11-1-2007

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Citation Details

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Habitat destruction has driven much of the current biodiversity extinction crisis, and it compromises the essential benefits, or ecosystem services, that humans derive from functioning ecosystems. Securing both species and ecosystem services might be accomplished with common solutions. Yet it is unknown whether these two major conservation objectives coincide broadly enough worldwide to enable global strategies for both goals to gain synergy. In this article, we assess the concordance between these two objectives, explore how the concordance varies across different regions, and examine the global potential for safeguarding biodiversity and ecosystem services simultaneously. We find that published global priority maps for biodiversity conservation harbor a disproportionate share of estimated terrestrial ecosystem service value (ESV). Overlap of biodiversity priorities and ESV varies among regions, and in areas that have high biodiversity priority but low ESV, specialized conservation approaches are necessary. Overall, however, our findings suggest opportunities for safeguarding both biodiversity and ecosystem services. Sensitivity analyses indicate that results are robust to known limitations of available ESV data. Capitalizing on these opportunities will require the identification of synergies at fine scales, and the development of economic and policy tools to exploit them.

Keywords: ecosystem services, biodiversity conservation priorities, natural capital

Conserving Earth's biological diversity and safeguarding the benefits, or "ecosystem services," that functioning ecosystems provide to humans are two major objectives of nature conservation (Ehrlich and Wilson 1991, UNEP 1992). Ecosystem services directly support more than one billion people living in extreme poverty (World Bank 2006), thus protecting ecosystems is also critical for economic development and poverty alleviation. In terrestrial systems, the same process—human conversion of natural habitats—is the dominant threat to biodiversity and ecosystem services (Millenium Ecosystem Assessment 2005). Spatial concordance of biodiversity and ecosystem services would mean that, in many cases, similar actions could jointly secure both objectives. Some studies, however, have asserted low concordance (Kareiva and Marvier 2003), and it remains unclear whether biodiversity and ecosystem services co-occur only under narrow sets of conditions, or concord broadly enough that global strategies for both objectives could realize widespread and productive synergy (Balvanera et al. 2001).

In this article, we use existing estimates of the value of ecosystem services worldwide, together with published templates of global biodiversity priorities, to analyze potential synergies between conserving biodiversity and safeguarding ecosystem services. Global-scale prioritization for biodiversity conservation is essential because biodiversity,

threats to it, and the ability of countries to pay for its conservation vary in space (Balmford et al. 2003). To date, at least nine global prioritization templates for terrestrial environments have been published (WWF and IUCN 1994–1997, Bryant et al. 1997, Mittermeier et al. 1997, Olson and Dinerstein 1998, Stattersfield et al. 1998, Sanderson et al. 2002, Mittermeier et al. 2003, 2004, Hoekstra et al. 2005; see Brooks et al. 2006 for a review). Collectively, these approaches offer a broader basis for analysis than any single biodiversity metric or priority template.

Because some local- to regional-scale studies have found coincidence of ecosystem service value (ESV) with biodiversity (Naidoo and Adamowicz 2005, Chan et al. 2006, Naidoo and

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Ricketts 2006), bundling ecosystem service and biodiversity objectives is now a common conservation strategy (Kremen et al. 2000). Understanding the global generality of such "win-win" scenarios, however, requires analysis at broader scales. We therefore used a global map of ESV (Sutton and Costanza 2002) derived from a standard land-cover map (Loveland et al. 2000) and corresponding per-unit ESV estimates (Costanza et al. 1997). This approach assumes constant marginal values of ecosystem services within biomes; it does not account for within-biome variation. This assumption and several others of the analysis are obvious, admitted approximations (Costanza et al. 1997). Nonetheless, the ESV analysis is the only global compilation of valuations 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 scales (Balmford and Bond 2005). Here we use this global ESV map and published biodiversity conservation priority maps to assess the concordance between biodiversity conservation priorities and ecosystem services, to explore how the concordance of the two varies in space, and to examine the global potential for simultaneously safeguarding both biodiversity and ecosystem services.

