LETTER

Protecting ecosystem services and biodiversity in the world's watersheds

Gary W. Luck[1], Kai M.A. Chan[2], & John P. Fay[3]

[1] Institute for Land, Water and Society, Charles Sturt University, Albury, NSW 2640, Australia
[2] Institute for Resources, Environment and Sustainability, University of British Columbia, Vancouver, British Columbia, Canada
[3] Geospatial Analysis Program, Nicholas School of the Environment and Earth Sciences, Duke University, Durham, NC 27708-9328, USA

Keywords
Biodiversity; carbon storage; conservation investment; conservation policy; ecosystem services; flood mitigation; human well-being; water provision; watershed.

Correspondence
Gary W. Luck, Institute for Land, Water and Society, Charles Sturt University, Albury, NSW 2640, Australia. Tel: 61 2 6051 9945; fax: 61 2 6051 9897. E-mail: galuck@csu.edu.au

Received: 24 March 2009; accepted: 7 May 2009.

doi: 10.1111/j.1755-263X.2009.00064.x

Abstract

Despite unprecedented worldwide biodiversity loss, conservation is not at the forefront of national or international development programs. The concept of ecosystem services was intended to help conservationists demonstrate the benefits of ecosystems for human well-being, but services are not yet seen to truly address human need with current approaches focusing mostly on financial gain. To promote development strategies that integrate conservation and service protection, we developed the first prioritization scheme for protecting ecosystem services in the world's watersheds and compared our results with global conservation schemes. We found that by explicitly incorporating human need into prioritization strategies, service-protection priorities were squarely focused on the world's poorest, most densely populated regions. We identified watersheds in Southeast Asia and East Africa as the most crucial priorities for service protection and biodiversity conservation, including Irrawaddy—recently devastated by cyclone Nargis. Emphasizing human need is a substantial improvement over dollar-based, ecosystem-service valuations that undervalue the requirements of the world's poor, and our approach offers great hope for reconciling conservation and human development goals.

Introduction

Despite a worldwide biodiversity crisis (Foley *et al.* 2005) and negative impacts of biodiversity loss on humanity, conservation is not as prominent in political agendas as some believe it should be (e.g., Christensen 2005). This is largely because most conservation strategies fail to incorporate the flow of benefits from ecosystems to people (ecosystem services; Daily 1997; Millennium Ecosystem Assessment (MA) 2003). Various organizations promote global prioritization schemes for biodiversity conservation (e.g., Olson & Dinerstein 1998; Stattersfield *et al.* 1998; Mittermeier *et al.* 2004) that may influence spending by other international bodies (e.g., The World Bank; Halpern *et al.* 2006) and are fundamental to effective conservation given spatial variation in the diversity of nature and the capacity to pay for its protection (Balmford *et al.* 2003; Wilson *et al.* 2006). Yet, for conservation to gain greater prominence in political agendas, these schemes must demonstrate how conservation efforts can also meet human needs.

Conservationists seeking to marry conservation and development are increasingly turning to the concept of ecosystem services for guidance (Naidoo *et al.* 2008; Tallis *et al.* 2008), but current measures of services fail to capture adequately the benefits humans derive from conservation. Some are represented principally by aggregate monetary values (e.g., Turner *et al.* 2007), which effectively neglect poor people's needs because individual economic values are capped by the valuer's ability to pay. Schemes that promote conservation and human well-being do not require such economic values, but rather an understanding that certain conservation actions in some places will benefit communities more than they will in other places.

We quantified spatial variation in human needs for ecosystem services and in global conservation priorities. Although human needs are many and varied, we focused on basic needs relative to the ecosystem services we analyzed—access to clean freshwater, and protection from displacement and death by flooding. We use the term "well-being" in its most general sense and assume that meeting basic needs is one of the most pressing ways to improve human well-being. Our intent is to motivate a closer connection between conservation and development, for example, through partnerships between conservation nongovernment organizations (NGOs) and global development organizations whose spending dwarfs that of conservation (James *et al.* 2001; The World Bank 2004). We aim to guide conservation investments of various kinds including land acquisition, ecosystem restoration, and payment for environmental services programs.

An assessment of the capacity of ecosystem services to benefit a given community requires identification and quantification of human-related benefits, costs, and the availability of alternatives to meet needs (Chan *et al.* 2006). We incorporated these factors into a global prioritization scheme for the protection of key ecosystem services (water provision, flood mitigation, and carbon storage) in the major watersheds of the world, and compared our results with global conservation priorities to identify the degree of concordance between human well-being and conservation objectives. We argue that a needs-based approach could yield vital funds (from, e.g., multinational NGOs and aid agencies such as the Canadian International Development Agency and United Nations Environment Programme) and promote conservation as a viable land-use option in the world's poorest regions (Rodríguez *et al.* 2007; see also Goldman *et al.* 2008).

