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Poverty and biodiversity loss are two of the world's dire challenges. Claims of conservation's contribution to poverty alleviation, however, remain controversial. Here, we assess the flows of ecosystem services provided to people by priority habitats for terrestrial conservation, considering the global distributions of biodiversity, physical factors, and socioeconomic context. We estimate the value of these habitats to the poor, both through direct benefits and through payments for ecosystem services to those stewarding natural habitats. The global potential for biodiversity conservation to support poor communities is high: The top 25% of conservation priority areas could provide 56%–57% of benefits. The aggregate benefits are valued at three times the estimated opportunity costs and exceed $1 per person per day for 331 million of the world's poorest people. Although trade-offs remain, these results show win–win synergies between conservation and poverty alleviation, indicate that effective financial mechanisms can enhance these synergies, and suggest biodiversity conservation as a fundamental component of sustainable economic development.

Keywords: ecosystem service flows, poverty alleviation, biodiversity conservation priorities, natural capital, valuation

The Convention on Biological Diversity, the Millennium Development Goals, and other international agreements explicitly connect conservation to poverty alleviation (Sachs et al. 2009), and ecosystem services, in principle, serve as links between biodiversity and human well-being (MA 2005). There is a general expectation that conservation actions should benefit human well-being, help secure livelihoods, and pose little risk to the poor (WCED 1987), and biodiversity and poverty often coincide at various scales (Fisher and Christopher 2007). Yet conservation is presented both as a constraint on development and as a tool for achieving poverty reduction (Adams et al. 2004, West et al. 2006, Andam et al. 2010), and analyses to date have been insufficient to inform decisionmakers about the role of conservation in socioeconomic development. Genuine synergy depends not only on spatial correlation but also on biophysical and economic connections: the means by which services flow across space and by which financial incentives are exchanged to protect these services. To evaluate these connections, we conducted the first global estimation of service flows from source habitats to human beneficiaries, with models spanning a range of services and different geographical delivery patterns.

We used four geographically explicit valuation alternatives to relate biodiversity conservation to the people benefiting from the ecosystem services that conservation delivers. To facilitate comparisons, we placed all data sources and spatial models on the same geographic grid.

In previous studies of ecosystem services, human well-being, or biodiversity, large analytical units have been used, such as biodiversity priority regions (Turner et al. 2007, Naidoo et al. 2008), drainage basins (Luck et al. 2009), countries (Ebeling and Yasué 2008), or the entire globe (critiqued by Duraiappah 2011, Raudsepp-Hearne et al. 2010), that suffer from three problems. First, the spatial variation relevant to ecosystem services is lost when it is aggregated to large regions, because much of the variation lies entirely within such regions. Second, the use of regions of unequal area complicates comparisons of both ecosystem services and biodiversity measures. Third, boundaries coincide with features such as country and habitat borders that are correlated with multiple variables of interest. The alternatives, including rectangular geographic or equal-area grids, are subject to oversampling and shape distortions away from the equator (Potere and Schneider 2007). To overcome these issues, we conducted all analyses on a global terrestrial grid of equal-area hexagons (Sahr et al. 2003; 2592 square kilometers [km²], standard deviation = 11.6 km², $N = 58{,}613$), which are also ideal for service-flow calculations, because each is equidistant from its neighbors.

The first of four valuation alternatives, *potential ecosystem services*, estimates the value of the services generated by habitats, regardless of whether people are close enough to receive those benefits. For this first method, we used existing land-cover- and service-specific ecosystem service value (ESV) estimates (Costanza et al. 1997) for all services except climate regulation and extrapolated to a land-cover map using an established technique (Sutton and Costanza 2002). This approach assumes constant marginal values of ecosystem services within biomes; it does not account for within-biome variation. This assumption and several others are admittedly approximations (Costanza et al. 1997). Nonetheless, the ESV

analysis is the only published global compilation of values for a range of services and habitat types and has been used as a source for ESV estimates at regional (Viglizzo and Frank 2006) and global (Balmford and Bond 2005, Turner et al. 2007) scales. We update this map with recent and finer-scale (finer than 500-meter resolution) land-cover data (Friedl et al. 2010) and with updated carbon storage and deforestation data. The three other valuation alternatives (described below) additionally incorporate socioeconomic factors in calculating ESV. We adjusted all monetary values to 2005 US dollars according to published estimates of annual global consumer price inflation.

