

Bundling ecosystem services in the Panama Canal watershed

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Land cover change in watersheds affects the supply of a number of ecosystem services, including water supply, the production of timber and nontimber forest products, the provision of habitat for forest species, and climate regulation through carbon sequestration. The Panama Canal watershed is currently being reforested to protect the dry-season flows needed for Canal operations. Whether reforestation of the watershed is desirable depends on its impacts on all services. We develop a spatially explicit model to evaluate the implications of reforestation both for water flows and for other services. We find that reforestation does not necessarily increase water supply, but does increase carbon sequestration and timber production.

water-regulation | evapotranspiration | baseflow

There is considerable evidence that land cover change in watersheds affects mean water flows (1–3), extreme flows (4, 5), and water quality (6). In so doing it also impacts a range of other ecosystem services, including timber production, habitat provision, and macroclimatic regulation through carbon sequestration (7–9). In all cases the precise effect of land cover change depends on local environmental conditions and land use. In this paper we consider the effect of the planned reforestation of the Panama Canal watershed on the bundle of ecosystem services it delivers. The reforestation plan is a reaction to the fact that forest cover has declined by over 40% since 1974 (10). At present 55% (1,598 km²) of the Panama Canal watershed is under forest (Fig. 1). Two-thirds of the forested watershed lies in protected areas—most established since 1980. Vegetation in the remaining areas comprises grassland (29%), shrubland (10%), commercial tree plantations (2%), and urban areas (3%). Agriculture accounts for less than 1% of the watershed area. Reforestation is the centerpiece of a 1997 regional land-use plan within the framework of Law 21. The plan aims to achieve a 94% reduction in land under pasture in the watershed by 2025 (11), and is supported by a series of forestry-incentive laws (12). It is expected to yield a number of benefits, the most important of which is an increase in the water flows needed to operate the Panama Canal in the dry season. Because the current expansion of the Canal (expected to be completed in 2014) will substantially increase demands from the watershed, the effect of reforestation on dry-season flows is of some importance. To evaluate the impact of reforestation on water flows and other ecosystem services, we constructed a spatially explicit model of ecosystem service flows (summarized in the final section and described in detail in *SI Text*). We then used this model to project the impact of changes in forest cover on dry-season water flows, timber production, and carbon sequestration across the watershed and to test the efficiency of alternative patterns of reforestation.

We first considered the impact of forest cover change on mean wet- and dry-season water supply. This depends on the balance between runoff, infiltration, and evapotranspiration. If infiltration gains dominate evapotranspiration losses, water flows may increase. If not, they may decrease (13, 14). The net effect accordingly depends on local environmental conditions. We assessed this in a spatially explicit way across the watershed. This extends work on the spatially explicit modeling of ecosystem services (15–17) to include the impact of reforestation on the regulation of seasonal water flows. Elsewhere, it has been shown that drought mitigation

achieved by increasing dry-season baseflow has positive economic value (18). In this case the value of dry-season flows derives from the value of Canal operations.

We next considered the interactions between distinct ecosystem services in the same spatially explicit way. Joint production of different services involves either synergies (more of one implies more of another) (19–21) or trade-offs (more of one implies less of another) (14, 16, 22) between services. In any given watershed, the relation between water supply, timber production, and carbon sequestration depends both on the forest species used and on the forest management regime applied. We evaluated the consequences of reforestation, using both native species and teak (*Tectona grandis*). To determine the impact of a change in forest cover on human well being, we estimated the value of the net effect of the change on all services across the watershed (23). We found that in much of the watershed reforestation will reduce, not increase, dry-season flows under any forest species and any forest management regime. The impact on timber production and carbon sequestration is, however, sensitive to both forest species and management regime used.