At a global scale, we consider watersheds to be a meaningful organizational unit independent of political boundaries and representing the connectedness of landscapes. Although many land-use decisions are made at local levels, global priority schemes serve as overarching, guiding frameworks that impact decision making directly and indirectly. Effective watershed management is vital to the future of humanity, but is a challenging endeavor. Predicted increases in population and consumption will stretch water resources (Arnell 2004). Climate change may exacerbate this problem, leading to an increasing number of people living in water-stressed watersheds (Hengeveld 1990; Schröter *et al.* 2005), although its likely effects are complex (Oki & Kanae 2006). Our approach provides a strategy for melding conservation and human development goals and demonstrates the concordance among broadly accepted conservation priorities and the protection of ecosystem services.

Our primary aims were: (1) to develop ecosystem-service indices to rank watersheds in order of priority for investing in the ecosystem services of water provision, flood mitigation and carbon storage; and (2) to compare the ranking of watersheds using ecosystem-service priorities and biodiversity-conservation priorities determined from established global conservation schemes.

Methods

General

We chose the ecosystem services of water provision, flood mitigation, and carbon storage based on the availability of global data sets and their relevance to watershed management (Loomis *et al.* 2000; Reid 2001; Zedler 2003; Postel & Thompson 2005). The biodiversity conservation priority of each watershed was determined by calculating the proportion of the watershed designated as a biodiversity Hotspot ("Hotspot"; Mittermeier *et al.* 2004), Global 200 ecoregion ("Global 200"; Olson & Dinerstein 1998) or endemic bird area ("EBA"; Stattersfield *et al.* 1998), and through a new priority index using a recently published database on freshwater ecoregions (Abell *et al.* 2008; see below and Supporting Information). We refer to these measures from hereon as biodiversity indices. We focused on four key trends in relation to ecosystem-service and biodiversity priorities: (1) mutual-high priorities—where watersheds have high priority for both biodiversity conservation and service protection and represent vital investment priorities; (2) mutual-low priorities—where watersheds have low priority for both biodiversity conservation and service protection; (3) ecosystem-service priorities—where watersheds have high priority for service protection and represent opportunities for investment in conservation; and (4) biodiversity-conservation priorities—where watersheds have high priority for biodiversity conservation and should be assessed for the potential to provide ecosystem services.

The priority index for each ecosystem service is composed of multipliers based on the benefit:cost ratio (where benefits are not measured in monetary units, in keeping with our focus on human need and the inability of dollars to capture that need; MA 2003), threat to the service, opportunity for enhancement, capacity to meet demand and availability of alternatives, incorporating a variety of metrics (below and Table S1). In general, watersheds are prioritized when human need for an ecosystem service is great, supply can be protected at relatively low cost, service provision is threatened, but not completely disrupted, and there is limited potential to develop alternatives. While our functions do not capture all the relevant dynamics, they account for considerable variation sufficiently well to provide guidance for global prioritization. We selected mathematical functions for our priority multipliers that are as simple as possible; in some cases, we have elected linear functions (or linear components of functions) for our multipliers even when underlying ecological or social dynamics likely contain nonlinearities, because the nature of the nonlinearities is often poorly understood or variable across contexts. Given the scale of our analysis, we required functions that are robust to uncertainties and represent the core of what is known dependably.

Watersheds

Watershed (basin) names, location, and boundaries were obtained from the World Resources Institute (WRI) Watersheds of the World database (http://earthtrends.wri.org/maps˙spatial/watersheds/index.php). Subbasins were used where possible (i.e., all those available in the WRI database) to improve the spatial resolution of the data. Not all watersheds were included in the WRI database and for others there were no data available for one or more of the parameters we measured. This limited our sample size to 128, but this represents an area of approximately 54 million km^2, or 41% of global ice-free land area. Omitted areas are mostly small coastal drainage basins or regions without permanent rivers. Watersheds ranged in size from 29,964 to 2,606,162 km^2 (mean = 455,119 km^2, median = 273,174 km^2).

Water provision

Water provision is interpreted in a broad sense to refer to the capacity of ecosystems to regulate water flows and quality in a fashion that may benefit humans (e.g., influencing seasonal availability or nutrient levels; Brauman *et al.* 2007). The water-provision (*WP*) index prioritizes watersheds in which the total supply of water is high and is relied on by a large number of people, and the relative financial costs of protecting this supply are low (*b*1); the watershed is just able or unable to meet human demands (*d*); there is substantial threat to this capacity through vegetation loss (*s*1); and there are limited options to employ alternatives to the provision of freshwater (*a*1). The *WP* index was devised for each watershed from these four components, which are described in detail in Table 1 (see Supporting Information for associated equations). Each component was expressed as a “priority multiplier” (*M*; Table S1 and Figure S1), as for all indices, and combined into the *WP* index using the following equation:

