

Global mapping of ecosystem services and conservation priorities

R. Naidoo^{*†}, A. Balmford[‡], R. Costanza[§], B. Fisher[¶], R. E. Green^{†||}, B. Lehner^{**}, T. R. Malcolm^{*}, and T. H. Ricketts^{*}

^{*}Conservation Science Program, World Wildlife Fund/United States, 1250 24th Street NW, Washington, DC 20037; [†]Conservation Science Group, Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, United Kingdom; [§]Gund Institute for Ecological Economics, University of Vermont, 617 Main Street, Burlington, VT 05405; [¶]Centre for Social and Economic Research on the Global Environment, School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ, United Kingdom; ^{||}The Royal Society for the Protection of Birds, The Lodge, Sandy, Bedfordshire SG19 2DL, United Kingdom; and ^{**}Department of Geography, McGill University, 805 Sherbrooke Street West, Montreal, QC, Canada H3A 2K6

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Global efforts to conserve biodiversity have the potential to deliver economic benefits to people (i.e., “ecosystem services”). However, regions for which conservation benefits both biodiversity and ecosystem services cannot be identified unless ecosystem services can be quantified and valued and their areas of production mapped. Here we review the theory, data, and analyses needed to produce such maps and find that data availability allows us to quantify imperfect global proxies for only four ecosystem services. Using this incomplete set as an illustration, we compare ecosystem service maps with the global distributions of conventional targets for biodiversity conservation. Our preliminary results show that regions selected to maximize biodiversity provide no more ecosystem services than regions chosen randomly. Furthermore, spatial concordance among different services, and between ecosystem services and established conservation priorities, varies widely. Despite this lack of general concordance, “win-win” areas—regions important for both ecosystem services and biodiversity—can be usefully identified, both among ecoregions and at finer scales within them. An ambitious interdisciplinary research effort is needed to move beyond these preliminary and illustrative analyses to fully assess synergies and trade-offs in conserving biodiversity and ecosystem services.

biodiversity | carbon | hotspots | Global 200 | conservation planning

Efforts to conserve wild nature have traditionally focused on biodiversity: the variety of life on earth at scales from genes to ecosystems (1). Recently, conservationists have become interested in another aspect of conservation: the goods and services from ecological systems that benefit people (e.g., water purification, carbon sequestration, and crop pollination). These “ecosystem services” are currently the focus of intensive research, development, and policy attention (2–4). The Millennium Ecosystem Assessment (5) documented the importance of ecosystem services to human well-being and showed that continued supply of these services is threatened by unsustainable anthropogenic activities (5, 6). Conservation groups have begun to promote ecosystem services and the benefits that biodiversity programs confer on people (7), but there is little direct evidence of this effect beyond a few local case studies (8–10). To effectively integrate ecosystem services into planned or existing conservation programs, we need to more broadly evaluate the spatial concordance between areas that produce ecosystem services and those that support biodiversity.

Such evaluation will require the best available data on the distribution of both ecosystem services and biodiversity. On the biodiversity side, the past 20 years have seen progress from extrapolations and general guesses about biodiversity in biomes such as tropical forests (11) to comprehensive, high-resolution global datasets on species ranges of a number of taxonomic groups (12–15). To accompany these improving data, researchers have developed sophisticated methods for prioritizing conservation efforts (16–18).

In contrast, the spatial estimation of global ecosystem service values remains quite crude. Similar to initial estimates of species richness, an early and controversial study on global ecosystem service values used localized, context-specific valuation studies to extrapolate economic values for the whole world (19). Ten years after this study was published, global and regional efforts to map ecosystem services continue to use these estimates (20–22), despite the well known limitations (23). In addition, few studies have taken advantage of recent technical advances in the selection of priority areas for biodiversity and adapted these advances to cover ecosystem services (but see refs. 24–26).

To move forward, global ecosystem service assessments must generate better maps of where ecosystem services are produced, quantify the likelihood of land use conversion and its probable impact on service provision, and understand the value and flow of benefits to nearby and distant human populations. This will require an extraordinary interdisciplinary effort (see Table 1) yet is vital for informed decision-making. For example, payments for ecosystem services (PES), which involve those who benefit from an ecosystem service compensating those who provide the service, will only benefit biodiversity conservation if there is spatial congruence between important areas for biodiversity and ecosystem services and if there is congruence in the particular land use regimes that best deliver both targets. Because characterizing multiple ecosystem services and biodiversity across the same region has only recently emerged as a field of study (27, 28), these levels of congruence are poorly understood, and the little quantitative evidence available to date has led to mixed conclusions (26, 29).