Forest Ecosystem Services

The capacity of the Panama Canal is limited by the dry-season water flows required to operate the locks that raise ships the 26 m needed to traverse the Isthmus via Gatun Lake. Rainfall is strongly seasonal (24). Each lockage (*SI Text, section S6*) currently uses ~211,200 m³ of freshwater. Of total annual rainfall in the watershed, 51% is lost to evapotranspiration, 13% is used in hydroelectric generation at the Gatun power plant, 3% is for municipal use, 29% is used for the operation of the locks, and ~4% is spilled through the Gatun spillway for flood control during the rainy season (25). The reliability of low season flows has been around 93% at current lock capacity. That is, flows have been low enough to restrict Canal operations one year in fifteen. An El Niño event in 1997–1998, for example, caused the Panama Canal Authority (ACP) to impose draft restrictions on Canal users for over 4.5 mo, with significant implications for Canal revenue, forgone energy sales from the Gatun hydroelectric plant, and additional dredging costs, as well as economic damages suffered by carriers (26). The Panama Canal expansion includes several measures designed to increase dry-season reliability, including raising the maximum operating level of Gatun Lake by 45 cm, the deepening and widening of navigation channels, and the introduction of water-saving basins for the new locks that will reduce the quantity of freshwater required per lockage. However, total dry-season water demand will still increase. At the same time, most climate change projections indicate a decline in dry-season rainfall (27).

The reforestation plan is based on the proposition that reforestation may have a positive impact on the water flows needed to support water supply for Canal navigation and other uses (28).

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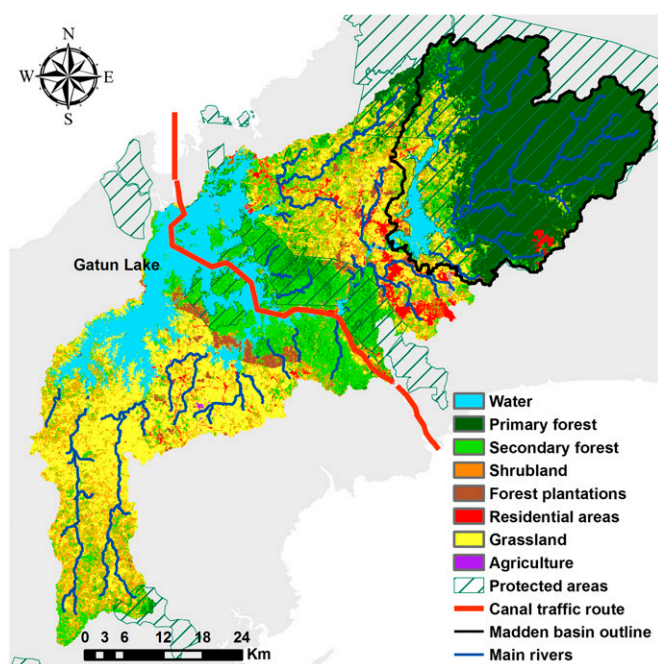


Fig. 1. Land use land cover in the Panama Canal watershed. Source: Authors' representation of the GIS dataset "Forest Cover 2008 by ACP" available at <http://mapserver.stri.si.edu/geonetwork/srv/en/main.home>.

The evidence on the effect of vegetation change on water flow in the tropics is generally mixed. Average annual water yields have generally been shown to be a decreasing function of forest cover (29–31), but the effect on low flows has been variable (32, 33). A paired catchment experiment conducted within a 9-mo period in two small (around 100 ha) subbasins in the Panama Canal watershed, one forested and the other deforested, found that wet-season stream flow was higher in the deforested catchment, but that dry-season stream flow was higher in the forested catchment (34). On the other hand, model-based estimates of the impact of reforestation of pasture land in the larger Chagres and Trinidad catchments found a reduction in runoff of 18% for the wetter to 29% for the drier Trinidad catchment (35).

The net impact of vegetation change on water flows depends on its effects on surface runoff, infiltration, and evapotranspiration (36). Transitions between vegetation types alter all three. Compared with grasslands, forests have a greater leaf area index and canopy roughness, as well as root systems that access deeper water sources (37). Because of this, reforestation potentially results in higher evaporative water losses. On the other hand, diminished surface runoff due to the "roughness" of forests and the impact of the root system on soil micro- and macropore characteristics potentially increases water infiltration and groundwater recharge (38).

