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Bundling ecosystem services in the Panama Canal watershed

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Abstract

Land cover change in watersheds affects the supply of a number of ecosystem services, including water supply, the production of timber and non-timber 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 other services. We find that reforestation does not necessarily increase water supply but does increase carbon sequestration and timber production.

Key words

Ecosystem services, water flow regulation, carbon sequestration, timber production.

Introduction

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 Km^2) 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. Since 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 supplementary on-line information). 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 run-off, infiltration and evapotranspiration. If infiltration gains dominate evapotranspiration losses, water flows may increase. If not, they may fall (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 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 wellbeing, 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 employed.

Forest ecosystem services in Panama

The capacity of the Panama Canal is limited by the dry-season water flows required to operate the locks that raise ships the 26m needed to traverse the Isthmus via Gatun Lake. Rainfall is strongly seasonal (24). Each lockage (see SI text S6) currently uses approximately 211,200 m^3 of freshwater. Of total annual rainfall in the watershed, 51% is lost to evapotranspiration, 13% in hydroelectric generation at the Gatun power plant, 3% is for municipal use, 29% is used for the operation of the locks, and approximately 4% is spilled through the Gatun spillway for flood control during the rainy season (25). The reliability of low season flows has been around 95% at current lock capacity. The failure of low season flows implies restrictions on Canal operations. An El Niño event in 1997-98, for example, caused the Panama Canal Authority (ACP) to impose draft restrictions on Canal users for over four and a half months, with significant implications for Canal revenue, forgone energy sales from the Gatun hydroelectric plant, 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 45cm, the deepening and widening of navigation channels, and the introduction of water saving basins for the new locks which will reduce the quantity of freshwater required per lockage. But 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). 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-month period in two small (around 100 ha) sub-basins in the Panama Canal watershed, one forested 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 macro-pore 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 macro-climatic stabilization. There is some evidence that these values dominate the value of forest products in many cases (39, 40). However, neither 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

We found the effect of current forest cover on dry-season water flow (see SI Text S1 and Table S1) 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 325mm and 2,010mm for the dry and wet seasons respectively. While 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 (see SI Text 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 the Gatun spillway. It is positive if the water level is below the spillway, and is increasing in the difference between the actual water level and the spillway. Declining water levels affect both the number of transits and toll revenue per transit if water level falls below the lower threshold (since 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 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 (see SI Text 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 m^3 of seasonal flow, equivalent to 176 lockages. We estimated the marginal revenue generated by an additional m^3 of flow to be US$ 0.44 (see SI Text S6). At this value the revenue generated by water flows from this portion of the existing forest cover is US$ 16.37 million. Since 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 m^3 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), 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 (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.S3a.

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 Tab.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.S3b and Tab.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) (see SI Text 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 have 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 to natural forest (see SI text 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 (Tab.1). Teak is a commercially valuable product yielding revenue on the order of 2,800 US$ ha^{-1} yr^{-1} under sustainable forestry management (see SI Text 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 Tab.1). In other words, if we only considered 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 sub-basin entirely covered by forest in the upper watershed (see SI Text S2), the parameter values for other land covers were derived from the literature using the 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 (see SI Text 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.S4). There do exist parameter values that reverse the effect of reforestation on dry-season flows, but these lie outside of 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.S5).

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 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.S6a). The higher the marginal value of water and livestock products, the lower the proportion of grassland it would be efficient to convert. The higher the marginal value of sequestered carbon, 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 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 (Fig.2d). 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.S6b). 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 supplementary on-line information), 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 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. But 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 three services discussed are located within the watershed. While carbon sequestration is a global public good, and while timber and livestock production are largely local private goods, 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 round 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, non-timber forest products) or global (e.g. conserving the genetic information contained in endangered endemic species, international ecotourism, pharmaceuticals). It may be possible to estimate the global value of habitat from expenditures by the Global Environment Facility or the 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 versus natural forests. Second, we do not consider non-convexities 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 non-convexity 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. But 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 the supplementary on-line information. 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 by 30 meter resolution. In order 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 S4, we estimated flows due both to surface runoff and dry-season baseflow using the equation:

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

where D^d, water discharge into both Madden and Gatun lakes during the dry season, 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, 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 then 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 was estimated using the SCS Curve Number approach (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 S3 for details of groundwater recharge and evapotranspiration estimation, and SI Text S2 for details of runoff estimation.

