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Global-scale mapping of economic benefits from agricultural lands: Implications for conservation priorities

Robin Naidoo^{a,*}, Takuya Iwamura^{b,1}

^aConservation Science Program, WWF-US, 1250 24th Street NW, Washington, DC 20009, United States

^bNicholas School of the Environment and Earth Sciences, Duke University, Box 90328, Durham, NC 27708, United States

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ABSTRACT

Research in systematic conservation planning has focused heavily on biological considerations, even though a growing number of studies demonstrate that integrating economic costs into the planning process markedly increases the efficiency of resulting plans. At the global scale, the availability of biodiversity maps is increasing, but analogous maps for economic factors that affect biodiversity conservation are rare, and no study has examined global conservation planning at high resolution using both biodiversity and cost information. Here, we integrate spatial information on crop productivity, livestock density, and prices to produce a global map of the gross economic rents from agricultural lands. We then illustrate the importance of including such opportunity costs in global planning for the conservation of endemic vertebrate species. Plans that consider costs represent endemic species at 10–33% of the opportunity cost of plans that do not, and produce priority sets that diverge from existing schemes. Given scarce resources and the great cost-effectiveness of plans that consider both biodiversity and costs, mapping of the economic costs of conservation should receive similar levels of research attention as mapping of biodiversity.

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1. Introduction

Our understanding of the spatial distribution of the world's biodiversity has increased dramatically in recent years. The publication of comprehensive, fine resolution spatial databases of the world's mammals (Ceballos et al., 2005), birds (Orme et al., 2005), and amphibians (Stuart et al., 2004) has helped improve our knowledge of patterns of vertebrate species richness and endemism at the global scale (Lamoreux et al., 2006). Recent studies have shown how such databases can be used to systematically identify priority areas for conservation investments (Ceballos et al., 2005; Orme et al., 2005). But as in most conservation planning studies, these global-level priority setting examples did not consider the spatial heterogeneity of economic factors that may influence

conservation outcomes (Naidoo et al., 2006). Studies at smaller scales have demonstrated that the spatial distribution of costs can be just as important as that of biodiversity in determining optimal conservation investments (Ando et al., 1998; Polasky et al., 2001; Ferraro, 2003). Without a high-resolution global database on the distribution of opportunity costs of conservation, it has not been possible to test whether this result also holds for global conservation priority-setting.

Here, we construct a map of opportunity costs of field-based conservation (Balmford et al., 2003) by producing a spatial database, at 5' resolution, of the gross economic benefits derived from agricultural lands. We considered 42 of the world's most important crops and integrated information on their potential yields (Fischer et al., 2002) and actual distribu-

* Corresponding author. Tel.: +1 202 861 8301; fax: +1 202 293 9211.

E-mail addresses: robin.naidoo@wwfus.org (R. Naidoo), takuya.iwamura@gmail.com (T. Iwamura).

¹ Current address: School of Integrative Biology, The University of Queensland, St. Lucia, Brisbane, Qld 4072, Australia. 0006-3207/\$ - see front matter © 2007 Elsevier Ltd. All rights reserved.

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tions (Leff et al., 2004) to develop a global map of yield per hectare, and then used producer prices (<http://faostat.fao.org>; accessed June 2005) to derive the gross economic rents per hectare for the world's croplands. We used a similar approach for livestock, integrating global maps of livestock densities (Wint and Robinson, 2006) with meat yields and producer prices (<http://faostat.fao.org>; accessed June 2005) to derive per-hectare livestock rents for pastures and rangelands. Combining the values for crops and livestock yielded the overall map for agricultural economic benefits, in 2000 US dollars per hectare per year.

We use this map to quantify the change in efficiency (i.e., the amount of conservation target achieved per unit cost) that results from the inclusion of conservation costs in planning processes. We also assess the efficiency of current global conservation priority schemes as compared to potential cost-effective priority sets. Our results show that including opportunity costs in global conservation planning can result in the expenditure of substantially fewer resources to achieve conservation goals.

2. Materials and methods

2.1. Developing the global map of opportunity costs

In the absence of a comprehensive spatial database on global land prices, we model the opportunity costs of conservation by estimating the flow of economic benefits derived from crops and livestock. This theoretical framework is commonly used in the agricultural economics literature when modeling the rental value of agricultural land (Goodwin et al., 2003). In addition, using agricultural land values as proxies of conservation costs has precedent in the conservation planning literature (Ando et al., 1998; Polasky et al., 2001), since they represent the income forgone if land is conserved instead of cultivated, and are capitalized into agricultural land values (Goodwin et al., 2003).

We here present only brief mention of the steps used in developing the opportunity costs layer (Fig. 1); see Appendix for more details. We used spatially explicit information (5' grid cells over the terrestrial surface of the earth) on potential productivities of 42 crop types (Fischer et al., 2002), then used maps of actual crop distributions (Leff et al., 2004) to estimate the current distribution of crop productivities across the earth's surface. We then used producer prices (<http://faostat.fao.org>; accessed June 2005) to estimate gross rents for each crop, and took a weighted average for each grid cell to arrive at an estimate of per unit-area crop rents.

We followed a similar procedure for livestock, using predicted density estimates for different livestock species, estimates of meat derived from an average carcass (we used regional estimates because carcass weight varied greatly by region; note also we ignored non-meat products), and producer price per unit weight of meat to come up with a gross rent for each species. After aggregating to get an overall livestock gross rent, we took the maximum of crop rent and livestock rent to be the gross returns to land from agriculture from each grid cell.