The choice of forest species and the type of forest management depends on the benefits forests are expected to yield. The species chosen to regulate water supplies will not necessarily be the same as those chosen for timber production, carbon sequestration, or habitat provision. The ACP is interested in the regulation of water flows to the Panama Canal, but private landholders in the watershed are typically focused on timber products or livestock production. In the absence of markets for water regulation or carbon sequestration, landholders have little incentive to take account of any benefits their management of the land offers to off-site or downstream users. The value of timber and livestock products is largely determined in well-functioning markets. It accrues to landholders and reflects the strength of demand for such commodities. The value of water regulation, on the other hand, stems from the importance

downstream users attach to floods, sedimentation, erosion, or the seasonality of water flows. The value of carbon sequestration similarly reflects global willingness to pay for macroclimatic stabilization. There is some evidence that these values dominate the value of forest products in many cases (39, 40). However, neither value is currently reflected in the market prices of land, timber, or livestock products. They are "external" effects of land use (41, 42).

The efficient management of watersheds requires that the costs and benefits of all relevant ecosystem services be taken into account, whether or not landholders themselves have an incentive to do so. Indeed, current enthusiasm for the development of systems of payments for ecosystem services (43–45) is largely focused on the "co-benefits" of reforestation (7). We applied principles for the optimal management of multiple-use natural resources (46, 47) to test the efficiency of the land cover changes envisaged by the watershed reforestation plan (11), given best estimates of the value of the different ecosystem services. Taking account of precipitation, topography, vegetation, and soil characteristics and the spatial distribution of these characteristics, we modeled the trade-offs and synergies between water flow regulation and other watershed services and used this to evaluate the economic consequences of alternative reforestation options in the Panama Canal watershed.

Results

After calibrating and validating the model (*SI Text, section S2*, and *Tables S1* and *S2*), we found the effect of current forest cover on dry-season water flow (*SI Text, section S1* and *Table S3*) to be positive in the wet Madden basin, increasing flow by 4.7%, but negative in the dry Gatun basin, decreasing flow by 13%. We therefore expect reforestation to have different effects in different parts of the watershed, depending on site-specific variables such as slope, the hydraulic characteristics of the soil, the amount of precipitation during both dry and wet seasons, and the characteristics of the forest species. Each of these variables influences the relationship between runoff and baseflow net of evapotranspiration. Our model results show that only where there are high precipitation rates, flat terrain, and soil types with high potential infiltration is reforestation likely to enhance dry-season flows.

Fig. 2A reports the distribution of existing forest cover and our estimates of the average value of the dry-season water flows secured by that forest cover. Taking a 5% slope and soil type with low infiltration potential as a reference point, we found that natural forest currently has a positive effect on dry-season hydrological flows in areas where precipitation rates are above 325 mm and 2,010 mm for the dry and wet seasons, respectively. Although forest cover increases infiltration, it also increases evapotranspiration, leading, in many parts of the watershed, to greater soil moisture deficiency. This is what determines baseflow.

The marginal value of dry-season flow is the value of the services it supports—in this case the lockages required for ships to transit the Isthmus—multiplied by the marginal impact of a change in flow on the number of lockages possible (*SI Text, section S6*). As a first approximation, we took the value of a lockage to be equal to the toll revenue it generates. This is a lower bound. Although the toll would be expected to reflect the shipping costs saved by using the route, it does not include the social value of emissions avoided by routing vessels through the Canal. The marginal impact of water flow on the number of lockages depends on the volume of water in Gatun Lake relative to the Gatun spillway and the threshold below which draft in the locks is reduced. The marginal value of water flow is zero if the water level is at or above that of the Gatun spillway. It is positive if the water level is below that of the spillway and is increasing in the difference between the actual water level and that of the spillway. Declining water levels affect both the number of transits and toll revenue per transit if water level falls below the lower threshold (because tolls are based on vessel and cargo tonnage).