Accurate consideration of the climate regulation benefits of ecosystems is critical, because climate change is of great concern worldwide, because mitigation of greenhouse gas emissions may be the payments-for-ecosystem-services (PES) scheme closest to widespread implementation, and because carbon-storing habitats are often essential for biodiversity conservation (Myers 1992). We used carbon stock data and country-level deforestation-rate data from the Food and Agriculture Organization of the United Nations to derive climate-regulation value. We used a global map of estimated carbon stored in above- and belowground biomass (Reusch and Gibbs 2008) and calculated the value of emissions avoided as $S \times D \times P$. In this equation, S is stored carbon (in tons of carbon per hectare). D is the deforestation rate, the national-level forest-cover-change rate for the period between 2000 and 2005 (FAO 2006) or a global mean of 0.23% per year, whichever is higher; this accounts for high-forest-cover countries with low historic deforestation (da Fonseca et al. 2007). P is the shadow price of carbon (Stern 2007) of $36.46 per ton of carbon dioxide (CO_2). We repeated analyses with a conservative price of $5 per ton of CO_2 and found that the chosen price of carbon had little influence on the results.

People often value more highly those services that can be captured by human beneficiaries. Our second valuation alternative estimates these *realized services.* For realized services, we classified 17 ecosystem services into three service-flow models (figure 1) to estimate the population able to capture services provided by habitats in a given cell. We adjusted the ESV of each cell according to the size of the human population (using the LandScan database; *www.ornl.gov/sci/landscan*) reached by the services originating from it. For these calculations, pairwise distances between all cells were computed with Vincenty's

great-circle algorithm on a WGS-84 ellipsoid. In principle, the generalized functional relationships between realized-service value and socioeconomic context could be derived from ESV estimates at a large number of sites and from the corresponding population and poverty characteristics of those sites. In practice, approximation is necessary because the socioeconomic contexts of the original service valuations are difficult to standardize and are generally unavailable. We therefore assumed a service-benefit curve (figure 2) that estimates ESV according to the population able to realize the services originating from a given location. This curve increases linearly from (0,0) to (p',v') and then flattens for populations greater than p', where p' is the median number (across all terrestrial cells) of people in a window relevant to the given service (figure 1), and v' is the full value of that service under the potential services valuation alternative. This method conservatively considers all services as rival (i.e., any benefits used by one person are not available to another). For the set of ecosystem services that follow hydrological drainage patterns in flowing from source habitats to human beneficiaries, we used 30-arc-second drainage-direction data (Lehner et al. 2008) where it was available, and Hydro1k drainage-direction data (*http://eros.usgs.gov/Find_Data/Products_and_Data_Available/gtopo30/hydro*) elsewhere, to compute the set of cells downstream of each hex cell, up to 500 kilometers, as the window over which nearby populations were calculated.

People vary in their capacity to create or pay for alternatives if ecosystem services are lost. Poor communities, in particular, often depend critically on ecosystem services to sustain their lives and livelihoods (Luck et al. 2009). We considered *essential services* to be those flowing directly to the poor and providing immediate benefits. Therefore, essential-services

Ecosystem services

Proximal: 30 km
biological control
disturbance regulation
habitat/refugia
pollination
soil formation
waste treatment