2.2. Hypothetical conservation planning approaches

We explored how accounting for opportunity costs of conservation affects global conservation priorities. We formulated three hypothetical conservation planning problems that each involved selecting a set of priority areas using the number of endemic vertebrate species as a target. Our analysis units were the 825 ecoregions of the world. We assumed simplistically that a conservation program that conserves 30% of an ecoregion would result in the conservation of all endemic species in that ecoregion. We therefore calculated opportunity costs for each ecoregion as [30% minus % area protected in IUCN category I–VI protected areas], multiplied by [total agricultural rents in the ecoregion] (Svancara et al., 2005). We used an integer programming approach, implemented with the lpSolve package in the R statistical language, to solve each of these optimization problems (Buttrey, 2005).

Cost-effectiveness – The cost-effective strategy maximized the number of endemic species subject to the total opportunity costs of the resulting set of ecoregions being less than the budget. This formulation by definition results in the greatest number of endemic species conserved per dollar of cost. Each site could only be selected once, and optimizations were repeated for a range of budgets.

Endemics-only – The endemics-only approach ignored opportunity costs of individual ecoregions; the only constraint is that there is a limit to the number of ecoregions that can be considered in the solution set. This approach is equivalent to ranking ecoregions from highest number of endemics to lowest and selecting down the list until the conservation budget is exhausted (Ferraro, 2003). Optimizations were repeated for a range of possible ecoregions in the final set.

Cost-minimization – The cost-minimization approach ignored the number of endemic species in an ecoregion. The focus was exclusively on minimizing the costs, given a target number of ecoregions to be conserved. This approach is equivalent to ranking ecoregions from lowest cost to highest and selecting down the list until the conservation budget is exhausted (Ferraro, 2003). Optimizations were repeated for a range of ecoregions in the final set.

2.3. Comparing the Global 200 and biodiversity hotspots with analogous cost-effective approaches

We investigated how a consideration of opportunity costs might influence two prominent conservation schemes that are being used to direct global conservation investments. The Global 200 ecoregions (G200) represent the most biologically distinct of the world's 825 terrestrial ecoregions across biomes and biogeographic realms (as determined by parameters such as species richness and endemism, ecological phenomena, and taxonomic uniqueness) (Olson and Dinerstein, 1998). Biodiversity hotspots focus on different criteria, and identify ecoregions with high plant endemism and a high degree of threat (Myers et al., 2000).

We formulated a conservation planning problem that contained similar elements as the approach used to develop the

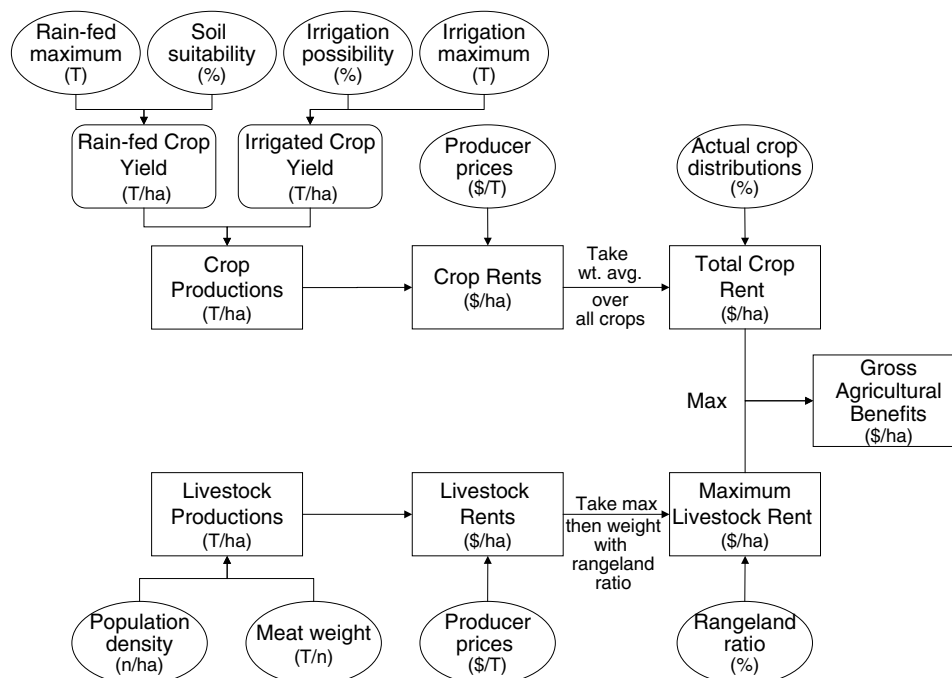


Fig. 1 – Flow chart describing steps involved in producing the global map of gross agricultural benefits at 5' resolution. See Appendix for detailed explanation of steps.

Global 200 ecoregions (Olson and Dinerstein, 1998), but that included opportunity costs of conservation. We minimized the opportunity costs of conservation subject to: (1) an equivalent number of endemic species as found in the G200 ecoregions (4941); and (2) biome/realm representation that is proportional to the actual geographic distribution of terrestrial ecoregions (i.e., there are 82 tropical moist forest ecoregions in the Neotropics, but only three tropical dry forest ecoregions in the Afrotropics).

The biodiversity hotspots approach focuses on conserving the greatest number of threatened endemic species per dollar invested (Myers et al., 2000). We therefore contrasted the hotspots with an approach that captures the same number of threatened endemic vertebrate species as found in hotspots (1274), while minimizing opportunity costs.

