns of irrigation and fertilizer use. Without these types of future assessments, the magnitude of the human footprint on Earth is open to much speculation.

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9. Here we use the "intermediate calculation" of Vitousek *et al.* (1), which includes all TNPP appropriated by humans (indirectly or directly) and by human-altered ecosystems:

$$\Sigma(HTNPP) = (A_{ag} \times PR_{ag}) + (A_{gcp} \times PR_{gcp})$$
$$+ (NPP_{lse} \times P_{lse/nl} \times P_{lgnp/gp}) + (A_s \times P_{sb} \times B_{sh} \times P_{gbnl})$$
$$+ (A_{tp} \times PR_{tp}) - P_{tp} \times \{NPP_{fwd} + P_{fb/mf} \times [(V_{fhct} \times \rho_w)$$
$$+ (V_{fhctr} \times \rho_w)] + (NPP_{fwd} \times P_{nhfwd})\} + ([[(V_{fhct} \times \rho_w)$$
$$+ (V_{fhctr} \times \rho_w)] \times P_{fb/mf}] - [(V_{fhct} \times \rho_w)$$
$$+ (V_{fhctr} \times \rho_w)]) + (POP_{sc} \times CR_{sc} \times P_{scstrf} \times B_{strf})$$

Fig. 3. Sensitivity analysis showing key independent parameters that strongly influence uncertainty in our estimate of HTNPP. Analysis was performed by systematically holding all variables (except one) constant and equal to their mean. Each parameter was allowed to vary randomly 1 million times.
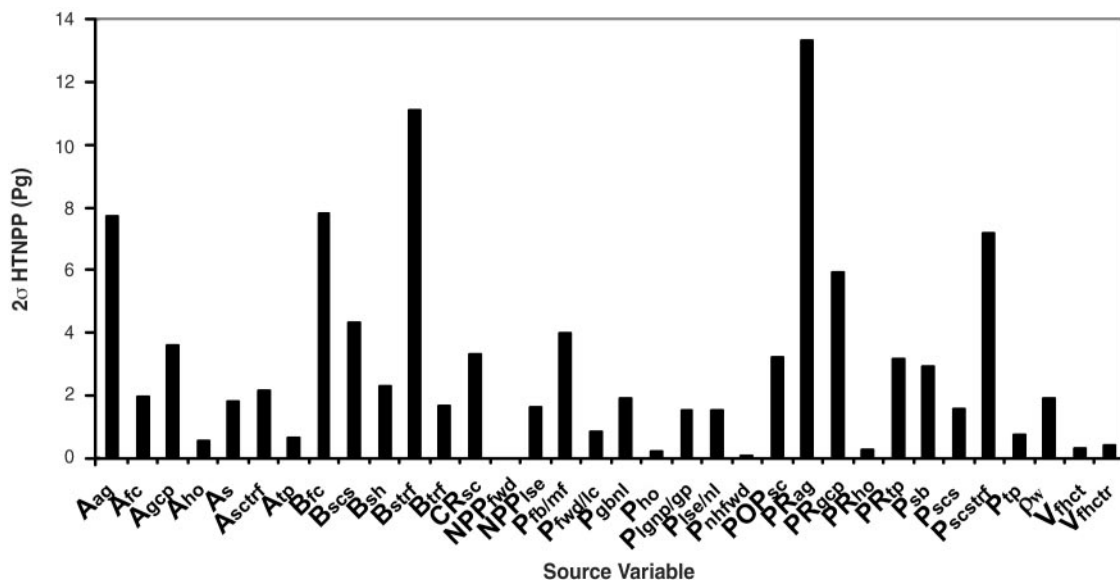
$$+ \ (POP_{sc} \times CR_{sc} \times P_{scs} \times B_{scs}) + (A_{sctrf} \times B_{trf})$$
$$+ \ (A_{fc} \times B_{fcs}) - (NPP_{fwd} \times P_{fwd/lc}) + (V_{fhct} \times \rho_w)$$
$$+ \ (V_{fhctr} \times \rho_w) + NPP_{fwd} + (A_{ho} \times P_{ho} \times PR_{ho})$$

The "low calculation" of Vitousek et al. (1), because it deals only with direct consumption, by design yields an unrealistically low assessment of human impact. The "high calculation" requires speculation on the TNPP lost as a result of human activities.

10. Data in the literature usually are presented as (i) means ± standard deviations, (ii) ranges, or (iii) means. Where a choice was available, we selected the data format according to the above order. We consider global-scale studies to be those whose data are chosen to represent the country scale or larger. To reduce subjectivity, we filtered out data that would require significant manipulation (e.g., incorporating allometric rules) to be used by our model.
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17. Four of the parameters (P_{gbnl}, P_{ho}, $P_{lgnp/gp}$, P_{nhfwd}; see Table 1 for definitions) are difficult to estimate because of the absence of data in the literature. We used the ad hoc estimates of (1).
18. The ad hoc estimate of error we use, 0.50, is slightly less than the mean error for parameters with multiple data, 0.60.
19. It would be possible to derive some of the uncertainty in our estimate of HTNPP analytically, especially for aspects that involve simple summation of independent parameters. However, given that many of the parameters are multiplied and that we wished to constrain parameters to be non-negative, the Monte Carlo approach is necessary.
20. We assumed that TNPP is 120 Pg, which is a mean value derived from 30 references since 1990. For these estimates and references, see *Science* Online (www.sciencemag.org/cgi/content/full/294/5551/2549/DC1).
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28. Our estimates of uncertainty are conservative in that (i) estimates of parameters are not independent (i.e., they are influenced by older literature, and some newer estimates are reworkings of older ones), and (ii) uncertainty due to assumptions in the model used (template, Fig. 1) is not included.
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A DNA Microarray-Based Genetic Screen for Nonhomologous End-Joining Mutants in *Saccharomyces cerevisiae*

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We describe a microarray-based screen performed by imposing different genetic selections on thousands of yeast mutants in parallel, representing most genes in the yeast genome. The presence or absence of mutants was detected by oligonucleotide arrays that hybridize to 20-nucleotide "barcodes." We used this method to screen for components of the nonhomologous end-joining (NHEJ) pathway. Known components of the pathway were identified, as well as a gene not previously known to be involved in NHEJ, *NEJ1*. Nej1 protein interacts with the amino terminus of LIF1/XRCC4, a recently recognized "guardian of the genome" against cancer.

A worldwide effort to create a comprehensive genetic resource has resulted in a nearly complete collection of deletion alleles

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corresponding to the yeast open reading frames (ORFs) (1, 2). Over 5800 of the estimated 6000-plus yeast ORFs have been systematically disrupted. In each mutant the ORF is precisely replaced by a *kanMX* cassette that confers G418 resistance. In addition, each cassette contains two 20-nucleotide (nt) "barcodes" uniquely assigned to that gene. The sequences, called UPTAGs and DOWNTAGs, are flanked by universal priming sites and can be used as