Proximal: 150 km
cultural
food production
raw materials

Downstream
erosion control
nutrient cycling
water regulation
water supply

Global
climate regulation
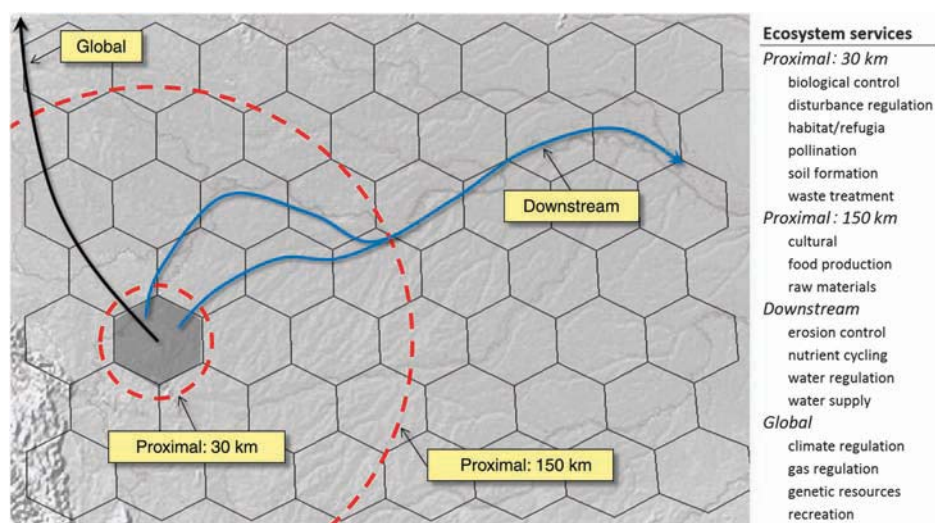gas regulation
genetic resources
recreation

Figure 1. Spatial models by which different ecosystem services flow from source habitats (shaded cell) to human beneficiaries. Global, benefits to the entire world; Proximal, fixed linear distance over which service may be realized; downstream, service follows hydrological drainage patterns.
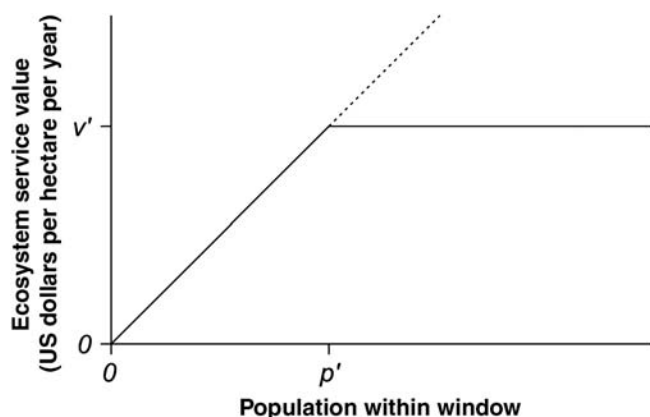
Figure 2. Service-benefit curve (solid line) for ecosystem-service value as a function of population within a service-specific window around the habitats generating the service. The dashed line, which was not used in our calculations, indicates the theoretical increase in value if the services were considered nonrival at all population levels.

calculations resemble those of realized services but value only those benefits flowing to poor individuals and exclude indirect or longer-term benefits (specifically excluded are climate regulation, gas regulation, nutrient cycling, genetic resources, and recreation). We used a subnational malnutrition map (CIESIN 2005) of underweight children under the age of five as an indicator of poverty rate. Although other indicators or proxies for poverty exist (e.g., stunting or per capita income), we are aware of no near-globally available indicators at a subnational resolution. A few countries and subnational units did lack malnutrition data. For the subnational units, we assigned rates equal to the mean malnutrition rate of the remainder of the country. For countries, we estimated missing values from a linear regression of country-level mean malnutrition rates against per capita caloric intake values (FAO 2008), an established technique (Fisher and Christopher 2007).