The above represents an ambitious research agenda for at least the coming decade, but how far can we get today? Here we explore this question by using available data of global extent and find only four ecosystem services for which we could map proxies at a global scale, and even those data are imperfect (Table 1). We assess these maps against the elements necessary for comprehensive mapping of global ecosystem services. Then, using this incomplete set, we illustrate the potential synergies and conflicts between the conservation of ecosystem services and more conventional biodiversity targets. We use ecoregions as the individual planning units because they are widely accepted as a useful template on which to base global-scale priority-setting (30) and because comprehensive data on vertebrate species

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[†]To whom correspondence should be addressed. E-mail: robin.naidoo@wwfus.org.

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Table 1. Elements required for mapping and valuation of ecosystem services in a spatial context

Element	Ecosystem service			
	Carbon sequestration	Carbon storage	Grassland production of livestock	Water provision
Rate of service production	Process model	Extrapolated observations	Statistical model	Production map attributed upstream
Flow of service away from production area	Global flow	Global flow	Approximately zero flow	Process-based hydrological model
Presence of beneficiaries	Global flow	Global flow	Restricted to livestock areas	Initially mapped at point of use
Economic value per unit service	Globally uniform	Globally uniform	Local net value of pasture to meat yield	Local net value of water to human uses
Probability of system being converted to another state	Fine-scale conversion probabilities	Fine-scale conversion probabilities	Fine-scale conversion probabilities	Fine-scale conversion probabilities
Change in service value if converted	Difference in service value between unconverted and converted states	Difference in service value between unconverted and converted states	Difference in service value between unconverted and converted states	Difference in service value between unconverted and converted states

Entries in bold are those we were able to address for the four services examined here.

distributions have recently become available for all terrestrial ecoregions (15). We ask four main questions: (i) How well correlated across space are the four ecosystem services? (ii) How do conservation priorities focused on biodiversity capture ecosystem services, and vice versa? (iii) Which of the world’s terrestrial ecoregions represent “win-win” locations for biodiversity and ecosystem services (given current data on both) and which represent trade-offs? and (iv) Do these global patterns hold at within-ecoregion scales, where conservation investments are typically made?

Results

Ecosystem Service Maps. We found only four ecosystem services for which we could develop spatial proxies (maximum resolution 0.5°) to represent their global geographic distribution (Table 1). Clearly, these four represent only a small subset of all important ecosystem services, but we were unable to locate global data for any others (we did not consider marine services, despite their economic and nutritional importance). Below we define each service, describe the proxies we developed to map them, compare these proxies with the ideal elements in Table 1, and highlight the major limitations of each proxy. See *Materials and Methods* for more details on proxy development.

Carbon sequestration is the net annual rate of atmospheric carbon added to existing biomass carbon pools, helping to slow global climate change. Our proxy for the spatial distribution of carbon sequestration across the globe was net carbon exchange (NCE) produced in simulations using the Terrestrial Ecosystem Model (TEM) (31, 32) [supporting information (SI) Fig. S1A]. Because this service is, in principle, enjoyed everywhere, irrespective of its point of production, spatially explicit models of service flows (Table 1, row 2) to beneficiaries (Table 1, row 3) are unnecessary. However, mapping the actual benefits of carbon sequestration would require additional spatial data on (i) the probability that a given parcel of land of a given biome is converted from its current state and (ii) the differences in rates of carbon sequestration between previous and new states (Table 1, rows 5 and 6). The main limitation of our proxy is that it is model-based, not observational, and therefore depends heavily on the assumptions, input variables, and time scales that defined the particular TEM simulation we used (simulation S3 in ref. 31).

Carbon storage is the amount of carbon stored in vegetation (both aboveground and belowground) and, therefore, an avoided flow of carbon into the atmosphere. Our proxy for carbon storage (Fig. S1B) was Olson’s classic estimates of above-

and belowground carbon stored in various biomes, updated using the Global Land Cover 2000 (GLC2000) land cover map (33) (Table 1, row 1). Because carbon storage avoids the prospect of further exacerbating global climate change, its remaining elements in Table 1 are identical to those for carbon sequestration. The main limitations of this proxy measure are that it is based on data that were originally published more than 20 years ago and that the original measures only coincide with 18 biome types that are mapped globally and assigned a single carbon value. Nevertheless, this is still the only globally consistent dataset based on observations of carbon in vegetation biomass (N. Ramankutty, personal communication).