$$WP = M_{b1} \cdot M_d \cdot M_{s1} \cdot M_{a1} \qquad (1)$$

Flood mitigation

Flood mitigation refers to an ecosystem’s capacity to reduce the impact of floods on local communities through physical barriers (e.g., forest cover) and the capacity of soil, wetlands, and associated vegetation communities to reduce runoff (Bayley 1995; Gore & Shields 1995; Tockner & Stanford 2002; Bradshaw *et al.* 2007). The flood-mitigation (*FM*) index prioritizes watersheds in which demand for flood protection is high (owing to a high number of floods and people affected) and the relative costs of providing this protection are low (*b*2); opportunities for landscape (and hence service) restoration are high (*op*1); threats to natural flood mitigation are high (*s*2); and the capacity to pay for alternatives to ecosystem-service provision is low (*a*2). The *FM* index was devised for each watershed from these four components (see Table 1 and Supporting Information for details) using the following equation:

$$FM = M_{b2} \cdot M_{s2} \cdot M_{op1} \cdot M_{a2} \qquad (2)$$

Carbon storage

Carbon storage refers to the ability of ecosystems to mitigate climate change by storing carbon above and below ground in vegetation and soils. The carbon-storage (*CS*) index prioritizes watersheds in which the current stores of carbon are high and the costs of protection are low (*b*3); and the opportunities for ecosystem service enhancement are high (*op*2). Based on these two components (Table 1 and Supporting Information), the *CS* index was calculated using the following equation:

$$CS = M_{b3} \cdot M_{op2} \qquad (3)$$

The benefits of carbon storage are a function of the total amount of carbon in the global atmosphere, for which it does not matter how much carbon is stored in any particular watershed. Accordingly, unlike the other ecosystem services we consider, the storage of carbon (for climate change mitigation) is substitutable across watersheds and for this reason our carbon index did not include a term for threats in the watershed.

Biodiversity priorities

We determined the area of each watershed classified under the different biodiversity schemes by overlaying

Table 1 A description of the variables used in the calculation of the water-provision index, flood-mitigation index, carbon-storage index, and freshwater-biodiversity index

Variable	Title	Description
Water provision		
*b*1	Benefit–cost ratio	Prioritized watersheds were those with a high population density and water supply per unit area (the benefit side of the equation), and where the costs of protecting supply (e.g., land acquisition and labor) were relatively low.
d	Capacity to meet human water use demands	Watersheds were prioritized when total water supply just met, or did not meet, total demand.
*s*1	Security of/threats to water supply capacity	We used vegetation cover in each watershed, rates of vegetation loss and area of protected land as indicators of the capacity of ecosystems to regulate the availability of clean water. Watersheds with mid-range values of vegetation cover and protected land, and mid to high rates of loss were prioritized. A low priority was given to watersheds with high proportions of vegetation/protected area, as we considered these to be under little threat, and those with low proportions, since these would require a large investment (of time and money) to improve capacity relative to return.
*a*1	Availability of alternatives	We used the financial status of countries associated with each watershed, measured using Gross National Income (GNI), as an estimate of the capacity of these countries to pay for alternatives to freshwater provision from ecosystems (e.g., water filtration and desalinization plants). Watersheds with low average GNI were prioritized.
Flood mitigation		
*b*2	Benefit–cost ratio	Watersheds were prioritized when there was a high number of floods and a high level of impact on the human population, and low management costs for protecting ecosystems that mitigate floods. Flood activity and impact were determined using historical data on number of floods in each watershed, number of people killed or displaced, duration of floods, and land area affected. The potential for impact was estimated using population density (Supporting Information).
*op*1	Opportunities for enhancement of flood mitigation	This component prioritized watersheds that had a greater proportion of degraded land that could be restored to contribute to natural flood mitigation.
*s*2	Security of/threats to natural flood mitigation	Watersheds with a high rate of loss in forest and woodland cover, as a proportion of all land, were deemed under threat and therefore priorities. We considered that loss of forests and woodlands undermines the capacity for natural flood mitigation (Bradshaw *et al.* 2007), although acknowledge that this issue is controversial (see Supporting Information).
*a*2	Availability of alternatives	This component was treated as for *a*1 reflecting the financial capacity of countries associated with a watershed to pay for alternatives to natural flood mitigation (e.g., dams and levee banks).
Carbon storage		
*b*3	Benefit–cost ratio	Watersheds were prioritized when the amount of carbon stored in their vegetation and soils was high and the costs of protecting this storage (e.g., through land acquisition) were low.
*op*2	Opportunities for enhancement of carbon storage	As for *op*1, where degraded land could be restored to improve its carbon storage capacity (e.g., through revegetation).
Freshwater biodiversity		
*b*4	Benefit–cost ratio	Watersheds were prioritized when species richness and the number of endemic species were high, and the costs of protecting species were low (e.g., purchasing and managing conservation reserves).
*s*3	Security of/threats to species persistence	We considered that water use by humans represents a threat to the persistence of freshwater species and prioritized watersheds where water withdrawals were high relative to supply.