Payments for ecosystem services (Wunder et al. 2008), by which beneficiaries of services provide financial compensation to resource stewards, could in principle provide even greater potential for simultaneous benefits to both nature and people. In our final valuation scenario, *essential services with transfers*, we assumed that direct benefits are realized by some set of people according to their spatial relationship to source habitats as they were described above and that these beneficiaries (excluding those classified as *poor*) financially compensate the local individuals who manage or incur the opportunity cost for sustaining the source habitats (i.e., people within the same hexagonal cell as those habitats). We assumed that payments are distributed equitably among all local inhabitants, such that the value of PES flowing to the poor in a given cell is the total PES value flowing to the cell multiplied by the cell poverty rate, recognizing that financial mechanisms that target poor people in

particular could deliver even greater PES value to the poor than that estimated here. The value of the essential services with transfers in a given cell, then, is equal to the value of all PES transfers to the cell thusly calculated plus the value of the essential services themselves originating from the cell.

We defined areas of high biodiversity conservation priority on the basis of mapped distributions of all of the threatened vertebrates in taxa comprehensively assessed by the International Union for Conservation of Nature Red List (IUCN 2008). Therefore, we used range maps for 4388 threatened terrestrial species, including amphibians (Stuart et al. 2008; 1905 threatened of 6260 species total), birds (Birdlife International 2008; 1222 of 9990), mammals (Schipper et al. 2008; 1141 of 5488), and tortoises and turtles (Iverson et al. 2007; 120 of 273). Recognizing the importance of irreplaceability and vulnerability for informing conservation priorities (Margules and Pressey 2000), we mapped endemic, threatened biodiversity (figure 3e) and defined priority areas for biodiversity conservation as the top quarter of cells according to this metric. To do so, we computed threatened endemism as range-size rarity (Williams et al. 1996) of the threatened species, or 1/(species range size), summed across all threatened species occurring in a cell. All species having range sizes smaller than a single cell received the cell area of 2592 km^2. These conservation priority cells and those identified as priorities by other methods align well, with 73% of priority cells falling into three or more of the diverse global biodiversity conservation strategies in use (reviewed by Brooks et al. 2006). To evaluate the role of vulnerability in existing global conservation priority strategies, we compared ESV under the four valuation alternatives between the set of 34 biodiversity hotspots (Myers et al. 2000, Mittermeier et al. 2004) and the set of 5 high-biodiversity wilderness areas (Mittermeier et al. 2003).