Concordance of biodiversity conservation priorities and ecosystem services

To assess the potential overlap of each biodiversity priority template with ecosystem services, we computed the total ESV represented by all terrestrial land covers within the template. In each case, we compared total observed ESV with that expected by chance alone by sampling 10,000 random sets of 1-square-kilometer (km^2) cells, without replacement, from the global map of terrestrial land cover and corresponding per-unit ESVs. We found general positive concordance of biodiversity priorities with areas of high ecosystem service value. Eight of nine templates include significantly higher ESV than random areas have; templates' ESV exceed that of comparable random areas by an average of 71.6 percent (table 1).

Proper assessment of the ESV of each template requires comparison with both random and maximum values as reference points. To measure the extent to which the observed ESV exceeds that expected at random, relative to the maximum possible, we computed a concordance index, based on the surrogacy index of Ferrier and Watson (1997):

$$(observed - random) / (maximum - random).$$

We determined the maximum possible ESV for each template by accumulating 1-km^2 cells, highest ESV first, until the template area was reached. This comparison is conservative, as both ESV and biodiversity objectives would most likely suffer in practice if only dispersed, disconnected 1-km^2 cells were protected. Nonetheless, the biodiversity templates perform well: concordance index values indicate that several templates include a substantial proportion (up to 40.3 percent) of the maximum ESV possible beyond that expected at random (table 1). Overall numbers are favorable in comparison with other surrogacy index applications. For example, a recent review of existing tests of cross-taxon and

environmental surrogates for biodiversity found a median surrogacy index of 12 percent, with the maximum between 50 percent and 60 percent, and 41 percent of the values below zero (Rodrigues and Brooks 2007).

The role of vulnerability

Conservation planning theory revolves around a framework of vulnerability, which measures the risk to species in an area, and irreplaceability, which measures the extent to which spatial substitutes exist for securing the biodiversity present in an area (Margules and Pressey 2000). To assess the relationship between vulnerability and ESV, we created two derived templates based on figure 3 in Brooks and colleagues (2006). Each of the nine raw templates is binary: areas are either high biodiversity conservation priorities or they are not. The two derived templates combine these raw templates to capture variation in vulnerability. The "most proactive" template includes any area found in at least one template for which low vulnerability is a priority (proactive strategies; Bryant et al. 1997, Sanderson et al. 2002, Mittermeier et al. 2003) and in at least four templates overall. The "most reactive" template includes any area found in at least one template for which high vulnerability is a priority (reactive strategies; Mittermeier et al. 2004, Hoekstra et al. 2005) and in at least four templates overall.

The most proactive regions harbored a mean ESV of US$217,356 per km^2 per year, nearly three times that of the most reactive regions, although even those regions had significantly more ESV than did random regions. Moreover, concordance indices indicate that proactive regions include a substantially greater proportion of the maximum possible ESV (concordance index of 37.1 percent) than that represented by reactive regions (4.5 percent; table 1). Much of the difference between proactive and reactive strategies most likely reflects the fact that the ESV of high-vulnerability (reactive) areas has already been reduced by habitat loss. Indeed, when obviously anthropogenic land cover (croplands and developed areas) is ignored, the relative ESV of the most reactive regions increases substantially (concordance index = 11.7 percent). In contrast to the vulnerability pattern, no irreplaceability signal is present: concordance indices show no clear pattern between those templates that prioritize endemism or other measures of irreplaceability (mean concordance index of 18.7 percent; WWF and IUCN 1994–1997, Mittermeier et al. 1997, 2003, 2004, Olson and Dinerstein 1998, Stattersfield et al. 1998) and those that do not (17.5 percent; Bryant et al. 1997, Sanderson et al. 2002, Hoekstra et al. 2005).

Variation among ecosystem services

Because different ecosystem services may vary in importance to different countries and funding institutions, it is important to consider which services make up the ESV of global biodiversity conservation priorities. Whereas templates vary substantially in their inclusion of ESV overall, proportions of ESV from each service show less variation. This is in part because evergreen broadleaf forest is the leading source of ESV

Table 1. Estimated ecosystem service value (ESV) within templates for global biodiversity conservation.