Baseflow and runoff are not the only source of water flows to Gatun Lake and the Canal in the dry season. In fact, water stored

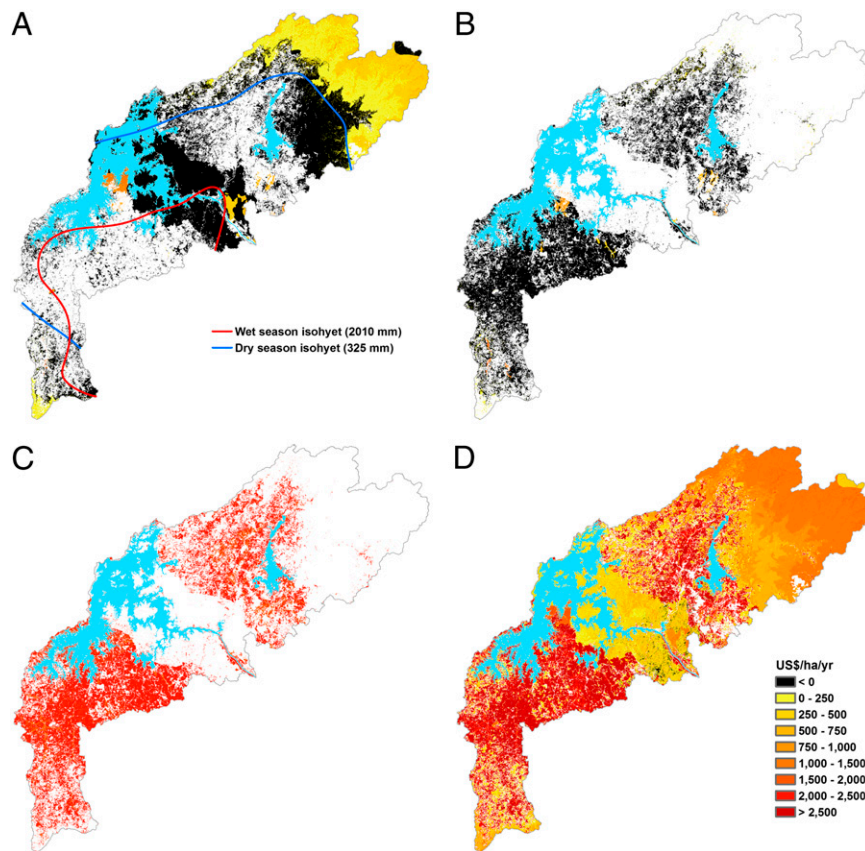


Fig. 2. Estimated steady-state annual average values for the ecosystem services in the Panama Canal watershed. (A) Value to the ACP of dry-season water flows generated by existing forest cover. (B) Value of dry-season water flows generated by conversion of grassland to “natural” forest. (C) Value of dry-season water flows plus timber production generated by conversion of existing grassland to commercial teak plantations and accounting for the opportunity cost of forgone livestock production. (D) Value of dry-season water flows, sequestered carbon, and timber production generated by conversion of existing grassland to teak production, accounting for the opportunity cost of forgone livestock production, and value of conservation of existing forest cover for water flow regulation and carbon sequestration (in D, land cover other than teak plantation and forest is shown in white). Source: Authors’ calculations. The figure shows the marginal value of dry season flows, using a water “price” of 0.44 US\$ m⁻³. The marginal value of sequestered carbon, 4 US\$ t⁻¹ C, derives from ref. 48. The marginal value of forgone livestock production from grassland conversion, 249 US\$ ha⁻¹ y⁻¹, was calculated from production data in ref. 59, assuming a livestock density of one animal per hectare. The marginal value of commercial teak plantation derives from sustainable extraction rates reported in ref. 60 and is based on a stumpage price of 280 US\$ m⁻³ from ref. 61.

in Madden Lake is the main dry-season reserve for Gatun and the Canal. However, we suppose that all water sources are perfect substitutes. This implies that the marginal value of water depends not on its origin, but on the current level of Gatun Lake. Nor are Canal operations the only source of water loss in the dry season. Additional losses are due to seasonal evaporation, municipal water demand, and hydroelectric energy production. Assuming that the reservoirs are refilled by the end of the wet season, we calculate the expected marginal revenue product of dry-season flow to be the expected toll revenue of the additional lockages allowed by a unit of flow at the expected level of precipitation, evaporation, and so on, given land use and land cover in the watershed (*SI Text, section S6*).