Grassland production of livestock is the annual production of livestock derived, at least in part, from grazing on unimproved natural grasslands (Fig. S1C). We mapped livestock production on natural grasslands by combining global data on livestock distributions (34), producer prices, and current and potential vegetation (35, 36) (Table 1, row 1). Because the economic benefits from livestock on grasslands are realized primarily at the point of production (Table 1, row 3), there is essentially no further flow before the service reaches its primary beneficiaries (Table 1, row 2). Limitations of these data include problems associated with mapping of pastures from remotely sensed imagery (e.g., it is difficult to determine from remote sensing whether grasslands have been “improved” by the introduction of nonnative species) and the lack of spatially explicit weightings that would reflect differences in the economic value of livestock species in different regions of the world.

Water provision is water used for irrigation, industry, domestic consumption, and livestock production. Our map of water provision (Fig. S1D) was based on the global hydrological model WaterGAP (37), which provides spatially explicit estimates of water availability and water use for various economic sectors (Table 1, row 3). We attributed the flows of this water upstream from their points of use to their points of production (Table 1, rows 1 and 2) by dividing the world into drainage basins (38) and distributing the total volume of water used in a basin among all basin grid cells in proportion to a cell’s runoff level. The main limitations of our proxy are that it ignores both spatial variation in water value (depending on scarcity and type of use) and, crucially, changes in water provision resulting from land use change (Table 1, rows 4 and 5). Hydrological responses to changes in vegetation are complex and controversial (39); our global surface, therefore, shows only where any such changes would impact the most water as currently provided.

Table 2. Correlations among log-transformed, per-unit-area ecosystem service production levels ($n = 574$ ecoregions; Pearson correlation coefficients)

	Carbon storage	Carbon sequestration	Grassland production	Water provision
Carbon storage	1	—	—	—
Carbon sequestration	0.17	1	—	—
Grassland production	-0.19	-0.02	1	—
Water provision	0.002	-0.07	0.20	1

Comparisons Between Ecosystem Services and Biodiversity. To assess the spatial concordance among ecosystem services at the global scale, we calculated mean per-unit-area ecosystem service production for each ecoregion. Log-transformation of these averages, and subsequent Pearson correlation analyses, revealed little correspondence among services; no pair of services had a correlation coefficient >0.2 (Table 2).

Next, we tested how well areas selected to maximize biodiversity capture ecosystem services, and vice versa. We used integer programming optimization methods (40) and ecoregion distribution data for mammal, bird, reptile, and amphibian species as our measures of biodiversity, conducting separate analyses for each taxonomic group. We first maximized species representation, determining the set of ecoregions that together contained the most species for a given total area. We compared the resulting species accumulation curves with the equivalent curves derived by choosing ecoregions to maximize total ecosystem service provision. On average for all taxa, we found that (for levels up to 90% of species representation) optimizing for individual ecosystem services conserved only 22–35% as many species for a given area as did optimizing for species, that is, no more than were conserved by selecting ecoregions at random (Fig. 1A).

We then conducted the converse analysis, selecting ecoregions to maximize ecosystem service provision and comparing these results with service levels captured while maximizing species. We found that maximizing species representation for a given area captured only 17–53% of maximum ecosystem service provision, depending on which service was considered and at which area limit the comparison was made. These levels of ecosystem service capture from species optimization were, again, no greater than those from a random selection of ecoregions (Fig. 1B).

How effectively do existing priority areas conserve ecosystem services? We asked this question for three contrasting global biodiversity priority schemes (Fig. S2): biodiversity hotspots (41), high-biodiversity wilderness areas (HBWAs) (42), and Global 200 ecoregions (43). The relative performance of the three prioritization schemes varied markedly across the four ecosystem services (Fig. 2). For carbon storage and sequestration, HBWAs had the highest mean levels, whereas biodiversity hotspots had the lowest levels. Hotspots were, in fact, net emitters of carbon during the 1980s. In contrast, water provision and grassland production of livestock were highest in biodiversity hotspots and lowest in HBWAs (Fig. 2). For all four services, Global 200 ecoregions offered intermediate levels of ecosystem service provision that were near to global averages (Fig. 2).