Global template	Area (million km²)	Mean ESV (US$ per km² per year)	Total ESV (billion US$ per year)			Percentage above random[c]	Concordance index[d] (percentage)
			Observed	Random[a]	Maximum[b]		
High-biodiversity wilderness areas (Mittermeier et al. 2003)	11.5	200,720	2314	701	4708	230	40.3
Frontier forests (Bryant et al. 1997)	13.2	188,224	2487	803	5151	210	38.7
Most proactive	7.6	217,356	1659	464	3681	257	37.1
Global 200 ecoregions (Olson and Dinnerstein 1998)	53.8	86,857	4671	3270	7466	43	33.4
Last of the wild (Sanderson et al. 2002)	35.0	98,356	3440	2127	6838	62	27.9
Megadiversity countries (Mittermeier et al. 1997)	49.8	77,457	3860	3031	7340	27	19.2
Endemic bird areas (Stattersfield et al. 1998)	13.8	88,710	1222	838	5301	46	8.6
Centers of plant diversity (WWF and IUCN 1994–1997)	12.2	83,779	1023	743	4888	38	6.8
Most reactive	12.1	76,057	917	734	4849	25	4.5
Biodiversity hotspots (Mittermeier et al. 2004)	23.0	69,071	1588	1398	6289	14	3.9
Random terrestrial km²	–	60,813	–	–	–	–	0.0
Crisis ecoregions (Hoekstra et al. 2005)	42.7	46,038	1967	2598	7112	–24	–14.0

Note: All monetary values are in 2005 US dollars.
a. ESV in randomly selected 1-km² cells, with the total area equivalent to that of each template.
b. Maximum ESV attainable for the total area equivalent to that of each template.
c. Significance of percentage deviation from random is evaluated with a randomization test ($N = 10,000$, $p < .001$ in all cases).
d. Percentage of ESV represented beyond that expected at random, relative to the maximum attainable.

in all biodiversity prioritization templates, accounting for a mean 59.5 percent of ESV among the nine templates, compared with 40.0 percent of total global terrestrial ESV (figure 1a). Nonetheless, variation among the templates in terrestrial land cover causes important patterns in ESV-by-service comparisons. Of 17 services, just 4 (nutrient cycling, waste treatment, food production, and climate regulation) account for the majority (54 percent to 66 percent) of the ESV of each template. Food production, biological control, and pollination make a much greater proportionate contribution to the ESV of the most reactive approaches (14.3 percent) than to the most proactive approaches (2.9 percent; figure 1b), which reflects the fact that most conversion of natural habitat is to agricultural and mixed natural or agricultural landscapes (Vitousek et al. 1997).

Spatial variation
Although the ESV represented by individual templates suggests moderate positive concordance between biodiversity conservation priorities and ecosystem services, of even greater relevance for planning is how alignment of the two objectives

varies among regions. We therefore overlaid biodiversity templates with the global terrestrial ESV map to explore correspondence (or lack thereof) between the two across geographic space. As an indication of the relative consensus priority of different areas for biodiversity conservation, we summed the number of templates intersecting each 1-km² cell. We then aggregated both ESV and biodiversity template maps to 100-km² cells. Each 100-km² cell received the mean value over its 100 constituent cells. This increased the number of unique values possible across cells, and thus enabled display of more underlying detail. We then assigned each cell a color (Williams and Gaston 1998)—red for biodiversity and green for ESV—with the intensity of the color increasing with the rank of the value.