2.4. Quantifying overlap and dispersion of cost-effective priority sets

To statistically compare the spatial pattern of the biodiversity hotspots/G200 ecoregions and the analogous cost-effective solutions, the geographical centroids of each ecoregion in each priority set were calculated and used in spatial point pattern analyses (Baddeley and Turner, 2005). We used nearest-neighbour analysis and compared the mean nearest-centroid distance between either biodiversity hotspots or G200 ecoregions and their analogous cost-effective solutions. Because there were more ecoregions in hotspots/G200 than in the corresponding cost-effective solution sets, for each comparison we randomly selected an equivalent number of ecoregions, calculated the mean nearest-neighbour distance, and repeated this procedure 5000 times (see Fig. 2).

3. Results

Annual economic benefits from agricultural lands were spatially heterogeneous and varied from 0 to about \$6 500 per hectare, with mean of 55\$/ha/year and standard deviation of 130\$/ha/year (Fig. 1). The highest value lands (those in the top 90% of per-hectare values) were concentrated in a few regions throughout the world. In the Americas, most of these were in the United States, with California's central valley (grapes), Florida (citrus fruit), and large areas in the Midwest (corn) having high opportunity costs of conservation. Other areas with high agricultural economic benefits included the coast of Chile (grapes) and parts of eastern Argentina, Uruguay, and southeastern Brazil (livestock production).

In Europe, the Middle East, and North Africa, areas along the Mediterranean had the highest agricultural values due to their mix of high value crops such as olives, grapes, almonds, and citrus fruit. Other areas in Europe also had high economic benefits from agriculture due to a mix of high livestock production and high production of a variety of crops such as barley, corn, wheat, potatoes, sugar beet, pulses, and rapeseed. In Africa, relatively little area was in the highest agricultural benefit class, with a few parts of South Africa (grapes/oranges) qualifying.

In Asia, much of the Indian subcontinent provides high economic returns from agriculture, due to a combination of high livestock production and high crop production from a mix of rice, maize, and assorted other crops. Much of southeast Asia (livestock production, rice) and eastern China (cotton, rapeseed, wheat, rice, maize, plus some high livestock areas) are also high value lands. In Australasia, only New Zea-

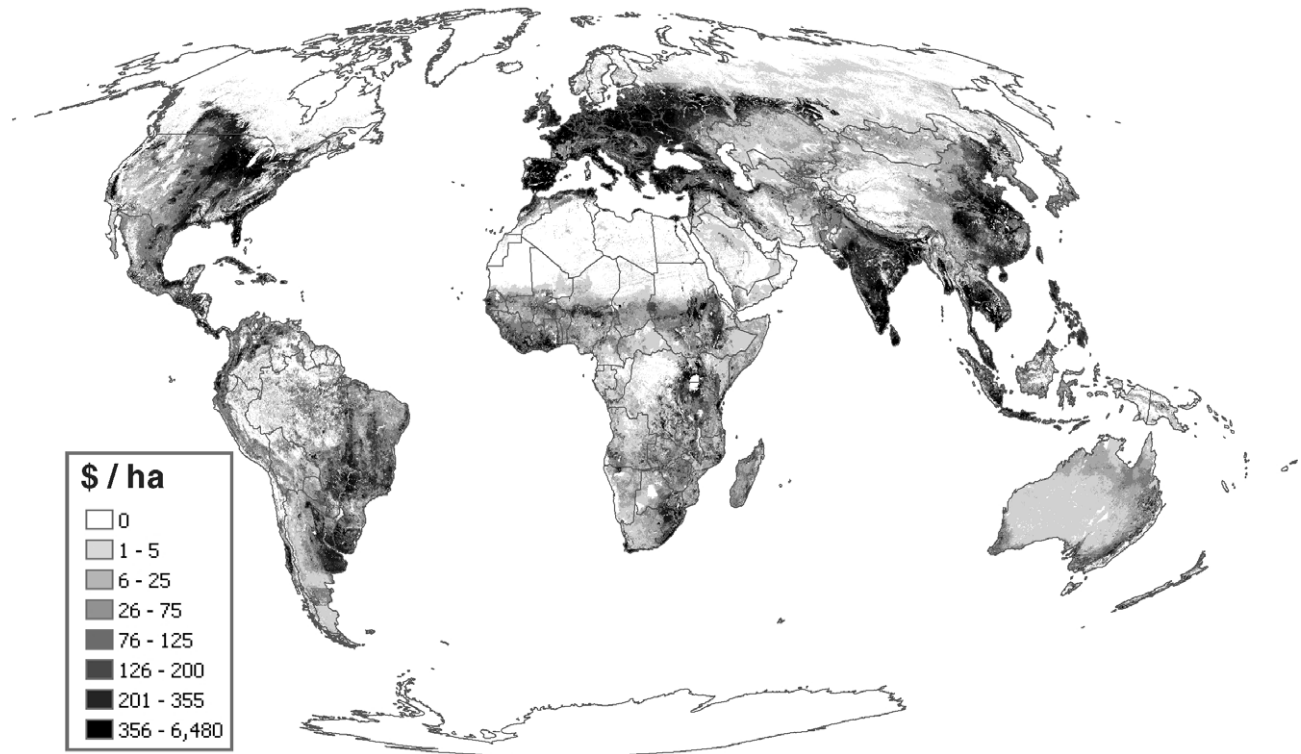


Fig. 2 – Annual gross economic rents (\$/ha) of the world's cropping and grazing lands. Areas in gray indicate 5' cells in which no agriculture occurs.

land has any significant area of globally high economic returns from agriculture, due to high livestock production.