As a simple illustration of how ecoregions might be prioritized for both biodiversity and ecosystem services, we plotted ecoregions on axes that quantify their rank importance for both attributes (Fig. 3). We defined biodiversity importance as the number of endemic vertebrate species, adjusted for area. Combining ecosystem services is difficult without valuations to weight each service relative to others, so, for the purposes of this analysis, we defined ecosystem service importance by using carbon storage alone. We divided Fig. 3 into four quadrants, based on median values for each variable. Despite a lack of correlation between the two variables, many ecoregions lie in quadrant 4, with importance for both biodiversity and ecosystem services. These win–win ecoregions tend to be located in tropical forested regions (Fig. S3), whereas ecoregions with low priority for both carbon storage and biodiversity are mostly in desert or tundra regions.

Finally, we used data from one specific ecoregion to examine whether global patterns hold at the smaller scales where conservation decisions are typically made. Chan *et al.* (26) divided

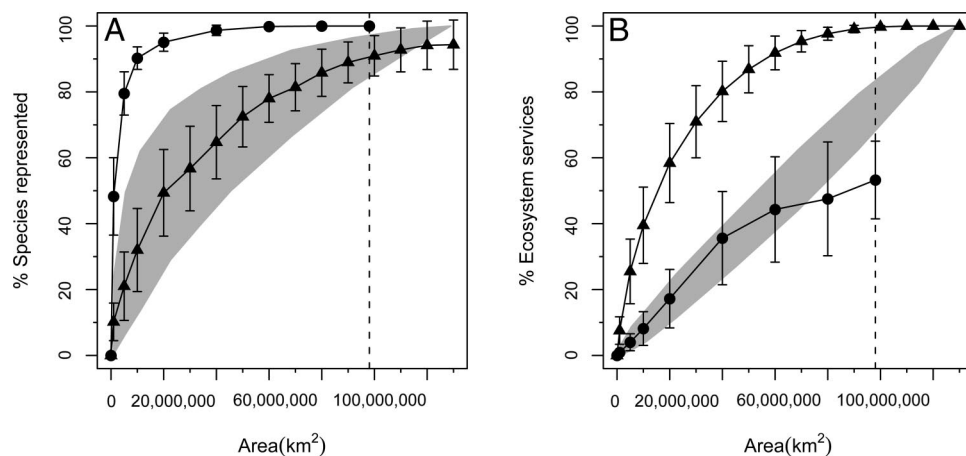


Fig. 1. Percentage accumulation of species (A) and ecosystem services (B) as total area selected for conservation increases. Circles represent optimizations of species representation (mean results from separate optimizations of birds, mammals, reptiles, and amphibians; error bars = 1 SD). Triangles represent optimizations of ecosystem services (mean results from separate optimizations of each of the four ecosystem services we considered). Shaded areas indicate 95% confidence limits from 500 sets of ecoregions selected at random. Dashed vertical lines indicate area at which all vertebrate species are represented.

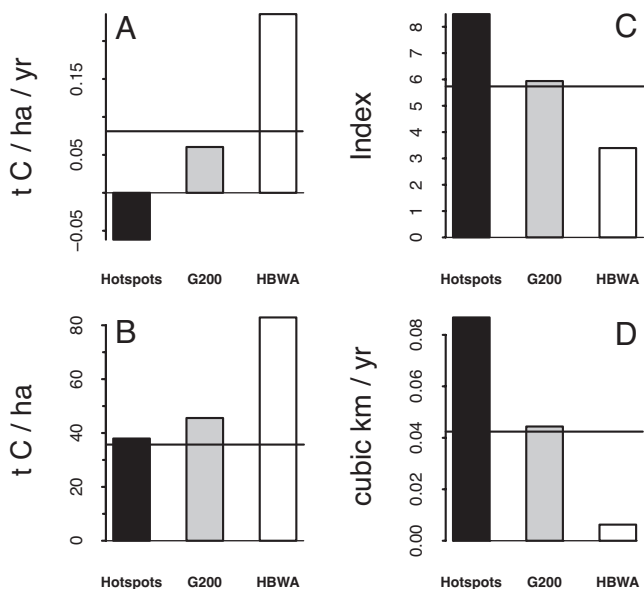


Fig. 2. Mean amount of ecosystem services per unit area provided by three global conservation priority schemes. (A) Carbon sequestration. (B) Carbon storage. (C) Grassland production of livestock. (D) Water provision. Horizontal lines represent the global mean for each service.

the California Central Coast ecoregion of the United States into $\approx 12,000$ hexagonal planning units and assessed levels of biodiversity and ecosystem services in each. This ecoregion occupies quadrant 4 in Fig. 3, identifying it as a global win-win for conserving biodiversity and stored carbon. However, mapping the quadrant scores of individual hexagons within the ecoregion indicates an abundance of both win-win and trade-off locations (Fig. S4, and see figure 2 in ref. 25 for similar results from more sophisticated analyses).