The resulting concordance map (figure 2) shows that high biodiversity priorities coincide with high ESV over broad regions such as Congo and the Amazon, in smaller areas such as central Chile and India's Western Ghats, and patchily within regions such as Southeast Asia. These and similar regions (black in figure 2) offer the most promising opportunities for simultaneously safeguarding biodiversity and
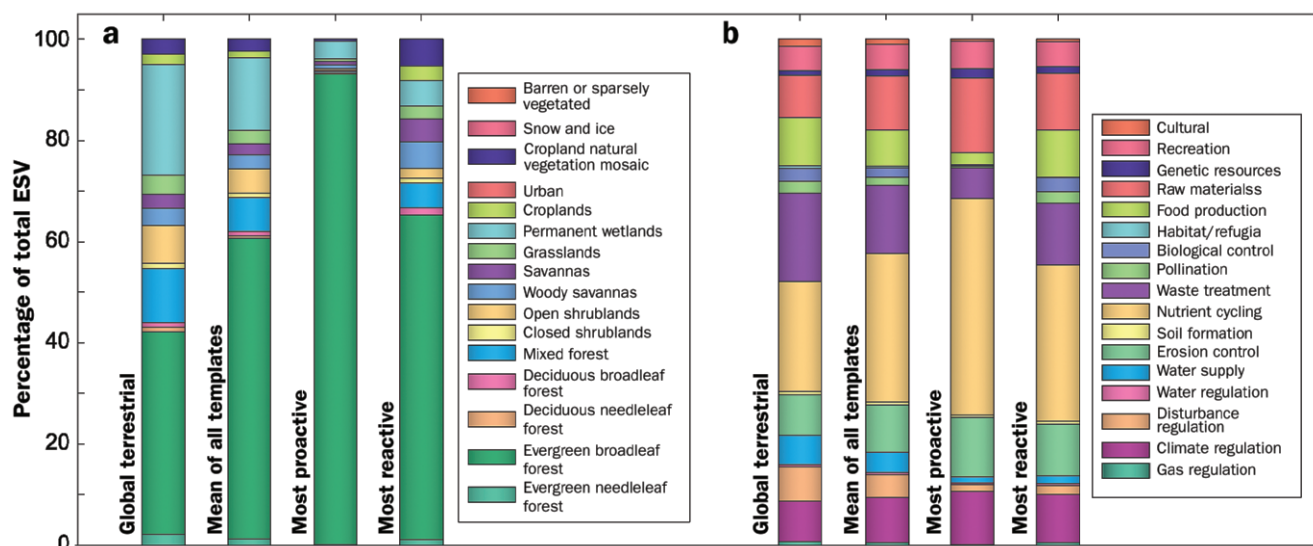
Figure 1. Ecosystem service value (ESV) of biodiversity conservation priorities, by land cover and service. "Most proactive" comprises those regions (e.g., wilderness) favored by proactive global templates. "Most reactive" comprises high-vulnerability regions favored by reactive templates. (a) Percentage of total ESV arising from each of 16 terrestrial land covers, and (b) percentage of total ESV from each of 17 ecosystem services.

ecosystem services. In many cases, these overlaps are driven by the importance of tropical forests (evergreen broadleaf forest) for biodiversity and the concomitant high value of ecosystem services they provide (Myers 1992).

That some win-win situations exist is apparent from figure 2, but a fundamental question remains: quantitatively, for what part of the highest-priority biodiversity conservation areas might synergy with ecosystem services conservation be a viable conservation strategy? The 10.7 million km^2 in areas prioritized by five or more templates represent 7.0 percent of global land area. Of this area of greatest biodiversity conservation consensus, 70.9 percent lies in areas with estimated ESV in the top 30 percent. This 7.0 percent of land harbors an estimated US$1.1 trillion per year in ESV, 158 percent more than the US$425 billion per year expected at random.

While the map of ecosystem service value overlaid on conservation priorities suggests potential synergies, it also highlights areas where caution is needed. Of particular interest are those regions (red in figure 2) that rank highly as biodiversity conservation priorities yet appear to offer little prospect for capturing ecosystem services. The factors underlying these mismatches are not uniform. Some regions important for biodiversity are low in ESV because the original habitat is ESV poor (e.g., arid regions such as South Africa's Succulent Karoo). Elsewhere, most of the higher-ESV original habitat has been destroyed, as in Brazil's cerrado and Atlantic forest, the Mediterranean, southern Australia, and much of Southeast Asia. These regions' total ESV would be substantially higher—and their biodiversity more secure—had their original habitats been better conserved. In contrast to this largely tropical pattern, most regions where ESV is high relative to biodiversity priority (green in figure 2) are in temperate

countries (the main exception is dryland Africa). The world's deserts and polar regions hold comparatively less biodiversity and ESV (white and near white in figure 2).