Inaccessible or unsuitable areas with no current agricultural value include tundra regions of North America and Eurasia, the ice shelves of Greenland and Antarctica, deserts such as the Saharan and Arabian, and large tropical forest areas of the Amazon and Congo basins.

Compared to the endemism-only approach, selecting priority ecoregions using the hypothetical cost-effective approach resulted in much lower opportunity costs. For example, conserving one-quarter (25%) of all endemic species was less than one-tenth the costs of the endemism-only approach, despite the fact that the cost-effective solution had seven times as much ecoregion area as the endemism-only approach. Conserving two-thirds (67%) of endemic species was less than a quarter of the costs of the endemism-only approach, again with a greater ecoregion area (Fig. 3). While it was three to four times more expensive than the cost-effective strategy for most endemic target levels, the cost-minimization approach actually performed better than the endemics-only strategy for all but the highest targets (Fig. 3).

The hypothetical cost effective approach also had much lower opportunity costs for an equivalent conservation performance as compared to the two existing priority schemes. For the G200, the same number of endemic vertebrates can be represented at 27% of the opportunity costs by optimizing over both endemic species and opportunity costs, while the same number of threatened endemic species as found in the biodiversity hotspots could be conserved for just 12% of

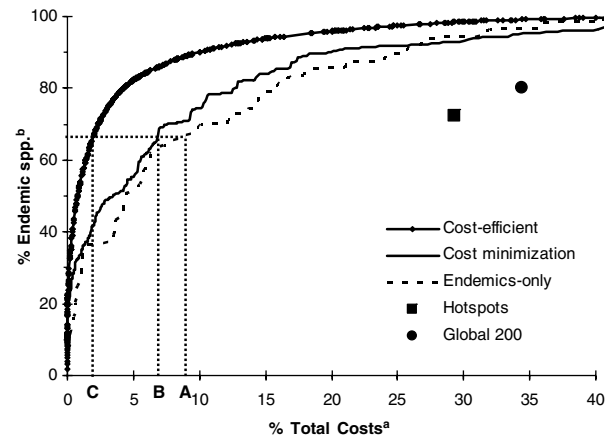


Fig. 3 – Cumulative number of endemic species conserved as the conservation budget increases for three generic conservation strategies (cost-effective, cost-minimization, and endemics-only), along with opportunity costs and endemic species levels of two actual investment schemes, the Global 200 ecoregions and the biodiversity hotspots. Relative to the cost of an endemics-only approach (A), the cost of conserving 67% of all endemic species is less than one quarter of the cost when using the cost-effective approach ($C/A < 0.25$), and even the cost-minimization approach conserved the same number of species for fewer costs than did the endemics-only approach ($B < A$). ^a percent of the total opportunity costs required to conserve all 6177 endemic species. ^b percent of total number of endemic species found in all ecoregions.

Table 1 – Area overlap, by biogeographic realm (Olson and Dinerstein, 1998), of cost-effective approaches with the biodiversity hotspots and the Global 200 ecoregions

Realm ^a	Hotspots				Global 200			
	Area ^b	Cost-effective area	Overlap area	% Overlap ^c	Area	Cost-effective area	Overlap area	% Overlap
AA	1041	2537	476	15.4	5194	4115	2643	39.6
AT	4830	2749	1721	29.4	9904	7912	4721	36.0
IM	4756	1160	1126	23.5	4643	2237	1410	25.8
NA	585	759	175	15.0	6735	6,071	2113	19.8
NT	6944	5553	3004	31.6	11,931	7294	5327	38.3
PA	5134	1511	385	6.1	16,369	13,738	5802	23.9
Total	23,289	14,269	6887	22.5	54,776	41,366	22,016	29.7

a Biogeographic realms: AA: Australasia; AT: Afrotropic; IM: Indo-Malay; NA = Nearctic; NT = Neotropic; PA = Palearctic.

b Area units are 1000's of km².

c Percent overlap is calculated as [shared area/(hotspots area + cost-effective area – shared area)].

the opportunity costs by using a cost-effective approach (Fig. 3).

Global overlap between biodiversity hotspots and the analogous cost-effective planning approach was 23% (Table 1, Fig. 4a). Relative to the biodiversity hotspots, the analogous cost-effective scheme resulted in more priority areas in the low-opportunity-cost lands of the Nearctic and Australasia. In North America, these included temperate rainforests in the Pacific northwest, the Ozark mountains, Appalachian forests, the Mojave desert, and Baja California xeric areas. In Australasia, much of Papua New Guinea was highlighted, along with forests on the east coast of Australia, and deserts/shrublands in south-central and western Australia. The analogous cost effective scheme resulted in less land area being prioritized in the Palearctic and Indo-Malay realms where opportunity costs of conservation are high in hotspots such as Mediterranean basin, Indo Burma, and Sundaland hotspots. Important areas that were captured by both hotspots and the analogous cost-effective solution were most of Central America and the mountains of western South America, Madagascar, much of the southern tip of Africa, and most of the island of Borneo.