Discussion

The analyses presented here are clearly preliminary and are intended primarily for heuristic purposes. However, they do suggest some early lessons and important research priorities.

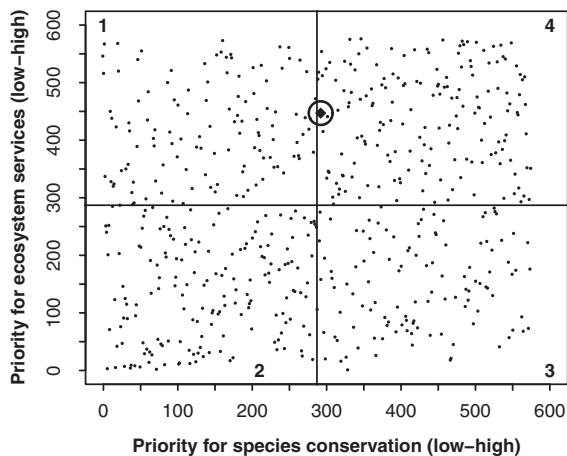


Fig. 3. Relationship between ecosystem service importance and conservation importance. Each axis is the rank order (low to high) of 574 terrestrial ecoregions in terms of per-area carbon storage (y axis) or area-corrected number of endemic species [x axis; calculated as (No. endemic species/area^{0.25})]. Lines indicate median values for each variable. Diamond in quadrant 4 represents the California Central Coast ecoregion.

One of our most striking findings is simply how few ecosystem services we were able to include in our analyses. This suggests that major new interdisciplinary efforts will be required in order to quantify and map even a fraction of the most important ecosystem services—and to assess their coincidence with biodiversity—at global scales.

Learning what we could from the available data, we found that conservation priorities aimed solely at biodiversity do not conserve optimal levels of the ecosystem services we examined, and vice versa. This can be seen by using both theoretical planning algorithms (Fig. 1) and actual portfolios for biodiversity conservation (Fig. 2). More complete analyses, including additional ecosystem services and other aspects of biodiversity, may show better concordance. Nevertheless, our findings emphasize that such concordance cannot be assumed and needs to be tested empirically.

The pattern of service capture among global conservation priority schemes (Fig. 2) reflects the distribution of service beneficiaries within these regions. The benefits of carbon storage and sequestration are globally dispersed and do not depend on local beneficiaries. Accordingly, these services were highest in the low-human-density HBWAs. On the other hand, water provision and grassland production of livestock, which benefit people closer to the point of service production, were highest in the densely populated biodiversity hotspots. The intermediate levels of service provision for Global 200 ecoregions reflect that these regions include both wilderness areas and areas of dense human settlement.

Despite the overall lack of spatial concordance between biodiversity and ecosystem services (Table 2), we were still able to identify win-win areas: ecoregions important for both types of targets (Fig. 3, quadrant 4). In these places, PES are more likely than elsewhere to achieve biodiversity conservation objectives. Perhaps more importantly, Fig. 3 also identifies areas of trade-off, where biodiversity conservation is crucial but is less likely to be supported by PES (quadrant 3) or where PES will likely have lesser impact on global conservation (quadrant 1). Mapping out all four quadrants (Fig. S3) illustrates that priorities for both ecosystem services and biodiversity can be located to guide conservation investment.

Although global analysis can inform broad-scale priorities, it is clear that actual conservation investments typically occur at more local scales. We found that, although a California ecoregion falls within quadrant 4 in our global analysis (Fig. 3), less than one-quarter of the planning units within it represent win-wins at more local scales (Fig. S4). Hence, even win-win ecoregions can contain areas that represent trade-offs between conservation and ecosystem services. By extension, ecoregions in quadrants 1–3 (Fig. 3) will almost certainly contain local win-win opportunities, especially when services that operate over relatively small scales (e.g., pollination by wild insects) are considered. Although finer scale analyses will be essential for targeting specific conservation action, global analyses remain useful for identifying broad areas where taking such actions is most likely to benefit people.