In a baseline exercise, we found that the 37% of currently forested area that has a positive impact on dry-season flows (Fig. 2A) provides an average of 37.2 million m³ of seasonal flow, equivalent to 176 lockages. We estimated the marginal revenue generated by an additional cubic meter of flow to be US\$ 0.44 (*SI Text, section S6*). At this value the revenue generated by water flows from this portion of the existing forest cover is US\$ 16.37 million. Because the regional land-use plan calls for a 94% reduction in land under pasture in the watershed by 2025, we then evaluated the consequences of the conversion of grassland to natural forest. The impact on the steady-state value of water flow was found to be negative in almost all areas of the watershed (Fig.

2B). Overall, we found that grassland conversion to natural forest would reduce dry-season flows by 8.4% in the entire watershed. The 4.3% of current grasslands capable of providing a potential water flow benefit if reforested could, at the biological steady state (at mean “climax” vegetation), yield an additional 3.54 million m³ to Canal navigation during the dry season, equivalent to US\$ 1.56 million in revenue to the ACP in 2009 dollars.

Dry-season water flow is not, however, the only ecosystem service provided by the watershed. We therefore considered, in addition, carbon sequestration (providing global benefits) and livestock and timber production (both providing local benefits). Consider, first, the effect of carbon sequestration. As part of the same baseline exercise, we found that in most areas the value of the hydrological losses due to existing natural forest would be compensated by the value of carbon sequestration at a price of 4 US\$·t⁻¹ C (where t denotes a metric ton) (48). For reference, this is above the March 2013 US Regional Greenhouse Gas Initiative auction clearing price (US\$ 2.80) and below the lowest European Spot Market price in the same month (US\$ 4.46). At 4 US\$·t⁻¹ C the average annual net value of current forest cover due to these two services ranges from -99 US\$·ha⁻¹ to 2,555 US\$·ha⁻¹. The spatial distribution of the average net value of existing forest, measured by the value of both dry-season flow and carbon sequestration, is shown in Fig. S14.

The proportion of grassland that would yield positive net benefits in terms of dry-season water flows if converted to natural forest would be only 4.3% (2.4% if the forgone benefits of livestock production are included) (Fig. 2B and Table 1). However, if the value of carbon sequestration is added (at a price of 4 US\$·t⁻¹ C), the area yielding positive net benefits would increase to 96.9% (59.6% if the forgone benefits of livestock production are included) (Fig. S1B and Table 1). We also tested the sensitivity of our findings to the greater range of carbon values commonly used in energy models (49) or observed in existing markets (50) (*SI Text, section S7*). We found that the extent of reforestation yielding positive net benefits ranges from 4.7% grassland conversion at 2 US\$·t⁻¹ C to 97.8% at 6 US\$·t⁻¹ C. A carbon price above 6.70 US\$·t⁻¹ C would justify 100% grassland conversion to natural forest.

Conversion of grassland to natural forest is not the only reforestation option, however. Nor is it necessarily the preferred reforestation option. The Smithsonian Tropical Research Institute's (STRI) Agua Salud project is investigating the consequences for ecosystem service provision of a range of land cover options, including high value timber crops (especially teak). We therefore considered reforestation with teak as the instrument of both carbon sequestration and water flow regulation. Elsewhere carbon sequestration via plantation monocultures has had an adverse effect on runoff and groundwater recharge, soil pH, base saturation, and soil fertility (14). We found that conversion to teak plantations would also reduce overall dry-season flow by 11.1%. In fact it would have a negative impact on dry-season flows in all but 142 ha of the area currently under grassland. It would also have a lower carbon storage capacity compared with natural forest (*SI Text, section S5*). Nevertheless, at 4 US\$·t⁻¹ C, the carbon sequestered by teak plantations would be sufficient to offset the value of the hydrological losses in 40.9% of grasslands (Table 1). Teak is a commercially valuable product, yielding revenue on the order of 2,800 US\$·ha⁻¹·y⁻¹ under sustainable forestry management (*SI Text, section S6*). Combining this with the value of water supply, net of the opportunity cost of forgone livestock production, we found that reforestation of existing grassland in teak would generate gains sufficient to offset the value of the hydrological losses in all areas currently under grassland (Fig. 2C and Table 1). In other words, if we considered only the impact of reforestation on dry-season water flows, we would have to conclude that reforestation under any species was not warranted. If we add the potential benefits offered by carbon sequestration and timber production, however, the position is different (Fig. 2D).