watershed boundaries with the boundaries of each Hotspot, Global 200, and EBA region using geographic information system software. To complement these, our freshwater-biodiversity (*BI*) index prioritizes watersheds in which fish and amphibian species richness and endemism are high in associated freshwater ecoregions (Abell *et al.* 2008) and the costs of species protection are low ($b4$); and high human water use, relative to supply, threatens species persistence ($s3$) (Table 1 and Supporting Information). The *BI* index was calculated using the following equation:

$$BI = M_{b4} \cdot M_{s3} \tag{4}$$

Analysis

We scaled the values for each ecosystem-service index and the freshwater-biodiversity index between 0 and

1 by dividing all values for an index by the largest value for that index. Pairwise correlations among the three ecosystem-service indices, the sum of these indices (i.e., an index combining all three services), each biodiversity index and a combined index (combining all schemes) were conducted using Spearman rank correlation to determine the general level of concordance among ecosystem-service and conservation priorities. The water regulation and flood mitigation indices were fourth-root transformed, and the carbon-storage and freshwater-biodiversity indices were square-root transformed prior to analysis and presentation. These transformations account for the number of multipliers in each index (two for carbon storage and freshwater biodiversity, and four for water regulation and flood mitigation) and correct for the left skew in the data, which was exacerbated by the addition of more multipliers.

We generated global maps of watersheds showing congruent or divergent ecosystem-service and biodiversity-conservation priorities, making pairwise comparisons between each service index and each biodiversity index. Watersheds were placed in one of four categories (mutual-high priority, mutual-low priority, ecosystem-service priority, or biodiversity priority—see above) by taking the median value for each index and comparing watersheds above or below this value. For example, when comparing watersheds ranked by the water-provision index versus the biodiversity-Hotspot index, watersheds could have values above the median for both (mutual-high priority), below the median for both (mutual-low priority), and above the median for one but not the other (either ecosystem-service or biodiversity priority). To determine a watershed's ranking within these four categories we calculated a combined measure (ecosystem service plus biodiversity) considering the watershed's value for each index relative to the median value for that index (Supporting Information).

Results

When watersheds were ranked using one of the three ecosystem-service indices, regardless of the index used, watersheds occurring in the top quartile were almost always in developing countries and often in the world's poorest regions. There were strong negative correlations between each index (and all indices combined) and per capita purchasing power parity-adjusted GNI for each watershed (Spearman rank correlations (r_s) ranged from –0.366 to –0.797). Although this result may be due partly to GNI occurring as a component of the *WP* and *FM* indices, the correlations between these indices and GNI were high even with the indices re-calculated with GNI held constant ($r_s = –0.568$ and –0.498, respectively). This strongly supports our claim that our approach focuses on human need, not profit.

There was a strong geographical bias for watersheds ranked highly using the *WP* index (Figure 1). Of the top quartile globally, 53% were in Central or Southeast Asia (including India and Pakistan) or China (whereas

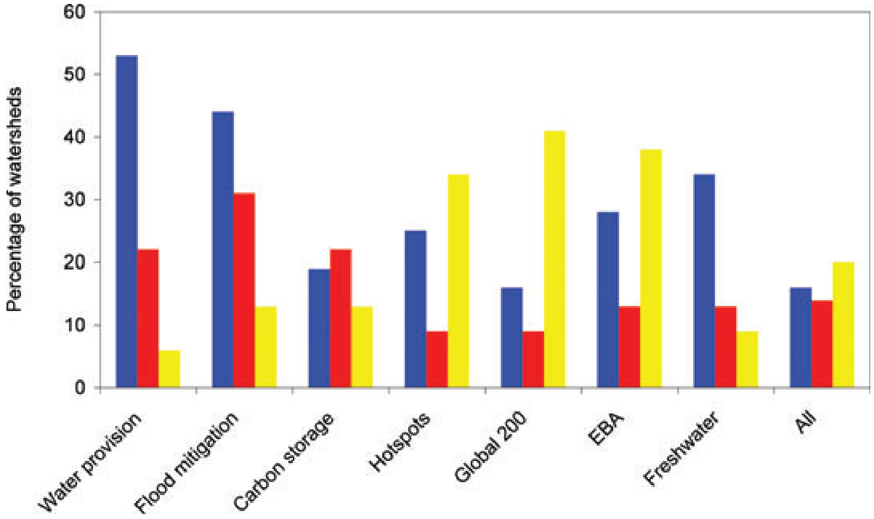

Figure 1 The proportion of watersheds ranked in the top quartile for each ecosystem-service and biodiversity index ("Freshwater" = the freshwater-biodiversity index) occurring in Asia (blue), Africa (red) and South America (yellow). "Asia" includes India, Pakistan, China, and Southeast Asia; "Africa" is mainland Africa only; and "South America" includes Central America. "All" is the proportion of all watersheds occurring in the three regions.