There were fewer differences among realms between the G200 and its comparison cost-effective planning approach because of the representation constraint (Table 1, Fig. 4b), but nevertheless global overlap among the two priority sets was only 30%. The lowest overlap was in the Nearctic and Palearctic. In the Nearctic, most of Alaska was selected by the analogous cost-effective solution, while the G200 instead includes areas boreal and tundra areas of northern Quebec, the Northwest Territories, Nunavut, and the Yukon. Further south, the analogous cost effective solution selected large areas such as the northern and southern Rockies, the Mojave desert, forests of the Cascade mountains, and swathes of the eastern deciduous forests, whereas large ecoregions in the G200 included the Northern Great Plains, southeastern forests, and the Chihuahan desert. In the Palearctic, large areas selected by the analogous cost-effective solution included the northern and southern fringes of the Sahara, Japan, the Gobi desert, and the northern Tibetan plateau. Large G200 ecoregions not selected by the analogous cost-effective solution included the east Siberian taiga, much of the Mediterranean basin, central Asian deserts, and southeastern Chinese ever-

green forests. Globally, important areas that were captured by both the G200 and the cost-effective analogue included most of Madagascar and Borneo, much of the northern, southern and western parts of the Amazon basin, the northern Andes, Patagonia, much of the Congo basin, Somalia bushlands, central Siberian tundra, and parts of the central and southern Tibetan plateau.

The mean nearest-neighbour distance of ecoregions in the cost-effective sets were significantly larger than in either the biodiversity hotspots (3.37° vs. 2.82°, $p = 0.00$; p -value taken to be percentage of trials where cost-effective distance exceeded hotspots distance) or in the G200 ecoregions (3.52° vs. 3.29°, $p = 0.00$). Both results indicate that conservation priority sets that result from a process that includes opportunity costs are more geographically dispersed than existing global conservation plans (Fig. 4).

4. Discussion and conclusions

Our map is not a definitive assessment of the costs of global-scale conservation. We focused only on opportunity costs of land, whereas others have demonstrated that dimensions of conservation costs such as management costs can also vary geographically (Balmford et al., 2000; Balmford et al., 2003). Some of the global data inputs into our calculations need updating (e.g., maps of crop distributions) or need more extensive field validation (e.g., maps of crop bioclimatic suitability).

Economic benefits associated with agricultural lands can be considered opportunity costs of conservation under the following assumptions: the most cost-effective conservation plans are field-based programs (James et al., 1999), agriculture is the dominant form of anthropogenic land use that competes with natural habitat (Leff et al., 2004), and agricultural activities result in more difficult conditions for biodiversity persistence as compared to natural habitat (Green et al., 2005). Under these conditions, more agriculturally valuable lands have greater economic costs of conservation (Polasky et al., 2001).

The extent to which each of these assumptions holds needs further investigation. We have probably underestimated opportunity costs in certain regions of the world where activities such as forestry and petroleum exploration are the dom-