Although we estimated the hydrological parameters for natural forest directly from the hydrograph of a subbasin entirely covered by forest in the upper watershed (*SI Text, section S2*), the parameter values (Table S4) for other land covers were derived from the literature using the Soil Conservation Service (SCS) Curve Number approach to estimate runoff (51). We therefore tested the sensitivity of our results on dry-season flows and the warranted extent of grassland conversion to variation in these values (*SI Text, section S7*). We found predicted dry-season flows to be robust to a wide range of values for the hydrological parameters. Reforestation has negative hydrological impacts over the whole range of parameter values reported in the literature (Fig. S2). There do exist parameter values that reverse the effect of reforestation on dry-season flows,

but these lie outside the range reported in the literature. We did, however, find that the extent of grassland conversion that would be warranted for different bundles of ecosystem services was sensitive to variation in the hydrological parameters (Fig. S3).

The efficiency of grassland conversion within the watershed accordingly depends on the bundle of ecosystem services at issue (52). Our results suggest that the value of sequestered carbon and timber may dominate the value of water regulation in much of the watershed. Because there is uncertainty about our estimates of the marginal value of different ecosystem services, however, we also tested the sensitivity of our findings to variation in the marginal values of the services considered (see *SI Text, section S7* for details). We found that the percentage of grassland it would be efficient to convert to natural forest was sensitive to the marginal value of water, carbon, and meat production (Fig. S4A). The higher the marginal value of water and livestock products was, the lower the proportion of grassland it would be efficient to convert. The higher the marginal value of sequestered carbon was, the higher the proportion of grassland that could be efficiently converted. Given our estimate of the forgone revenue from livestock production and value of dry-season water flows to the ACP, for example, reforestation of all existing grassland for water regulation and carbon sequestration would be viable at a carbon price above 6.7 US\$·t⁻¹ C for natural forest and 10.6 US\$·t⁻¹ C for teak. Moreover, once we included the value of timber production, we found that water flow losses could be offset at significantly lower carbon prices. At the same time we found that the percentage of grassland it would be efficient to convert to production forest under teak was much less sensitive to the marginal value of other ecosystem services (Fig. S4B). Only if the marginal value of water was significantly above that corresponding to the end of the dry season, or if the stumpage value of teak was significantly below the current market value, would it be efficient to convert less than 100% of existing grassland.

Discussion

We have already noted that there is a body of research that seeks to identify ecosystem services at the landscape scale, linked to the development of decision-support tools at that same scale (53). Much of this body of research is spatially explicit and maps ecosystem services to the landscape in question. It also examines trade-offs between services in particular locations (54). Our approach is similarly spatially explicit in its treatment of local ecosystem service flows (although using the modeling architecture described in *SI Text*) and also identifies the physical trade-offs and synergies involved in local ecosystem-service provision. It extends previous work in two respects. First, because we model the regulating services, we focus on intra-annual variability of ecosystem service flows. Second, because we are interested in off-site ecosystem service flows, we pay special attention to the scale of the externalities involved and hence the scale of the decision problem.