We found substantial positive correlations between biodiversity conservation and the provision of ecosystem services. The spatial distribution of ESV, and consequently, the strength of the relationship between ESV and biodiversity conservation priorities, varies, depending on the valuation alternative. For potential ESV, the distribution of service value aligns closely with the distribution of high-value habitats such as tropical rainforests and wetlands (figure 3a). In contrast with potential ESV, realized ESV (figure 3b) is lower in regions where relatively few people can capture services, including tundra, boreal forests, and much of Australia. In comparison, natural habitats in regions such as South Asia become comparatively more important sources for realized services because of large beneficiary populations located nearby or downstream. Both valuation alternatives reveal strong relationships between biodiversity conservation priorities (figure 3e) and ecosystem service provision. For example, conserving the 25% highest-priority areas for biodiversity would sustain a disproportionately large 39% of the global potential ESV. For realized services, this fraction rises to 50%, reflecting the spatial concordance of key intact habitats and human communities.
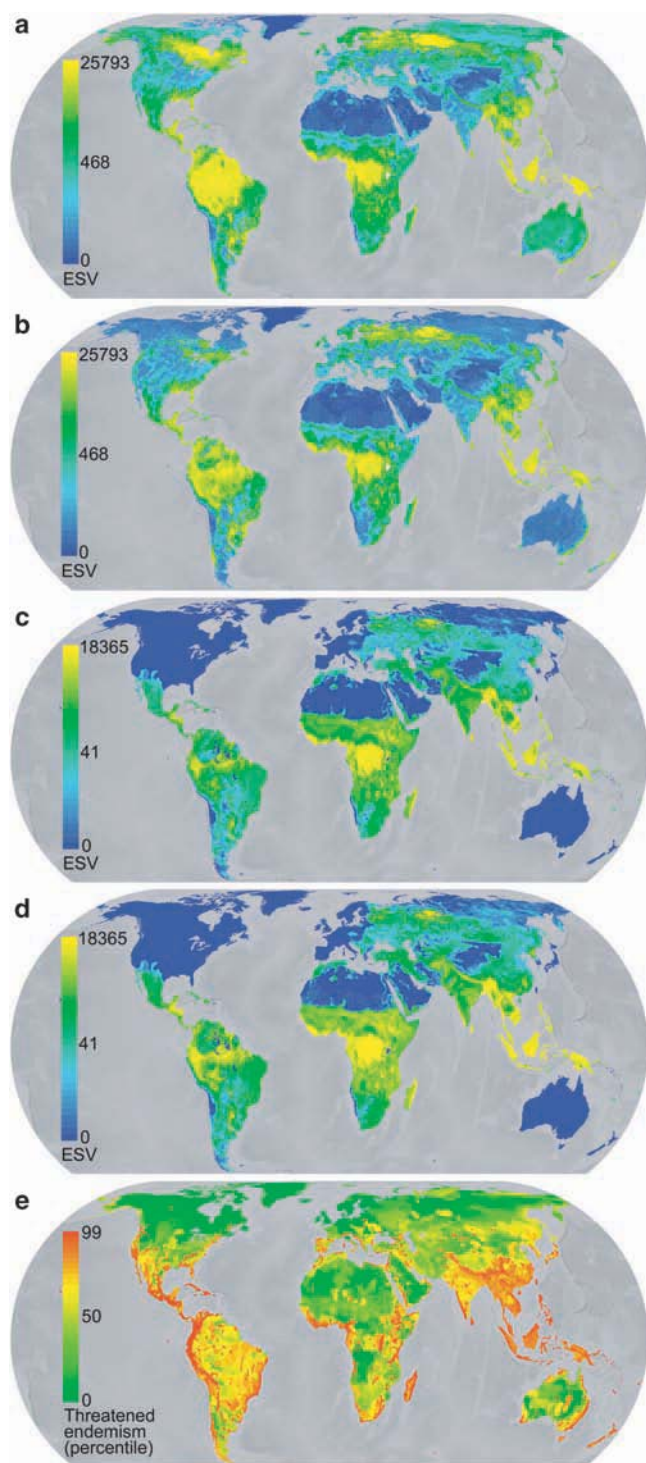
Figure 3. *Global distribution of ecosystem service value (ESV, in US dollars per hectare per year) and biodiversity conservation priorities. (a) Potential services. (b) Realized services. (c) Essential services to poor communities (excludes gas regulation, climate regulation, nutrient cycling, genetic resources, recreation). (d) Essential services with transfers (including payments for ecosystem services). (e) The percentile of biodiversity priority as measured by threatened species endemism. Panels (a) and (b) share the same scale; panels (c) and (d) share the same scale.*

Accounting for the socioeconomic status of people reveals an even stronger relationship between biodiversity conservation and human well-being. Essential services and essential services with transfers show that 56% and 57%, respectively, of global ESV benefiting the world's poorest people originates in high-biodiversity-conservation-priority areas (figure 4). These relationships are not limited only to a narrow set of top conservation priorities; 79% of essential services, for example, lie within areas of above-median value for biodiversity conservation.