Table 2 Spearman rank correlation matrix showing the relationships among ecosystem-service and biodiversity indices

	Ecosystem-service indices				Biodiversity indices			
	WP	FM	CS	CES	Hotspot	Global 200	EBA	CB
FM	0.643							
CS	0.372	−0.012						
CES	0.914	0.742	0.511					
Hotspot	0.385	0.425	0.019	0.368				
Global 200	0.250	0.096	0.125	0.199	0.547			
EBA	0.419	0.309	0.054	0.385	0.500	0.464		
CB	0.359	0.209	0.190	0.321	0.644	0.930	0.588	
BI	0.277	0.390	0.148	0.342	0.383	0.010	–0.007	0.021

WP = water-provision index; FM = flood-mitigation index; CS = carbon-storage index; CES = combined ecosystem-service index; Hotspot = Conservation International Hotspot; Global 200 = World Wildlife Fund Global 200 priority ecoregion; EBA = Birdlife International endemic bird area; CB = combined biodiversity index; and BI = freshwater-biodiversity index.

only 16% of all watersheds occur in these regions). A total of 22% were in mainland Africa (14% of all watersheds occur here; Table S2). When watersheds were ranked using the *FM* index, 44% of the top quartile occurred in Central or Southeast Asia or China, and 31% were in mainland Africa. For carbon storage, 22% were in mainland Africa and 19% in Southeast Asia or China (Figure 1). The dominance of Southeast Asia was underscored by watershed rankings based on a combined index (i.e., combining all ecosystem-service indices; Table S2).

Of the top quartile of watersheds ranked using the proportion of watershed area designated as a Hotspot, 25% were in Southeast Asia (including India) or China and only 9% in mainland Africa, while 34% were in Central/South America (20% of all watersheds occur in this region). For rankings based on the Global 200 scheme, 41% were in Central/South America, and results were similar using EBAs (Figure 1). Rankings based on our *BI* index diverged from this trend with the top quartile including a higher representation of watersheds from Southeast Asia and China (34%) and few watersheds in South America, consistent with our rankings based on ecosystem services. This may reflect stronger relationships between water-related ecosystem services and freshwater biodiversity and similar treatment of costs and threats across these indices (Supporting Information).

While watersheds ranked highly using either the ecosystem-service or biodiversity indices were mostly in developing regions, there were important differences in rankings. High priorities for ecosystem services were mainly in Central and Southeast Asia and to a lesser extent Africa, while biodiversity priorities were highest in Central/South America for the Hotspot, Global 200 and EBA schemes. Nevertheless, pairwise correlations among the ecosystem-service and biodiversity indices were always positive and there were strong correlations in some instances (Table 2). For example, watersheds indexed using *WP* versus EBAs ($r_s = 0.419$), *FM* versus Hotspots (0.425), and *FM* versus *BI* (0.390).

Congruence or divergence in global ecosystem-service and biodiversity-conservation priorities is presented spatially for all ecosystem services combined versus all biodiversity conservation schemes combined (Hotspots, Global 200 and EBA; Figure 2; see Figure S2 for further pairwise comparisons). Mutual-high priorities for ecosystem services and biodiversity were confined almost entirely to developing regions, especially Central/South America (including Mexico; 30% of mutual-high priorities), Southeast Asia (including China; 28%), and Africa (including Madagascar; 23%). Conversely, mutual-low priorities primarily occurred in developed regions, especially the United States and Canada (33% of mutual-low priorities) and Central and Western Europe (25%). Watersheds with high priority for ecosystem-service protection, but low priority for biodiversity conservation were evenly spread among Eastern Europe (including Russia), Africa and China/India (33% in each case), whereas for the converse, watersheds occurred primarily in Central/South America (42%).

Our results were remarkably consistent regardless of which pair (or combination) of ecosystem-service—biodiversity-conservation indices were being compared. Across 20 pairwise comparisons, 15% of the 128 watersheds always occurred in only one of the priority categories (i.e., mutual-high, mutual-low, ecosystem-service priority or biodiversity priority), 47% occurred in the same category at least 75% of the time, and 75% of