The services analyzed include two—timber production and carbon sequestration—that are synergistic (are complements in production), depending on institutional conditions (55) and production technologies (56). They also include one—the regulation of water supply—that trades off against the others (is a substitute in production), depending on environmental conditions. Across much of the Panama Canal watershed, the regulation of dry-season water

Table 1. Percentage of efficient grassland conversion under different bundles of ecosystem services

Conversion to	Water regulation and opportunity cost of land	Water regulation	Water regulation, carbon storage, and opportunity cost of land	Water regulation and carbon storage	Water regulation, timber production, and opportunity cost of land	Water regulation, timber production, carbon storage, and opportunity cost of land
Natural forest	2.4	4.3	59.6	96.9	—	—
Teak	0	0	40.9	73.0	100	100

flows trades off against both timber production and carbon sequestration. Bundling this set of services requires an understanding of both the production functions that generate them and the value they have to different groups of beneficiaries. Under the existing governance system, the negative impact of timber production on water flow regulation and the positive impact of timber production on carbon sequestration are both external to the decisions of plantation owners. However, whereas the negative water flow externality is at least partly local, the positive carbon externality is strictly global. Which services are included in any evaluation depends on the scale at which the problem is posed.

Multiple-ecosystem service flows generally imply the existence of multiple beneficiaries. In the case of the Panama Canal watershed only some of the beneficiaries of the services discussed are located within the watershed. Whereas carbon sequestration is a global public good, and whereas timber and livestock production is largely a local private good, water flow regulation offers a mix of public and private benefits at more than one scale. Although we have taken the Panama Canal Authority as the prime beneficiary of dry-season water flow regulation, and although we have taken the Canal toll revenue as a proxy for the benefits of dry-season water flow regulation, the existence of the Canal confers benefits on a much larger constituency. Like carbon sequestration within the watershed, the emissions saved from passage through the Canal rather than around Cape Horn benefits the global community.

The value of land cover as habitat for species also reflects benefits or costs that may be either local (e.g., pollination, pests and diseases, and nontimber forest products) or global (e.g., conserving the genetic information contained in endangered endemic species, international ecotourism, and pharmaceuticals). It may be possible to estimate the global value of habitat from expenditures by the Global Environment Facility or the Reducing Emissions from Deforestation and Forest Degradation (REDD+) scheme, but we were unable to identify biodiversity values with sufficient confidence to include them in this analysis. However, two points are worth making. First, we can say with certainty that the biodiversity value of conversion of grassland to natural forest would be expected to be significantly higher than the biodiversity value of conversion to teak plantations. Although we are unable to estimate the difference, it is partly what motivates our tests of the sensitivity of forest conversion to the relative value of plantations vs. natural forests. Second, we do not consider nonconvexities in the production of ecosystem services. It has been known for some time that differences in the optimal age of forests managed for timber only or for timber plus habitat may be a source of nonconvexity in the joint production function (46), leading to spatial and temporal specialization (57, 58). Both things might be expected to lead to greater heterogeneity in the optimal structure of forests than we find here.

The main point here is that separate evaluation of jointly produced ecosystem services and the focus on particular spatial or temporal scales can both lead to error. Understanding the spatial distribution of the costs and benefits of jointly produced services is important to the development of effective governance mechanisms and efficient incentive systems. The value of watershed protection is sensitive to demand for different services, and in some important cases markets for watershed protection services are already emerging. However, the spatial externalities of land use in forested watersheds persist. Addressing those externalities requires information both on the interdependence between multiple services and on the distribution of costs.

Methods

The methods used are described in detail in *SI Text*. Here we summarize the approach taken to the modeling of dry-season water flows and other ecosystem services. We adopted a spatially distributed approach to the identification of the processes and functions that underpin distinct ecosystem services, the i th spatial unit (pixel) having a 30×30 -m resolution. To evaluate the effect of land cover change on water flow regulation, we focused on dry-

season flows into Gatun and Madden Lakes. During the dry season, Madden Lake is drained into Gatun and so directly supports Canal navigation. Under the assumptions described in *SI Text, section S4*, we estimated flows due both to surface runoff and to dry-season baseflow, using the equation

$$D^d = \sum_i D_i^d(Z_{ij}) = \sum_i [B_i(G_i(Z_{ij}), E_i^d(Z_{ij}), R_i^d) + Q_i^d(Z_{ij})], \quad [1]$$