Robustness to data limitations

Few attempts have been made to grapple with questions of equitability, socioeconomics, and spatial relationships as they affect global-scale planning for biodiversity and ecosystem services. For example, ecosystem services may be relatively more valuable per unit of area in some parts of the most reactive templates, because these areas hold more people who depend directly on these services. Furthermore, ecosystem services vary in the spatial scales over which they may be captured by humans. For example, whereas carbon sequestration benefits humans worldwide, pollination services may provide benefits only to areas nearby. If so, then the ESV data set we used could overestimate the value of certain services in remote areas.

To evaluate whether this was the case with our results, we repeated our analyses on a subset of global-scale or broadscale services, excluding services that generally need to be captured at the source (e.g., soil formation, food production, raw materials) or near the source (e.g., disturbance regulation, waste treatment, pollination, biological control, refugia). Results for the global-scale or broadscale subset of services were similar to those obtained when we included all services. The same eight templates still harbored significantly more ESV than expected at random (mean 104.6 percent more ESV than random, compared with 71.6 percent when all services were included). The mean concordance index was 21.6 percent for the broadscale-only subset, compared with 18.3 percent for all services combined. The most proactive
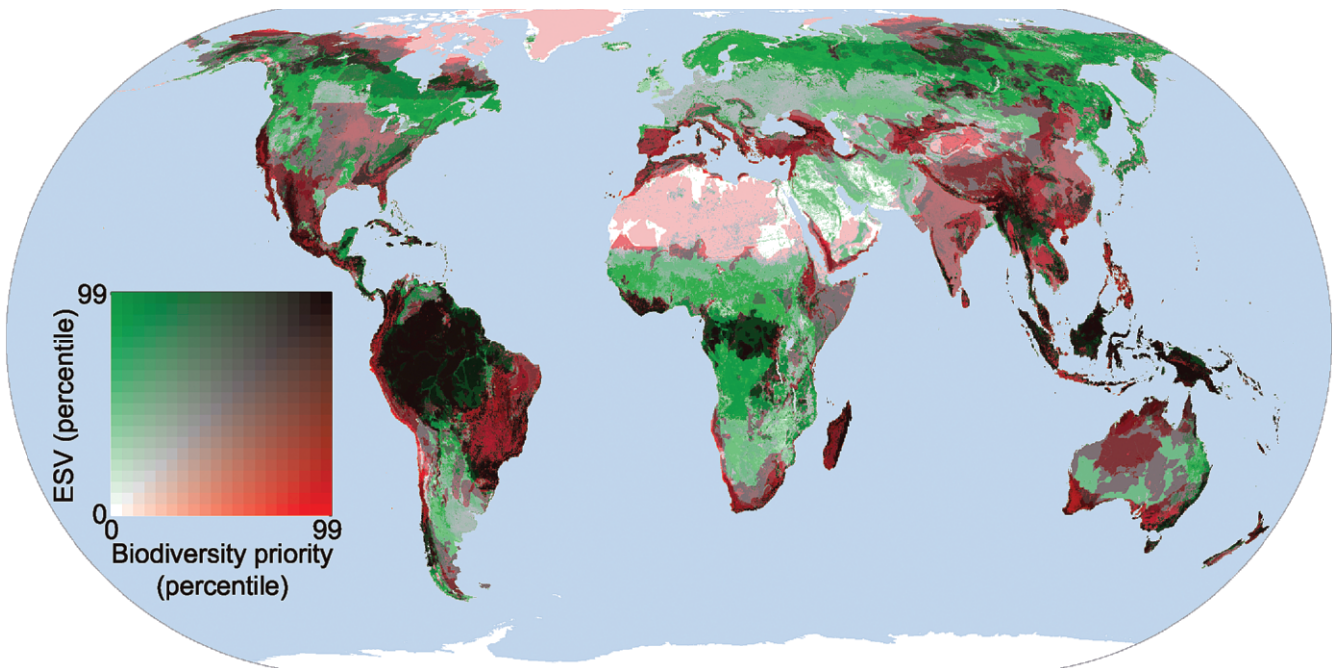
Figure 2. Spatial concordance of global biodiversity priorities and ecosystem service value (ESV). Increasing intensities of green and red represent, respectively, increasing rank ESV and increasing rank consensus biodiversity priority. White corresponds to low values for both variables, black to high values for both, and shades of gray to covarying values for both.