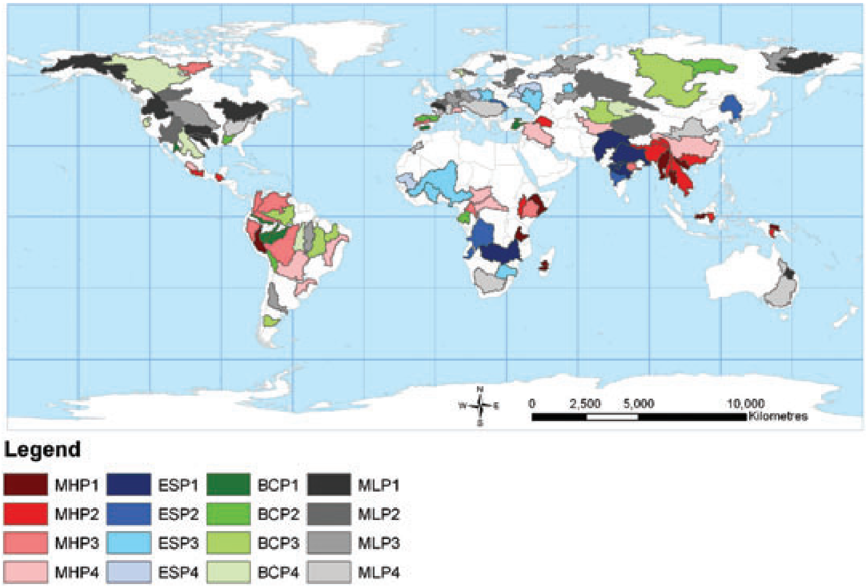

Figure 2 Global priorities for the protection of ecosystem services and biodiversity. Map shows all ecosystem-service indices combined and all biodiversity indices combined (Hotspots, Global 200, and EBA). Watersheds are split into four categories: mutual-high priorities (MHP; red) for protection of both ecosystem services and biodiversity; high priorities for protecting ecosystem services (ESP; blue); high priorities for protecting biodiversity (BCP; green); and mutual-low priorities (MLP; gray/black) for protecting both ecosystem services and biodiversity. White areas are not included in our analysis. Color intensity varies in each category to reflect the quartiles of values in that category with dark–light corresponding with the top–bottom quartiles (Supporting Information).

watersheds occurred in the same category at least 50% of the time. This suggests that our results are robust across different ecosystem services or biodiversity prioritization schemes.

Ten watersheds always occurred in the mutual-high-priority category regardless of which ecosystem-service and biodiversity combination was being considered (Table 3). A total of 50% of these were in Africa (including Madagascar) and 30% were in Southeast Asia (southern China, Vietnam, and Myanmar). According to our analysis, these watersheds are the most critical priorities for investing in the protection of both ecosystem services and biodiversity.

Table 3 Watersheds that were always ranked as mutual-high priorities for the protection of ecosystem services and biodiversity. Watersheds are sorted by mean ranking (highest to lowest). Countries that contain at least 10% of the watershed area are also listed.

Watersheds	Countries
Mania	Madagascar
Irrawaddy	Myanmar
Shaballe	Ethiopia, Somalia
Hong	China, Vietnam
Rufiji	Tanzania
Balsas	Mexico
Turkana	Ethiopia, Kenya
Salween	China, Myanmar
Jubba	Ethiopia, Kenya, Somalia
Rio Grande de Santiago	Mexico

Discussion

Our study is the first attempt to incorporate cost–benefit trade-offs explicitly in developing global priorities for protecting ecosystem services and biodiversity in the world's watersheds. Watersheds in Southeast Asia and Africa were prioritized for the protection of ecosystem services because often they had the highest benefit-to-cost ratio. For example, in Southeast Asia, investment in water provision is attractive because of an extensive supply servicing areas of high human population density with relatively low costs for service protection. Similarly, this region was also a priority for investing in flood mitigation services because of a high level of flood activity and damage.

Reassuringly, the ecosystem-service approach applied here yields similar results to conservation-based schemes that emphasize investment in regions with a high benefit-to-cost ratio (e.g., Asia and Africa; Balmford *et al.* 2003). Two points are crucial: first, only a small proportion of global conservation dollars is currently spent in these areas (James *et al.* 2001); and second, national governments in many of these regions do not have the capacity to invest heavily in conservation. This highlights the vital role of multinational NGOs and other global institutions in effectively protecting ecosystem services. Also, time is short. Costs of conservation positively correlate with human population density (Balmford *et al.* 2003) and the same is likely true for ecosystem-service protection. Human populations are growing rapidly in most developing regions, which suggests investment decisions need to be made now, perhaps even before more sophisticated decision-making frameworks can be employed.

Investment in ecosystem services could contribute to biodiversity conservation in watersheds of mutual-high or ecosystem-service priority, leaving designated conservation funding to focus on sites of high biodiversity (but low ecosystem service) importance (Naidoo *et al.* 2008). We argue that our focus on the *need* for services (which we capture through variables such as human population density in a watershed and the capacity to pay for human-derived alternatives to ecosystem services) rather than simple dollar metrics promotes conservation in poor regions. Local-scale examples suggest that it is possible to manage for both ecosystem-service protection and biodiversity conservation (Guo *et al.* 2000; Chan *et al.* 2006). Effective protection of ecosystem services may require transfer payments from service beneficiaries to landholders whose land is used to generate the service(s) and who may have to forgo other land-use opportunities (e.g., Guo *et al.* 2007), although there are many financial mechanisms for protecting ecosystem services (Reid 2001; Postel & Thompson 2005; Ruhl *et al.* 2007). Funding may occur through regional or international trading schemes for relevant services (e.g., carbon trading, which occurs at both levels).

Our approach can be applied at much finer spatial resolutions to guide region-specific land management strategies. Ultimately, we favor a systematic return-on-investment (ROI) strategy (Murdoch *et al.* 2007) that incorporates optimal resource allocation rules and dynamic decision-making frameworks, as that should yield greater benefits per dollar spent than simple ranking schemes like that developed here (Wilson *et al.* 2006). However, the improvement of an ROI approach over this one depends entirely on knowledge of impacts of management actions on each ecosystem service and biodiversity, which is sorely lacking. Our methods use readily available data and are applicable in data-poor circumstances, which is vital for real-world decision making. Moreover, our systematic, comprehensive approach provides valuable information on the congruence and divergence among broadly accepted conservation priorities and the protection of ecosystem services, and identifies regions where the protection of services can yield substantial benefits at low cost.