Effective PES mechanisms would change the magnitude but not the spatial distribution of poverty alleviation through biodiversity conservation. Such mechanisms could increase the total global benefits to poor communities by an estimated 49.7% ($1024 billion for essential services versus $1533 billion for essential services with transfers). By contrast, the spatial distribution of ESV benefits to poor communities is similar whether PES are incorporated (figure 3d) or not (figure 3c). Meanwhile, the differences between these two and the valuation alternatives that do not incorporate poverty (figure 3a, 3b) are marked: The natural ecosystems in sub-Saharan Africa and South and Southeast Asia become even more important because of the high poverty rates in
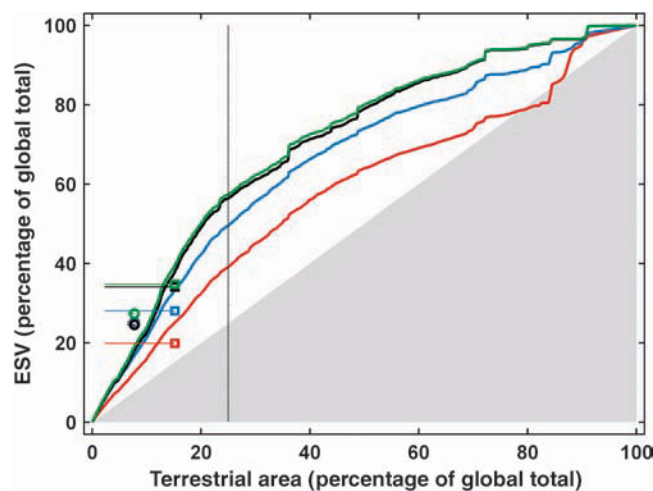

Figure 4. *Ecosystem service value (ESV) provided by areas selected for biodiversity. ESV accumulates faster when socioeconomic context is considered, with potential services (red) lying below realized services (blue), and both lying below the valuation alternatives in which poverty is considered: essential services (green) and essential services with transfers (black). All of the values are significantly higher than would be expected by chance (gray area) except potential services beyond 80% of the land area. Left of the dotted line is the top 25% of the land area for biodiversity. Also shown are biodiversity hotspots (squares; the remaining habitat is 2.3% of the terrestrial area, as is indicated by the whiskers) and high-biodiversity wilderness areas (circles; the remaining habitat is 6.5% of the terrestrial area).*

these regions, and less so in North Asia, whereas North America, western Europe, and Australia disappear from the comparison almost entirely.

Putting benefits in context: Comparisons with costs and income

Our findings of strong spatial concordance among biodiversity conservation priorities, ecosystem service provision, and human need would be less compelling if the aggregate value of services was low relative to opportunity cost or to per capita income. Therefore, we first compared ESV with the estimated opportunity cost of conservation. Because no global database of land prices exists, we used data on gross economic rent from agricultural lands (Naidoo and Iwamura 2007). This data set provides an approximation of alternative land-use values—based on crop productivity, livestock density, and producer prices—that is both spatially explicit and independent of the data used to compute ESV. Realized ESV generated by habitats in the top quartile of land for biodiversity conservation was more than triple (326%) the estimated opportunity cost of conserving these lands. Next, to assess the magnitude of ecosystem service benefits to the poor, we calculated the per capita value of ecosystem services—perhaps a more accurate assessment of the value of natural capital to individuals. If effective and equitable PES mechanisms were implemented comprehensively (as in the essential services with transfers valuation alternative), ESV where people live would exceed $1 per person per day for 30% (331 million) of an estimated 1.1 billion people living in poverty. This is but one way to quantify the magnitude of ESV to the poor. It does not include ecosystem services whose economic value, although not exceeding this per capita threshold, may nonetheless provide critically important benefits (such as freshwater services originating from the watersheds upstream of densely populated areas). The calculation is conservative, because it assumes that all services are rival and thus underestimates the per capita value of nonrival services, such as disturbance regulation.

Other studies, using different criteria, have shown substantial differences in the correlation between ecosystem services and conservation priorities (Turner et al. 2007, Naidoo et al. 2008), in part because of trade-offs among different services. For example, high-biodiversity wilderness areas (Mittermeier et al. 2003) are disproportionately important for carbon storage, whereas the estimated potential for livestock production from grasslands is generally highest in biodiversity hotspots (Myers et al. 2000) where most of the habitat has been cleared (Naidoo et al. 2008). We find that the fraction of global ESV included in the hotspots increases substantially, from 20% to 35%, when population and poverty are considered. By contrast, this fraction increases less (up 2%, from 25% to 27%) within wilderness areas, which underscores the fact that many of the ecological processes generated in these more-remote areas are not realized as ecosystem services. Nonetheless, the full set of these conservation priorities, which extend over a combined 23% of