Data availability severely limited our analyses. For the four ecosystem services we assessed, we were only able to assemble data on the first three elements that are needed for a comprehensive assessment (Table 1, rows 1–3). Relatively speaking, mapping of the biophysical production (row 1) and flows of ecosystem services has perhaps seen the most progress, but, as we have indicated, much remains to be done (44, 45). Identifying ecosystem service beneficiaries requires knowing who they are and where they live. Sociologists, anthropologists, and political scientists need to identify how social structure, cultural elements, and governance affect who benefits from ecosystem services and by how much (46). On the economics side (Table 1, row 4), no spatial data were available on economic values, preventing us

from “monetizing” our maps. Although there is a rich literature on economic valuation of the environment, research on how values vary spatially has only recently begun to emerge (24). Beyond economic valuation, quantifying the net benefits of ecosystem conservation also requires spatially explicit data on the probabilities of conversion to other land use types (Table 1, row 5), coupled with information on likely rates of service provision after conversion (Table 1, row 6). Different management regimes within the same land use type can also alter levels of service provision (47) and so are another important consideration.

These data limitations likely affect our comparative results in several ways. For example, natural pastures are difficult to distinguish from human-cleared areas by using remote sensing; therefore, we may have overestimated livestock production from natural pastures in the biodiversity hotspots, with their preponderance of cleared lands (Fig. 2). More generally, the particular services and species we considered may have led us to overestimate how poorly priority areas for species conservation deliver services, and vice versa. Two of our four species services (carbon storage and sequestration) peak in tropical and temperate forests and are, therefore, biased away from ecoregions with high vertebrate endemism, which are often island or montane areas (41). Similarly, given our endemics-based biodiversity measure, our species data were limited to taxa with relatively large ranges, reducing the importance of broad areas of tropical forests. Both of these data biases act to drive the curves in Fig. 1 further apart, thus underestimating the degree to which planning for ecosystem services would capture biodiversity, and vice versa. For these reasons, we reiterate that our analyses are only a first-cut attempt to illustrate the types of questions that could be asked, and approaches that could be used, once more comprehensive data on ecosystem services are available.

Despite the challenges discussed here, comparisons between biodiversity and ecosystem services have the potential to inform decision-making. To realize this potential, we need to learn how to rigorously quantify and map more elements of more services. Such an improved understanding would allow us to operationalize a principle that is becoming increasingly clear: that human welfare is linked in diverse ways to biodiversity conservation and that sustainable development should involve managing for both.

Materials and Methods

Carbon Sequestration. We used NCE results from the TEM model (32) as a proxy for carbon sequestration. TEM is a terrestrial biosphere model that simulates carbon exchange between the atmosphere and terrestrial biosphere on the basis of vegetation types, soils, climate, atmospheric CO₂, and land use history. We used results from the S3 simulation of TEM (31), in which atmospheric CO₂ concentrations, cropland expansion, and climatic conditions were all varied simultaneously. The model was run to equilibrium to 1880 and then run transiently through 1992. In ref. 31, annual NCE was calculated as heterotrophic respiration minus the sum of net primary productivity, carbon emissions from the conversion of natural vegetation to cropland, and carbon emissions from the decay of forest and agricultural products (units = $t_C ha^{-1} yr^{-1}$). Note that for our analyses, we multiplied NCE from ref. 31 by -1 , meaning that positive numbers indicate a net sequestration of carbon from the atmosphere to the biosphere, whereas negative numbers indicate a net release of carbon from the biosphere to the atmosphere. We used average NCE for the 1980s (the most recent decade for which simulation data were available) to most

closely approximate current carbon fluxes while also accounting for interannual variability.

Carbon Storage. Olson (33) originally estimated biome-level carbon values in preagricultural live vegetation through extensive field observations, inventories, and analyses of literature values. The updated dataset we used (33) mapped carbon values from Olson’s original biome types to land cover types of the GLC2000, hence providing an estimate of carbon stored in vegetation circa the year 2000. Although the dataset enjoys widespread use in carbon cycling research, its major deficiency is that whole biomes are assigned a single carbon value, neglecting major within-biome variability due to heterogeneity in climate, land use, soils, and topography.

Grassland Production of Livestock. To map livestock production on natural pastures, we used recently developed 5’-resolution global maps of livestock distributions (34). These maps use regression-based methods to estimate the expected density of cattle, sheep, goats, pigs, poultry, and buffalo across the earth’s surface. For each livestock type, we used these density estimates and data on the mass of edible meat per animal (estimated by country from United Nations Food and Agriculture Organization data) to estimate the tons of meat produced in each cell. A global producer price was used to weight different livestock types; using these weights, an aggregate index of livestock production was obtained by summing the weighted livestock meat weights. We then constructed a global map of natural pastures by combining a 5’-resolution potential vegetation dataset of savanna, grassland/steppe, and shrubland biome types (35) and then masking out all known human-altered landscapes by using the GLC2000 (36). We intersected the livestock production index and the map of natural pastures to produce a global map of livestock production on natural pastures, which, unlike for the other services we consider, restricts the production domain to wild nature. We aggregated the map of livestock production from 5’ to 0.5° spatial resolution for consistency with the other ecosystem service datasets evaluated here.