Acknowledgments

This work was supported by the Charles Sturt University Special Studies Program while GWL was a visiting scholar at the Institute for Resources, Environment and Sustainability, University of British Columbia. Sincere thanks to the following who assisted in data access and interpretation: R. Abell, D. Brito, X. Chen, L. Fishpool, M. Flörke, J. Howard, S. Minnemeyer, F. Nachtergaele, M. Parr, C. Revenga, J. Robertson and N. Sindorf. Thanks also to the following for insightful comments on the manuscript: P. Armsworth, P. Balvanera, K. Brauman, L. Hoshizaki, M. Johnson, C. Kremen, R. Naidoo, R. Pringle, J. Ranganathan, C. Revenga, M. Weiler, and two anonymous referees.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1 Graphical representation of the functions used to convert index components to multipliers: a, conversion of d (capacity to meet demand) to M_d (a multiplier constrained between 0.25 and 1); b, conversion of $s1$ (expected vegetation cover) to M_d (a multiplier constrained between 0 and 1); c, conversion of a (ability to pay for alternatives) to M_{a1} (a multiplier constrained between 0 and 1); and d, conversion of $s2$ (security of service) to M_{s2} (a multiplier constrained between 0 and 1).

Figure S2 Global priorities for the protection of ecosystem services and biodiversity. Pairwise comparisons are as follows: a, all ecosystem-service indices versus Hotspots; b, all ecosystem-service indices versus Global 200; c, all ecosystem-service indices versus EBA; and d, all ecosystem-service indices versus freshwater biodiversity. Watersheds are split into four categories: mutual-high priorities (MHP; red) for protection of both ecosystem services and biodiversity; high priorities for protecting ecosystem services (ESP; blue); high priorities for protecting biodiversity (BCP; green); and mutual-low priorities (MLP; gray/black) for protecting both ecosystem services and biodiversity. White areas are not included in our analysis. Color intensity varies in each category to reflect the quartiles of values in that category (noted as 1–4) calculated from equations 13–16 (Supporting Information). For example for MHP, the darkest red is the top quartile of watersheds in that category (i.e., those that have the highest priority for protection of both ecosystem services and biodiversity) and the lightest red is the bottom quartile. For MLP, black is the top quartile of values (i.e., those that have the lowest priority for protection of both ecosystem services and biodiversity).

Table S1 A summary of the multipliers, variables, data sources, and their resolution (where applicable) included in the calculation of each ecosystem service index and the freshwater biodiversity index. See text of Supporting Information for further details.

Table S2 The ecosystem-service and biodiversity-conservation indices for each watershed. Watersheds are sorted into regions and alphabetically. WP = water-provision index; FM = flood-mitigation index; CS = carbon-storage index; CES = combined ecosystem-service index; HS = Conservation International Hotspot; G200 = World Wildlife Fund Global 200 priority ecoregion; EBA = Birdlife International endemic bird area; CB = combined biodiversity index (HS + G200 + EBA); and BI = freshwater-biodiversity index. Subbasin names are in brackets.

(Correction statement added after online publication 21 May 2009: the calculation on line 421 of the Supplementary Material was originally incorrectly listed as 0.1.)

References

Abell, R., Thieme M.L., Revenga C. *et al.* (2008) Freshwater ecoregions of the world: a new map of biogeographic units for freshwater biodiversity conservation. *BioScience* **58**, 403–414.

Arnell, N.W. (2004) Climate change and global water resources: SRES emissions and socio-economic scenarios. *Global Environ Chang* **14**, 31–52.

Balmford, A., Gaston K.J., Blyth S., James A., Kapos V. (2003) Global variation in terrestrial conservation costs, conservation benefits, and unmet conservation needs. *Proc Natl Acad Sci USA* **100**, 1046–1050.

Bayley, P.B. (1995) Understanding large river–floodplain ecosystems. *BioScience* **45**, 153–158.

Bradshaw, C.J., Sodhi N.S., Peh K.S., Brook B.W. (2007) Global evidence that deforestation amplifies flood risk and severity in the developing world. *Global Change Biol* **13**, 1–17.

Brauman, K.A., Daily G.C., Duarte K., Mooney H.A. (2007) The nature and value of ecosystem services: an overview highlighting hydrologic services. *Annu Rev Env Resour* **32**, 67–98.

Chan, K.M.A., Shaw M.R., Cameron D.R., Underwood E.C., Daily G.C. (2006) Conservation planning for ecosystem services. *PLoS Biol* **4**, e379, doi:10.1371/journal.pbio.0040379.

Christensen, J. (2005) Sitting out the big game. *Conserv Pract* **6**, 156–157.