Earth's land area (8.7% if only natural habitats are included), coincides with a disproportionate share of potential ecosystem services (45%), which could benefit human communities (realized services, 53%), particularly the world's poor (essential services with transfers, 62%; figure 4). As a second means to assess trade-offs between services, we repeated our analyses but excluded services whose provision could compromise the intact habitats that provide the other services and sustain species (food production, raw materials) or that might require habitat fragmentation in order to be fully realized (pollination, soil formation, biological control). This changed the results modestly, decreasing the value of realized services in the top-quarter areas for biodiversity from 326% to 264% of opportunity costs, while increasing the concordance between biodiversity and ecosystem services by 1.19%–1.60% for each of the four valuation alternatives (see supplemental table S1, available online at *http://dx.doi.org/10.1525/bio.2012.62.1.13*).

We tested the robustness of our results by repeating our analyses with agricultural production area (Monfreda et al. 2008) added to the demand model for that subset of services that benefits agriculture (pollination, food production, soil formation, and biological control) and modeling demand for these services on the basis of the distribution of agricultural production. In this case, we computed the realized services for these four services using the original service-benefit curve approach (as was described above; figure 2) but with the area of agricultural production (Monfreda et al. 2008; summed across all 11 major crop groups) replacing human population, whereas the remaining services were computed as they were before. This revealed an even stronger correlation with biodiversity: Top-priority biodiversity lands generated 54.4% of realized services (compare with 49.5% when the agricultural production area was not considered explicitly). In addition, to test the sensitivity of our results to the (uncertain) price of carbon, we repeated the analyses with a conservative $5 per ton of CO_2, and found that the chosen price had little influence on the results. For example, the proportion of ESV found in the top quarter of the terrestrial area for biodiversity conservation (in figure 4, ESV at an *x*-axis value of 25%) differed by less than 1% between the two carbon prices for all of the four valuation alternatives. Low sensitivity to carbon price suggests that climate regulation is just one of a number of valuable services provided by natural habitats associated with high levels of biodiversity. These results reinforce the need to address not only climate change mitigation but a broad range of services in securing benefits for poor communities.

Conclusions

We find that biodiversity conservation priority areas are efficient targets for benefiting human well-being through the services those areas provide. The benefits to poor communities—both directly and through potential financial compensation schemes—are particularly strong. In previous research, a spatial concordance of biodiversity and poverty

has been reported (Fisher and Christopher 2007), and policy connections have been suggested (Adams et al. 2004, Sachs et al. 2009), but the spatial links by which global biodiversity conservation provides benefits to the people that most urgently need them have not been explored before. Our modeling of service flows improves on previous work that was focused only on spatial overlays (Turner et al. 2007, Sachs et al. 2009), and this more-detailed analysis reveals even greater scope for the synergy between biodiversity conservation and development goals. All communities rely on a balance of produced, human, and natural capital. Our results reinforce findings that natural capital plays a disproportionately important role in supporting all communities—but especially poor communities—through flows of ecosystem services (World Bank 2011). The results also provide spatially explicit detail on the distribution of key resources that the poor depend on most.

Some have argued that the idea of integrated conservation and development is conceptually flawed, is based on unrealistic assumptions about win–win solutions, and is doomed to reduced efficiency and effectiveness relative to the focused, independent pursuit of conservation and development objectives (e.g., McShane and Newby 2004, Salafsky 2011). Overall, our analyses bracketed a range of possible ecosystem service benefits, from the immediate benefits without transfers (essential services) to an optimistic valuation alternative that assumes complete PES effectiveness (essential services with transfers). The broadly similar results for these two very different alternatives (figure 4) indicate that the importance of biodiversity conservation priority areas for the poor is robust and not dependent on particular services or financial mechanisms. This finding suggests that, regardless of whether adequate transfer mechanisms emerge, biodiversity conservation provides both direct services (food, fuel) and indirect services (pollination, clean water) that the poor have difficulty replacing. Emerging evidence for this was found in recent quasiexperimental studies for Costa Rica and Thailand in which similar districts with and without biodiversity conservation were compared: The districts with protected areas experienced approximately 10% less poverty in Costa Rica and 30% less in Thailand (Andam et al. 2010). We suggest that effective policies to manage these stocks of natural capital will result in poverty-alleviation benefits, not simply as unintended side effects but as part of deliberate, targeted strategies based on the biophysical dependence of both biodiversity and human well-being on the same ecological systems.