Water Provision. We used a global hydrological model to map water provision for human consumptive use. The WaterGAP 2 model provides data at 0.5° spatial resolution on annual water availability (surface runoff and total discharge) and consumptive water use per sector (e.g., industrial, domestic, irrigation, and livestock), averaged over a 30-year period (1961–1990) (37). We summed consumptive water use across the four sectors to produce a spatially explicit map of total water use in biophysical units (cubic kilometers per year). We then attributed the volume of water consumption back to its points of origin by using a basin-level perspective of water production. Drainage basins for the globe were identified from a 0.5° global drainage direction map (DDM30) (38). We calculated the proportional contribution of each cell to the total water production of the basin in which it resides, calculated the amount of total water consumption for that basin, and then redistributed the total consumption according to the proportion of basin-wide water production at each grid cell. By redistributing the volume of water consumption in this manner, we arrived at a coarse estimate of total water use attributed to point of origin.

Additional Materials and Methods. For further details on the methods and materials used in this study, see *SI Materials and Methods*.

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- Brooks TM, et al. (2006) Global biodiversity conservation priorities. *Science* 313:58–61.
- Sachs JD, Reid WV (2006) Environment: Investments toward sustainable development. *Science* 312:1002.
- Wunder S (2007) The efficiency of payments for environmental services in tropical conservation. *Conserv Biol* 21:48–58.
- Daily GC (1997) *Nature’s Services: Societal Dependence on Natural Ecosystems* (Island Press, Washington, DC).
- Millennium Ecosystem Assessment (2005) *Ecosystems and Human Well-Being: Synthesis* (Island Press, Washington, DC).
- Balmford A, et al. (2002) Economic reasons for conserving wild nature. *Science* 297:950–953.

- Odling-Smee L (2005) Dollars and sense. *Nature* 437:614–616.
- Russ GR, Alcala AC, Maypa AP, Calumpong HP, White AT (2004) Marine reserve benefits local fisheries. *Ecol Appl* 14:597–606.
- Ricketts TH, Daily GC, Ehrlich PR, Michener CD (2004) Economic value of tropical forest to coffee production. *Proc Natl Acad Sci USA* 101:12579–12582.
- Becker CD (1999) Protecting a garúa forest in Ecuador: The role of institutions and ecosystem valuation. *Ambio* 28:156–161.
- Erwin TL (1988) The tropical forest canopy: The heart of biotic diversity. *Biodiversity*, ed Wilson EO (Natl Acad Press, Washington, DC), pp 123–129.
- Orme CDL, et al. (2005) Global hotspots of species richness are not congruent with endemism or threat. *Nature* 436:1016–1019.