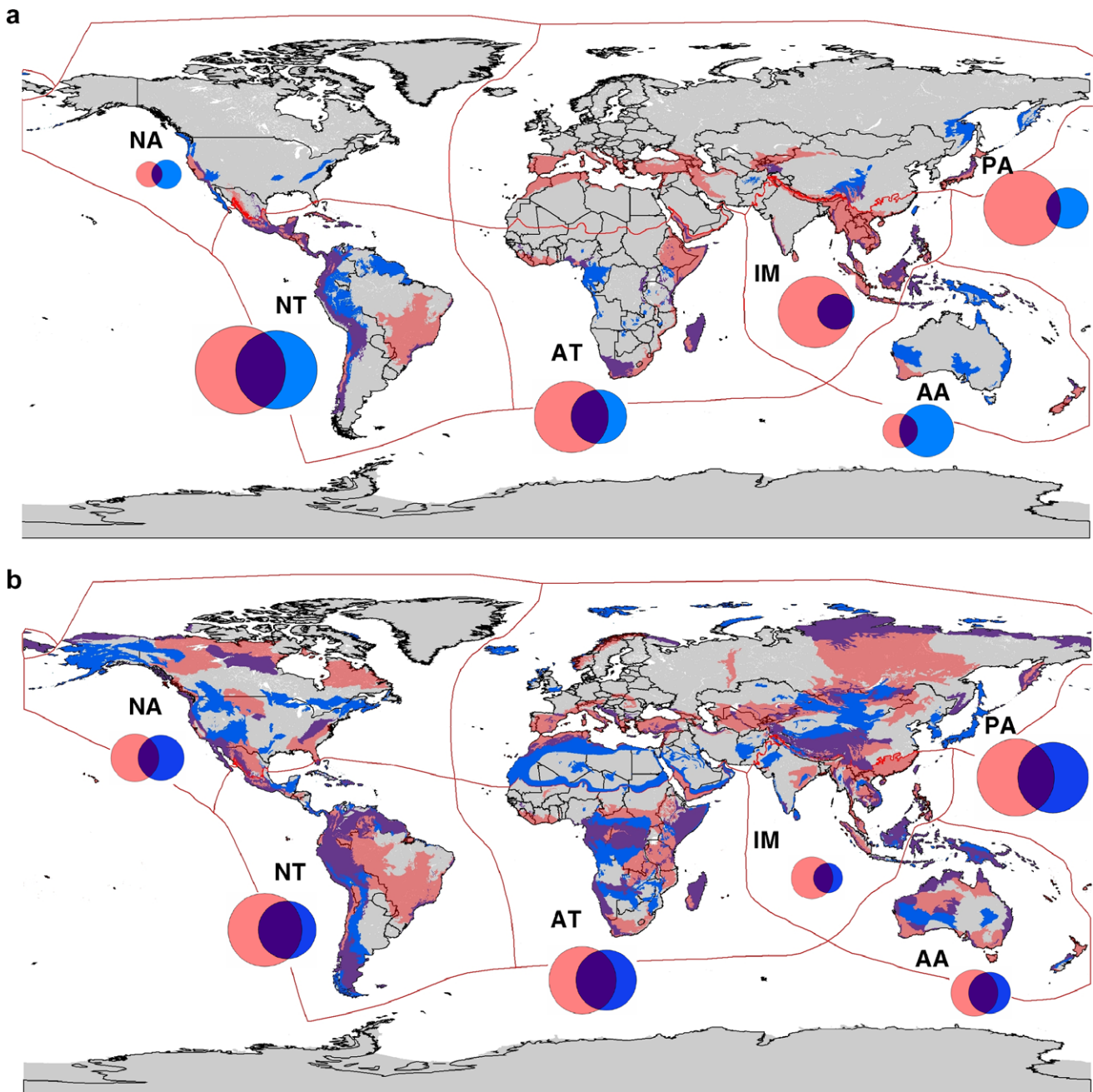


Fig. 4 – Overlap (purple) of the biodiversity hotspots (a; red) or the Global 200 ecoregions (b; red) with priority areas from an analogous cost-effective conservation planning approach (blue) Venn diagram circle sizes are proportional to area and further highlight overlap in six biogeographical realms: NA = Nearctic, NT = Neotropical, AT = Afrotropical, IM = Indo-Malayan, AA = Australasian, PA = Palearctic. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

inant land uses, for example in remote forest areas of the Amazon and Congo basins. On the other hand, we may have overestimated opportunity costs of conservation in extensive grazing systems where native species may coexist with certain livestock stocking rates. For many human-dominated land uses, some native biodiversity can persist at low to moderate levels of intensity (Pykala, 2000; Daily et al., 2001; Putz et al., 2001). A comprehensive analysis would estimate rents derived from all anthropogenic land uses, estimate the degree of compatibility of these land uses with biodiversity conservation, and

integrate these with the probability of conversion to such land uses to arrive at opportunity costs (Naidoo and Adamowicz, 2006). Such an analysis would better reflect the potentially high opportunity costs of conservation at the deforestation frontier in wilderness places such as the Amazon and Congo, and the potentially low opportunity costs of conservation in extensive and sustainably managed grazing systems.

We used global averages for producer prices of crop and livestock products, and considered gross, not net, rents. It would have been preferable to use regional or country-level

producer prices, but for many countries local currency prices appeared inconsistent when converted to US dollars, reflecting either inaccuracies in the price data or the difficulty of using official exchange rates to convert prices to a single currency. Net rents would have entailed obtaining spatially explicit data on production costs of the various crops and livestock groups we considered. These are sure to vary spatially, much as output prices do, in which case net rents may be distributed quite differently in space than gross rents. Unfortunately, spatially explicit data on production costs at the global scale are not yet available, making the use of gross rents the only recourse in modeling opportunity costs of conservation.

The conservation planning unit in our analyses was the ecoregion, and a species was judged conserved if at least one ecoregion in which it occurred was selected by a planning algorithm. Clearly, this is a gross oversimplification; alternative representations of conservation success that may be more realistic might include conserving a certain percentage of a species' range (e.g., [Pressey et al., 2004](#)), or conserving a certain number of site occurrences for each species (e.g., [O'Hanley et al., 2007](#)). In addition, the ecoregion-level resolution of the vertebrate species data set rendered us unable to address issues such as intra-ecoregion heterogeneity in both habitat suitability and economic benefits from agriculture. Finally, we incorporated biological value and conservation cost into our analyses, but did not account for variation in threat or vulnerability to ecoregion habitat ([Wilson et al., 2005](#)). A more sophisticated analysis would address all these issues by conducting analyses at a finer scale of resolution, using information on cost, threat, and biodiversity within a dynamic framework that would identify the sequence of priority investments for conservation ([Costello and Polasky, 2004](#)).

The cost-effective sets of ecoregions produced from our optimizations are meant to be illustrative, and are not alternatives to existing global priority schemes. There are many other values (e.g., strategic, historical, political) that factor into real-world conservation planning that are not accounted for in our stylized examples. In addition, both the Global 200 ecoregions and the biodiversity hotspots pre-date the ecoregion-level species data we use in our cost-effective approaches. Finally, although those species data comprise the most comprehensive dataset on the geographic distribution of terrestrial biodiversity, the vertebrate taxa we considered still comprise only a tiny fraction of all species.

Nevertheless, current global conservation priorities appear to be much less efficient in achieving their conservation goals than they could have been had they included economics in their planning approach. The Global 200 ecoregions could have achieved representation and biodiversity targets at about a quarter of the current opportunity costs. And despite being called a "silver bullet" strategy for biodiversity conservation ([Myers et al., 2000](#)), targets for threatened endemic vertebrates could have been achieved at a tenth the cost of the biodiversity hotspots. These results add an economic twist to a growing literature that calls into question a hotspots paradigm for biodiversity conservation ([Odling-Smee, 2005](#); [Orme et al., 2005](#); [Possingham and Wilson, 2005](#)), and more generally illustrate that any planning process that does not consider economic costs will likely spend more of its limited resources than necessary.

What the cost-effective examples also show is that priorities can change dramatically when the opportunity costs of conservation are explicitly incorporated into conservation planning. Not only are cost-effective areas largely different from existing global conservation priorities, the geographical distribution of these priority sets are also more widely dispersed, reflecting the heterogeneity of costs and flexibility in achieving biodiversity goals. This dispersion of conservation priorities has the added benefit of scattering conservation efforts over a wider range of ecological and biophysical conditions, thereby enhancing the representation of elements of biodiversity that may not be well-represented by taxonomic groups that are used as indicators in planning ([Olson and Dinerstein, 1998](#)).