where D^d , water discharge into both Madden and Gatun Lakes during the dry season (Fig. S5D), is the sum of the dry-season flows from all spatial units in the Panama Canal watershed. Dry-season discharge is a function of two flows: baseflow, B_i , and surface runoff, Q_i^d . Net dry-season baseflow is modeled as a function of groundwater recharge (Fig. S5C), G_i , dry-season evapotranspiration, E_i^d , and rainfall infiltration over the same period, $(R_i^d - Q_i^d)$. Potential baseflow in the dry season is equivalent to groundwater recharge in the wet season. Vegetation uses available soil moisture. If soil moisture is less than the actual evapotranspiration (i.e., $R_i^d - Q_i^d < E_i^d$), groundwater uptake of wet-season recharge will compensate for the dry-season soil moisture deficiency up to the point where uptake does not exceed recharge. Direct runoff (Fig. S5A) was estimated using the SCS Curve Number approach (Fig. S6) (51). If estimated on a monthly time frame, the direct runoff component in this approach includes monthly baseflow and not just the sum of event-based quick flows. See *SI Text, section S3* for details of groundwater recharge and evapotranspiration estimation and *SI Text, section S2* for details of runoff estimation.

Additional ecosystem services modeled were climate regulation through carbon sequestration and timber and livestock production, with X_1 denoting carbon storage, X_{12} denoting timber production, and X_{13} denoting livestock production. We considered each to be jointly produced as part of a bundle associated with one of three different types of land cover: natural forest, Z_{11} , production forest, Z_{12} , and grassland, Z_{13} . We denote the reference service, the regulation of dry-season water flows from the i th pixel, by $Y_{10} = Y_{10}(D_i^d)$. In addition, we have three carbon-product bundles corresponding to each land cover: natural forest, $Y_{11} = Y_{11}(X_{11}, 0, 0, Z_{11})$, production forest, $Y_{12} = Y_{12}(X_{11}, X_{12}, 0, Z_{12})$, and grassland, $Y_{13} = Y_{13}(X_{11}, 0, X_{13}, Z_{13})$. The impact of change in land cover on carbon stocks in each case was modeled using estimates obtained from local studies (*SI Text, section S5*). We did not separately account for soil carbon stocks because local studies indicate that changes in land cover have little effect on soil carbon (59). However, we did account for carbon stocks in litter accumulation, using ref. 60. Production of timber from teak plantations and livestock products from grassland was modeled using parameter estimates from local studies and assuming sustainable forest management and cattle production (*SI Text, section S6*).

The joint production of dry-season water flows and these three carbon-product bundles was then modeled using a spatially disaggregated implicit production function of the form

$$F_i(Y_{10}, Y_{1j}, Z_{1j}) = 0, \quad [2]$$

where $F_i(\cdot)$ defines, for the i th pixel, the output of a set of services comprising dry-season water flows, Y_{10} , plus the three carbon-product bundles, Y_{1j} , $j = 1, \dots, 3$, and the land covers that generate each bundle. The choice of land cover on each pixel accordingly determines both dry-season flows and the carbon-product bundle supplied by that pixel. Assuming that a single land cover type corresponds to each pixel, the requirements for land cover to be efficient may be obtained from the first-order necessary conditions for maximizing the net benefits yielded by this bundle of services,

$$\pi_i(Y_{10}, Y_{1j}, Z_{1j}, V, W) = V_0 Y_{10} + V_j Y_{1j} - W_j Z_{1j}, \quad [3]$$

with V_0 and V_j being, respectively, the marginal value of the dry-season water flows and a measure of the marginal value of the carbon-product bundle associated with the j th land cover type and W_j being the marginal cost of the j th land cover type. Because the rate of transformation between dry-season water flows and each carbon-product bundle should be equal to the ratio of their marginal values, we used estimates of the marginal value of each service (described in *SI Text, section S6*) to identify the land area for which this condition held for different bundles of services.

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