Nonetheless, the biophysical flows of life-sustaining or economically valuable services from natural habitats—however substantial—are not on their own sufficient to lift people from poverty. Financial mechanisms for transfers will need to be established, which may be complex and will incur transaction costs. Continued attention will be necessary to advance finance and governance mechanisms that minimize these costs and the potential for corruption. This highlights a dual role for development agencies with expertise on poverty alleviation, including multi- and bilateral institutions and foundations. First, the high level of support that ecosystems provide to the poor suggests a much greater need for development agencies to support biodiversity conservation (TEEB 2009). Second, their expertise is vital in designing value-transfer mechanisms, such as PES, designed to benefit the poor.

Although many services—for example, the ability of certain habitats to reduce flood risk—can benefit individuals of any socioeconomic status, other services cannot be fully realized by those lacking adequate land tenure or other means of legal claim to service flows. Although many services flow directly to beneficiaries, payments for ecosystem services, which the essential services with transfers results suggest could increase the net value to the poor by 49.7%, will additionally require that recipients have some means by which to receive payments. Continued effort will be required to ensure that the monetary benefits from natural ecosystems reach the rural poor, landless laborers, and others whom these benefits can help most. This will require mechanisms at multiple levels, including, for example, project- and landscape-level accounting and equitable distribution and national and subnational government policies. Many of these mechanisms and policies have been developed under rights-based approaches to the development and management of natural resources (Campese et al. 2009). Effective examples not only sustainably harness natural capital but also implement specific policy instruments—investments in health, education, infrastructure, technology, conditional cash-transfer systems, and the like—aimed at the produced- and human-capital dimensions of poverty alleviation. For example, the success to date of Ecuador's Socio Bosque program toward its explicit ecosystem-conservation and poverty-alleviation objectives can be partly attributed to its investments in production activities, conservation, education, and other areas across all three dimensions of capital (de Koning et al. 2011).

Any study in which a variety of services are globally estimated is subject to assumptions and caveats. Although we updated carbon and habitat data and improved the data's quality by accounting for socioeconomic context, the point valuations that contributed to our initial global ESV estimates (Costanza et al. 1997) must be improved in the future with more systematic compilation and with standardized protocols. Many benefits were not quantified or were not fully quantified here, including cultural values and the future or "option" value of biodiversity (MA 2005, McNeely et al. 2009). We have not accounted for the effects of the scarcity of ecosystem services (or their substitutes) on ESV. We used marginal valuations and US dollars as a common currency in order to evaluate the relative value of services provided across space. If large changes in supply of or demand for these services occur in the future, these valuations must be recomputed.

Although the benefits provided by healthy ecosystems are high relative to the estimated opportunity costs and

income, ecosystem services and the habitats providing them are vanishing at alarming rates (MA 2005), which indicates that they are being undervalued in markets, business decisions, and government accounting. Implementation of PES is often limited by inadequate policy frameworks and poor spatial planning (Wunder et al. 2008). However, our results suggest great potential if REDD+ (reducing emissions from deforestation and forest degradation) and other compensation mechanisms explicitly address key limitations (e.g., de Koning et al. 2011, Fisher et al. 2011) and are supported widely. Developing such mechanisms will be particularly critical in the future, because the importance of some ecosystem services is likely to increase and because healthy ecosystems can help ameliorate climate change and its negative impacts (Turner et al. 2009). These findings send an important message to policymakers: Protecting the places of highest priority for biodiversity conservation will deliver benefits to human well-being and poverty alleviation that are large, both in absolute terms and relative to costs and needs.

Acknowledgments

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