Our global map of agricultural values and the implications of these opportunity costs for conservation priorities illustrate the influence that costs can exert on the optimal investment portfolios for biodiversity. The counter-intuitive result that we can conserve more endemic species per dollar by ignoring the distribution of species and considering only the distribution of costs is a function of the correlation structure of costs and endemic species across ecoregions ([Ferraro, 2003](#)), and of the efficiency gains that can occur when costs are formally considered in conservation planning. This latter point is supported by results from studies that have formally incorporated opportunity costs of conservation at national ([Ando et al., 1998](#)) and sub-national ([Ferraro, 2003](#)) planning scales, as well as studies that have included management costs at regional ([Moore et al., 2004](#)) and international ([Balmford et al., 2000](#)) scales. A growing body of literature now demonstrates that integrating the spatial distribution of costs into conservation planning can dramatically improve the efficiency with which scarce resources are allocated ([Wilson et al., 2006](#)). Mapping of the costs of conservation should therefore be accorded high priority by those who wish to achieve the greatest bang for the buck in conservation planning.

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Appendix. Mapping gross rents from agriculture

We assume that the annual rental value R_i of a parcel of agricultural land i is equivalent to the sum of its expected annual net revenue flow from agricultural commodities:

$$R_i = \sum_{j=1}^J (P_{ij}Q_{ij} - C_{ij}I_{ij}) \quad (1)$$

P_{ij} and C_{ij} are the prices of outputs and inputs including labor, respectively, Q_{ij} is the quantity of output, and I_{ij} is the quantity of inputs to the agricultural production function, and j indexes the J commodities (crops and/or livestock types) produced in the plot of land i . We were unable to find reliable information on the variation of agricultural production costs across the globe for the crops and livestock groups we considered, therefore we only considered gross agricultural rents G_i in our estimations:

$$G_i = \sum_{j=1}^J P_{ij} Q_{ij} \quad (2)$$

While FAO data includes output (producer) prices at the national level, concerns regarding data quality for some crops and nations led us to construct a global producer price \bar{P}_j for each crop and livestock category. What we therefore estimate is:

$$G_i = \sum_{j=1}^J \bar{P}_j Q_{ij} \quad (3)$$

We constructed a producer price \bar{P}_j that we took to be broadly representative of the prices that most farmers in the world expect to receive. To reduce the effect of annual fluctuations we took the 12-year average (1991–2002) of producer prices paid in the top-5 producing countries, weighted by production quantity (<http://faostat.fao.org>; accessed June 2005). This set of countries typically covered 60–90% of global production for a given commodities.

Crops

We considered 18 globally important major crops and a suite of regionally important minor crops in calculating crop productivity (Leff et al., 2004). For each major crop, our starting point was a global map (at 5' resolution) of potential crop suitability, defined for each grid cell as the fraction of the maximum agro-climatically attainable yield (Fischer et al., 2002). This maximum agro-climatic yield depends on the climatic zone, soil conditions, the level of technical inputs (low, medium, high) into the farming process, the crop- and climatic-specific responses to irrigation, and the possibility of irrigation in a given grid cell. We assumed an intermediate level of inputs for all crops and then used GIS layers of climatic zones and irrigation potential (Fischer et al., 2002) to develop maps of potential crop yield, in tonnes per ha, for each 5' cell of the earth's terrestrial surface.

$$Q_{ij} = a_{ij} R_{ij} + b_{ij} I_{ij} \quad (4)$$

R_{ij} is the rain-fed maximum crop productivity and I_{ij} is the maximum additional productivity by irrigation. a_{ij} and b_{ij} indicate the suitability of the area for rain-fed and irrigation productivities which are dependent on differing temperatures of five broadly defined climatic zones (Fischer et al., 2002). Each grid cell had specific values for R_{ij} and I_{ij} based on soil characteristics. a_{ij} and b_{ij} were coarser level variables based again on climatic zones.

For minor crops we did not have as geographically detailed yield information as for major crops. We therefore adopted the 22 regional divisions for which regionally important crops were defined (Leff et al., 2004), and then calculated actual yields for each of the 25 minor crops based on total produc-

tion and total area under cultivation (<http://faostat.fao.org>; accessed June 2005) for each of these regions.

For each major crop, we multiplied the producer price by the potential crop yield for each grid cell, then, we multiplied this potential rent by the fraction of that cell that is estimated to be actually occupied (ca. mid 1990's) by the crop (Leff et al., 2004). Summing these per-hectare values over all crops resulted in a grid cell value of the gross economic rents of all major crops.

$$c_{ij} = \bar{P}_j Q_{ij} \quad (5)$$

$$C_i = \sum_j c_{ij} d_{ij} \quad (6)$$

c_{ij} is gross rent in \$/ha from crop production at cell i for crop j . d_{ij} is the actual crop distribution for crop j at the land i , and ranges from 0 (no fraction of cell occupied by the crop) to 1 (crop occupies all of cell area). C_i is the total gross rent from crop production at cell i , which results from a weighted average of all crops with d_{ij} as the weights.

For minor crops, we multiplied the producer price by the region-wide average yield of each minor crop in each geographic region of the world (Leff et al., 2004). We then took a weighted (by area occupied) average to get the region-wide per-hectare gross economic rents of minor crops. To assign these values spatially we multiplied the per-hectare rents by the fraction of a grid cell that was occupied by minor crops, using global distribution maps (Leff et al., 2004).

Finally, we summed the gross economic rents of major and minor crops, resulting in a value for each grid cell of the gross economic rents from crops.