Daily, G.C., editor. (1997) *Nature's services: societal dependence on natural ecosystems*. Island Press, Washington, D.C.

Foley, J.A., DeFries R., Asner G.P. *et al.* (2005) Global consequences of land use. *Science* **309**, 570–574.

Goldman, R.L., Tallis H., Kareiva P., Daily G.C. (2008) Field evidence that ecosystem service projects support biodiversity and diversify options. *Proc Natl Acad Sci USA* **105**, 9445–9448.

Gore, J.A., Shields F.D. Jr. (1995) Can large rivers be restored? *BioScience* **45**, 142–152.

Guo, Z., Li Y., Xiao X., Zhang L., Gan Y. (2007) Hydroelectricity production and forest conservation in watersheds. *Ecol Appl* **17**, 1557–1562.

Guo, Z., Xiao X., Li, D. (2000) An assessment of ecosystem services: water flow regulation and hydroelectric power production. *Ecol Appl* **10**, 925–936.

Halpern, B.S., Pyke C.R., Fox H.E., Haney J.C., Schlaepfer M.A., Zaradic P. (2006) Gaps and mismatches between global conservation priorities and spending. *Conserv Biol* **20**, 56–64.

Hengeveld, H.G. (1990) Global climate change: implications for air temperature and water supply in Canada. *Trans Am Fish Soc* **119**, 176–182.

James, A., Gaston K.J., Balmford A. (2001) Can we afford to conserve biodiversity? *BioScience* **51**, 43–52.

Loomis, J., Kent P., Strange L., Fausch K., Covich A. (2000) Measuring the total economic value of restoring ecosystem services in an impaired river basin: results from a contingent valuation survey. *Ecol Econ* **33**, 103–117.

Millennium Ecosystem Assessment (MA). (2003) *Ecosystems and human wellbeing: a framework for assessment*. Island Press, Washington, D.C.

Mittermeier, R.A., Gil P.R., Hoffmann M. *et al.* (2004) *Hotspots revisited: earths biologically richest and most endangered ecoregions*. Cemex, Mexico City, Mexico.

Murdoch, W., Polasky S., Wilson K.A., Possingham H.P., Kareiva P., Shaw R. (2007) Maximizing return on investment in conservation. *Biol Conserv* **139**, 375–388.

Naidoo, R., Balmford A., Costanza R. *et al.* (2008) Global mapping of ecosystem services and conservation priorities. *Proc Natl Acad Sci USA* **105**, 9495–9500.

Oki, T., Kanae S. (2006) Global hydrological cycles and world water resources. *Science* **313**, 1068–1072.

Olson, D.M., Dinerstein E. (1998) The global 200: a representation approach to conserving the Earth's most biologically valuable ecoregions. *Conserv Biol* **12**, 502–515.

Postel, S.L., Thompson B.H. Jr. (2005) Watershed protection: capturing the benefits of nature's water supply services. *Nat Resour Forum* **29**, 98–108.

Reid, W.V. (2001) Capturing the value of ecosystem services to protect biodiversity. Pages 197–225 in V.C. Hollowell, editor. *Managing human-dominated ecosystems: proceedings of the Symposium at the Missouri Botanical Garden, Saint Louis, Missouri, 26–29 March 1998*. Missouri Botanical Garden Press, Saint Louis.

Rodríguez, J.P., Taber A.B., Daszak P. *et al*. (2007) Globalization of conservation: a view from the south. *Science* **317**, 755–756.

Ruhl, J.B., Lant C., Kraft S. (2007) *The law and policy of ecosystem services*. Island Press, Washington, D.C.

Schröter, D., Cramer W., Leemans R. *et al*. (2005) Ecosystem service supply and vulnerability to global change in Europe. *Science* **310**, 1333–1337.

Stattersfield, A.J., Crosby M.J., Long A.J., Wege D.C. (1998) *Endemic bird areas of the world: priorities for biodiversity conservation*. BirdLife International, Conservation Series No. 7, Cambridge, United Kingdom.

Tallis, H., Kareiva P. Marvier M., Chang A. (2008) An ecosystem services framework to support both practical conservation and economic development. *Proc Natl Acad Sci USA* **105**, 9457–9464.

The World Bank. (2004) *Global development finance 2004: harnessing cyclical gains for development*. The World Bank, Washington, D.C.

Tockner, K., Stanford J.A. (2002) Riverine flood plains: present state and future trends. *Environ Conserv* **29**, 308–330.

Turner, W.R., Brandon K., Brooks T.M., Costanza R., da Fonseca, G.A.B., Portela, R. (2007) Global conservation of biodiversity and ecosystem services. *BioScience* **57**, 868–873.

Wilson, K.A., McBride M.F., Bode M., Possingham H.P. (2006) Prioritizing global conservation efforts. *Nature* **440**, 337–340.

Zedler, J.B. (2003) Wetlands at your service: reducing impacts of agriculture at the watershed scale. *Front Ecol Environ* **1**, 65–72.

Editor: Prof. Claire Kremen