13. Ceballos G, Ehrlich PR, Soberon J, Salazar I, Fay JP (2005) Global mammal conservation: What must we manage? *Science* 309:603–607.
14. Stuart SN, et al. (2004) Status and trends of amphibian declines and extinctions worldwide. *Science* 306:1783–1786.
15. Lamoreux JF, et al. (2006) Global tests of biodiversity concordance and the importance of endemism. *Nature* 440:212–214.
16. Wilson KA, McBride MF, Bode M, Possingham HP (2006) Prioritizing global conservation efforts. *Nature* 440:337–340.
17. Pressey RL, Watts ME, Barrett TW (2004) Is maximizing protection the same as minimizing loss? Efficiency and retention as alternative measures of the effectiveness of proposed reserves. *Ecol Lett* 7:1035–1046.
18. Margules CR, Pressey RL (2000) Systematic conservation planning. *Nature* 405:243–253.
19. Costanza R, et al. (1997) The value of the world's ecosystem services and natural capital. *Nature* 387:253–260.
20. Sutton PC, Costanza R (2002) Global estimates of market and nonmarket values derived from nighttime satellite imagery, land cover, and ecosystem service valuation. *Ecol Econ* 41:509–527.
21. Li R-Q, et al. (2007) Quantification of the impact of land-use changes on ecosystem services: A case study in Pingbian County, China. *Environ Monit Assess* 128:503–510.
22. Turner WR, et al. (2007) Global conservation of biodiversity and ecosystem services. *Bioscience* 57:868–873.
23. Bockstael NE, Freeman AM, Kopp RJ, Portney PR, Smith VK (2000) On measuring economic values for nature. *Environ Sci Technol* 34:1384–1389.
24. Naidoo R, Ricketts TH (2006) Mapping the economic costs and benefits of conservation. *PLoS Biol* 4:e360.
25. van Jaarsveld AS, et al. (2005) Measuring conditions and trends in ecosystem services at multiple scales: The Southern African Millennium Ecosystem Assessment (SAfMA) experience. *Philos Trans R Soc London Ser B* 360:425–441.
26. Chan KMA, Shaw MR, Cameron DR, Underwood EC, Daily GC (2006) Conservation planning for ecosystem services. *PLoS Biol* 4:e379.
27. Schroter D, et al. (2005) Ecosystem service supply and vulnerability to global change in Europe. *Science* 310:1333–1337.
28. Metzger MJ, Rounsevell MDA, Acosta-Michlik L, Leemans R, Schroter D (2006) The vulnerability of ecosystem services to land use change. *Agric Ecosyst Environ* 114:69–85.
29. Bohensky EL, Reyers B, Van Jaarsveld AS (2006) Future ecosystem services in a Southern African river basin: A scenario planning approach to uncertainty. *Conserv Biol* 20:1051–1061.
30. Wikramanayake E, et al. (2002) Ecoregions in ascendance: Reply to Jepson and Whitaker. *Conserv Biol* 16:238–243.
31. McGuire AD, et al. (2001) Carbon balance of the terrestrial biosphere in the twentieth century: Analyses of CO₂, climate and land use effects with four process-based ecosystem models. *Global Biogeochem Cycles* 15:183–206.
32. Tian H, Melillo JM, Kicklighter DW, McGuire AD, Helfrich J (1999) The sensitivity of terrestrial carbon storage to historical climate variability and atmospheric CO₂ in the United States. *Tellus Ser B Chem Phys Meteorol* 51:414–452.
33. Gibbs HK (2006) *Olson's Major World Ecosystem Complexes Ranked by Carbon in Live Vegetation: An Updated Database Using the GLC2000 Land Cover Product* (Oak Ridge Natl Lab, Oak Ridge, TN), Numeric Data Package (NDP)-017b. Available at <http://cdiac.ornl.gov/epubs/ndp/ndp017/ndp017b.html>.
34. Wint W, Robinson T (2006) *Gridded Livestock of the World* (FAO, Rome).
35. Ramankutty N, Foley JA (1999) Estimating historical changes in global land cover: Croplands from 1700 to 1992. *Global Biogeochem Cycles* 13:997–1027.
36. Bartholome E, Belward AS (2005) GLC2000: A new approach to global land cover mapping from earth observation data. *Int J Remote Sens* 26:1959–1977.
37. Alcamo J, et al. (2003) Development and testing of the WaterGAP 2 global model of water use and availability. *Hydrol Sci J* 48:339–348.
38. Döll P, Lehner B (2002) Validation of a new global 30-min drainage direction map. *J Hydrol* 258:214–231.
39. Bruijnzeel LA (2004) Hydrological functions of tropical forests: Not seeing the soil for the trees? *Agric Ecosyst Environ* 104:185–228.
40. Polasky S, Camm JD, Garber-Yonts B (2001) Selecting biological reserves cost-effectively: An application to terrestrial vertebrate conservation in Oregon. *Land Econ* 77:68–78.
41. Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* 403:853–858.
42. Mittermeier RA, et al. (2003) Wilderness and biodiversity conservation. *Proc Natl Acad Sci USA* 100:10309–10313.
43. Olson DM, Dinerstein E (1998) The Global 200: A representation approach to conserving the earth's most biologically valuable ecoregions. *Conserv Biol* 12:502–515.
44. Carpenter SR, et al. (2006) Millennium Ecosystem Assessment: Research needs. *Science* 314:257–258.
45. Kremen C (2005) Managing ecosystem services: What do we need to know about their ecology? *Ecol Lett* 8:468–479.
46. Chan KMA, et al. (2007) When agendas collide: Human welfare and biological conservation. *Conserv Biol* 21:59–68.
47. Steffan-Dewenter I, et al. (2007) Trade-offs between income, biodiversity, and ecosystem functioning during tropical rainforest conversion and agroforestry intensification. *Proc Natl Acad Sci USA* 104:4973–4978.