Livestock

To map out the gross economic rents associated with livestock, we used recently developed global maps of livestock distributions (Wint and Robinson, 2006). These maps use regression-based methods to estimate the expected density of cattle, sheep, goats, pigs, poultry, and buffalo at 3' resolution across the earth's surface. For each livestock type we used these density estimates and data on the mass of edible meat per animal (since carcass weights vary significantly over geographic space, yet many countries do not report average carcass weights, we divided the world into five broad regions and estimated average edible meat values; <http://faostat.fao.org>; accessed June 2005) to estimate Q_{ij} , the tons of meat produced in each cell:

$$Q_{ij} = p_{ij} w_{ir} \quad (7)$$

p_{ij} is the regression-estimated number of individuals of livestock species j in cell i . w_{ir} is the average meat weight per carcass in region r .

We then constructed a global producer price as for crops (\bar{P}_j) and multiplied this by the meat yield Q_{ij} to estimate l_{ij} , the annual gross economic rents, on a per-hectare basis, of a livestock group.

$$l_{ij} = \bar{P}_j Q_{ij} \quad (8)$$

Note that for simplicity we did not consider products such as hides and milk when calculating economic benefits from livestock production.

Unlike crops, for which we had global estimates of both potential yields and actual distributions, for livestock we only

had regression-based estimates of animal densities. Accordingly, we treated the economic rents associated with each livestock type as potential returns to land, and therefore instead of taking a weighted average of livestock we used the maximum over all types as our measure of the gross potential economic rents from livestock. Finally, we multiplied a cell's potential gross rent from livestock rent by the fraction of a cell that is estimated to be occupied by pastures or rangelands (Foley et al., 2005). This assumes that rearing of livestock occurs only in cells having some fraction of their land as pastures or rangelands.

$$L_i = f_i \text{Max}(l_{ij}) \quad (9)$$

L_i is the total gross rent from livestock production at cell i , and f_i is the fraction of cell i that is occupied by pasture or rangelands distribution.

Combining crops and livestock

Assuming land is put to its best possible use, we took the greater of crop rent and livestock rent and used this to represent the opportunity costs of conservation in each grid cell. Note that this ignores the possibility that a cell could have a mix of cropland and pastures/rangelands; this certainly does occur in reality but we cannot address intra-cell issues with our methodology.

$$G_i = C_i \quad \text{if } C_i \geq L_i \quad (10)$$

$$G_i = L_i \quad \text{if } C_i < L_i$$

Hypothetical conservation planning approaches

Formulation of cost-effective approach:

$$\text{Max} \quad \sum_{i=1}^I y_i \quad (11)$$

$$\text{Subject to} \quad \sum_{i=1}^I x_i m_i \leq B \quad (12)$$

$$x_i \leq 1 \quad (13)$$

where y_i is the number of endemic vertebrate species (fish excluded) found in ecoregion i , $x_i = 1$ if ecoregion i is selected and $x_i = 0$ if not selected, m_i are the opportunity costs of conservation in ecoregion i , and B is the budget available for conservation. Eq. (4) maximizes the number of endemic species, Eq. (5) ensures the opportunity costs of the resulting set of ecoregions is less than the budget, and Eq. (6) ensures that a site can be selected only once. Optimizations were repeated for a range of budgets.

Formulation of endemics-only approach:

$$\text{Max} \quad \sum_{i=1}^I y_i \quad (14)$$

$$\text{Subject to} \quad \sum_{i=1}^I x_i \leq S \quad (15)$$

$$x_i \leq 1 \quad (16)$$

In this problem, opportunity costs of individual ecoregions are ignored, but S represents the maximum number of ecoregions that can be considered in the solution set. This approach is equivalent to ranking ecoregions from highest number of endemics to lowest and selecting down the list until the conservation budget is exhausted (Ferraro, 2003). Optimizations were repeated for a range of S .

Formulation of the costs-minimization approach:

$$\text{Min} \quad \sum_{i=1}^I x_i m_i \quad (17)$$

$$\text{Subject to} \quad \sum_{i=1}^I x_i \leq S \quad (18)$$

$$x_i \leq 1 \quad (19)$$

Here, the number of endemic species is ignored, and the focus is exclusively on minimizing costs for a given number of ecoregions S that can be conserved. This approach is equivalent to ranking ecoregions from lowest cost to highest and selecting down the list until the conservation budget is exhausted (Ferraro, 2003). Optimizations were repeated for a range of S .

Comparing the Global 200 and biodiversity hotspots with analogous cost-effective approaches

G200 and analogous cost-effective approach:

$$\text{Min} \quad \sum_{i=1}^I x_i m_i \quad (20)$$

$$\text{Subject to} \quad \sum_{i=1}^I y_i \geq Y \quad (21)$$

$$a_k \geq p_k A \quad (22)$$

$$x_i \leq 1 \quad (23)$$

Y is the number of endemic species found in the G200 ecoregions. Eq. (15) specifies that the number of ecoregions in biome-realm combination a_k must equal the proportion of ecoregions that actually occur in each biome-realm (p_k) multiplied by the total number of ecoregions in the G200 (A).

Biodiversity hotspots and analogous cost-effective approach:

$$\text{Min} \quad \sum_{i=1}^I x_i m_i \quad (24)$$

$$\text{Subject to} \quad \sum_{i=1}^I t_i \geq T \quad (25)$$

$$x_i \leq 1 \quad (26)$$

This approach captures the same number of threatened endemic vertebrate species as found in hotspots (1274), while minimizing opportunity costs. Constraint (18) specifies that the sum of threatened endemic vertebrates t_i must be no less than the total number of threatened endemic vertebrates T that are found in the biodiversity hotspots.

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