(low-vulnerability) areas still harbored more ESV (concordance index 54.6 percent) than did the most reactive areas (6.5 percent). Finally, the spatial patterns of concordance between ESV and biodiversity priorities were similar and nearly indistinguishable from figure 2. This analysis indicates that our results are generally robust to variation in the spatial arrangement of human population and in the spatial scales over which services may be captured. Nevertheless, this is an area ripe for research. For example, coincidence of biodiversity priorities, human population, and poverty (Balmford et al. 2001) suggests that synergies even greater than those indicated here could exist.

Although our ESV data came from the only global data set currently available (Sutton and Costanza 2002), these estimates are subject to a variety of uncertainties (Costanza et al. 1997). To reduce these, our study suggests that research priorities in ecosystem services should include, first, better spatial articulation of services and valuations regionally and globally, and, second, more sophisticated modeling of the biophysical origin and flow of services spatially and temporally. That said, further sensitivity analysis shows that over- or underestimation of key unit ESVs would produce little change in results. A substantial part of the ESV of biodiversity conservation templates is driven by the area and ESV of evergreen broadleaf forest. We thus evaluated the effect of twofold underestimation or overestimation of the ESV of evergreen broadleaf forest. The same eight templates harbored significantly more ESV than random in any case. Quantitative changes were also minor: the magnitude and ranking of templates' concordance indices changed only slightly from the original case (mean concordance index across templates 17.6 percent, maximum 38.7 percent) to either the underestimation of evergreen broadleaf forest ESV (mean 14.3 percent, maximum 40.7 percent) or the overestimation of it (mean 25.0 percent, maximum 53.9 percent).

Discussion

These results should be interpreted carefully for two reasons. First, we considered only terrestrial biodiversity, and although freshwater and marine environments harbor substantial biodiversity and ESV—global ESV for marine systems has been estimated to exceed terrestrial ESV by a significant margin (Costanza et al. 1997)—similar analyses for these environments cannot proceed until sufficient biodiversity data are available (Brooks et al. 2006). Second, there is a difference in scale between the ESV data (1 km^2) and the biodiversity prioritization templates (regions varying from 10^3 to 10^6 km^2). While biodiversity and ESV are quite evenly distributed across the most proactive templates, both are concentrated in the scattered remaining natural habitat of the most reactive templates. This artifact will increase the apparent overall ESV of the former relative to the latter.

Given the growing awareness of ecosystem services and their increasing use as a biodiversity conservation tactic (Millennium Ecosystem Assessment 2005), our findings have far-reaching consequences. Although our results support the idea that ecosystem services are a promising way to motivate biodiversity conservation, regional variation in the concor-

dance between biodiversity conservation priorities and ESV needs to be considered when devising strategies for securing conservation objectives. The greatest opportunities for synergy may be in areas such as tropical forests, where the overlap of priorities is highest (figure 2) and the benefits of transforming the area to agriculture are low (Gorenflo and Brandon 2005). By contrast, regions of relatively high ESV but low biodiversity fall mainly in wealthy temperate countries, where budgets to support internal conservation activities are often large and do not have to compete for meager global biodiversity conservation funds. Meanwhile, in biodiverse but ESV-poor regions, it is necessary to do more than conserve remnant habitat patches: restoration must be an important tactic for both ecosystem services and biodiversity conservation.

Capitalizing on the opportunities highlighted in this article will require further research into the causes of observed regional variation, identification of synergies at fine scales, development of economic and policy tools to exploit synergies, and greater recognition and investment from development organizations and governments into the fundamental contributions of conservation efforts to human welfare.

Acknowledgments

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