Additional ecosystem services modeled were climate regulation through carbon sequestration, timber and livestock production: X_{i1} denoting carbon storage, X_{i2} denoting timber production, and X_{i3} 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_{i1}, production forest, Z_{i2}, and grassland, Z_{i3}. We denote the reference service, the regulation of dry-season water flows from the i^{th} pixel, by $Y_{i0} = Y_{i0}(D_i^d)$. In addition, we have three carbon-product bundles corresponding to each land cover: natural forest, $Y_{i1} = Y_{i1}\left(X_{i1}, 0, 0, Z_{i1}\right)$, production forest, $Y_{i2} = Y_{i2}\left(X_{i1}, X_{i2}, 0, Z_{i2}\right)$ and grassland, $Y_{i3} = Y_{i3}\left(X_{i1}, 0, X_{i3}, Z_{i3}\right)$. The impact of change in land cover on carbon stocks in each case was modeled using estimates obtained from local studies (see SI Text S5). We did not separately account for soil carbon stocks since 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 (60). Production of timber from teak plantations and livestock products from grassland were modeled using parameter estimates from local studies, and assuming sustainable forest management and cattle production (see SI Text 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:

$$F_i\left(Y_{i0}, Y_{ij}, Z_{ij}\right) = 0 \qquad \textbf{[2]}$$

where $F_i(\cdot)$ defines, for the i^{th} pixel, the output of a set of services comprising dry-season water flows, Y_{i0}, plus the three carbon-product bundles, Y_{ij}, $j = 1,...,3$, 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:

$$\pi_i\left(Y_{i0}, Y_{ij}, Z_{ij}, V, W\right) = V_0 Y_{i0} + V_j Y_{ij} - W_j Z_{ij} \qquad \textbf{[3]}$$

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. Since 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 S6) to identify the land area for which this condition held for different bundles of services.

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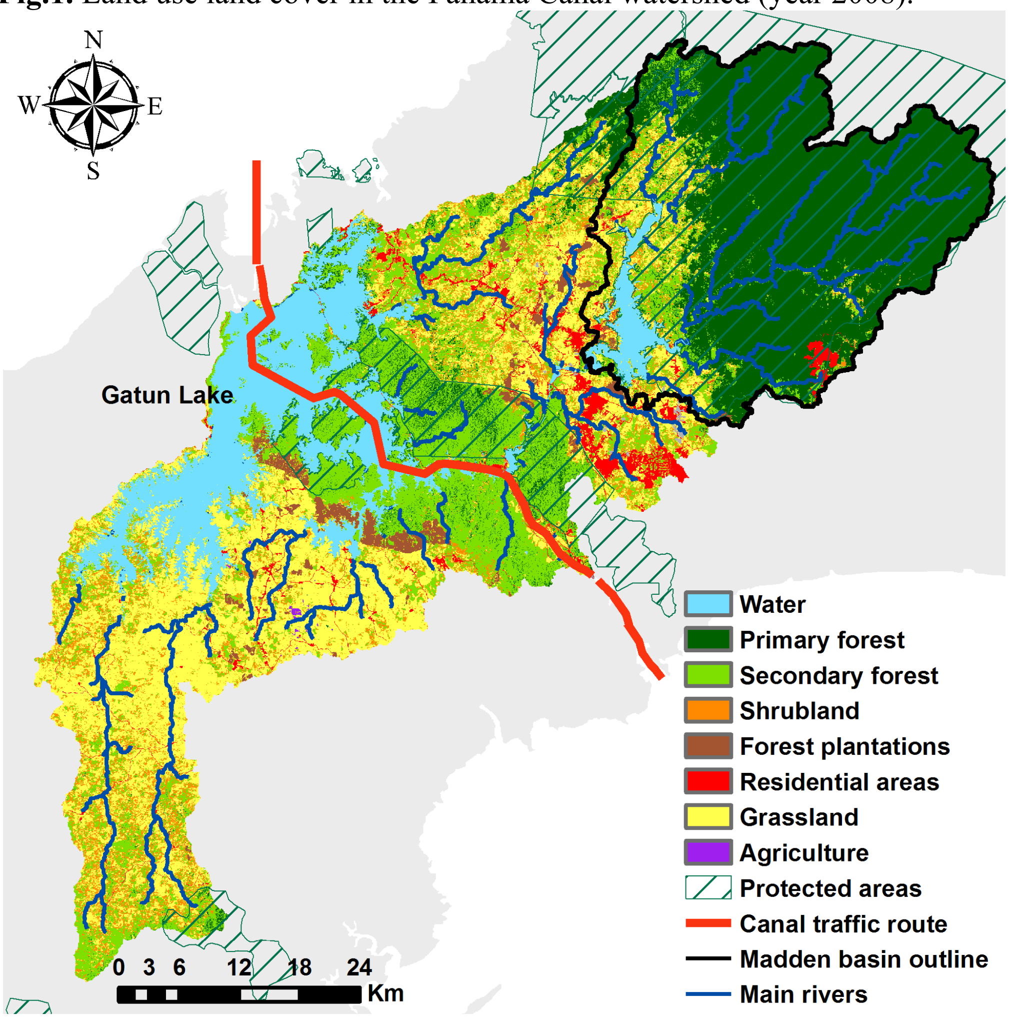
Table 1. Efficient grassland conversion (%) under different bundles of ecosystem services.

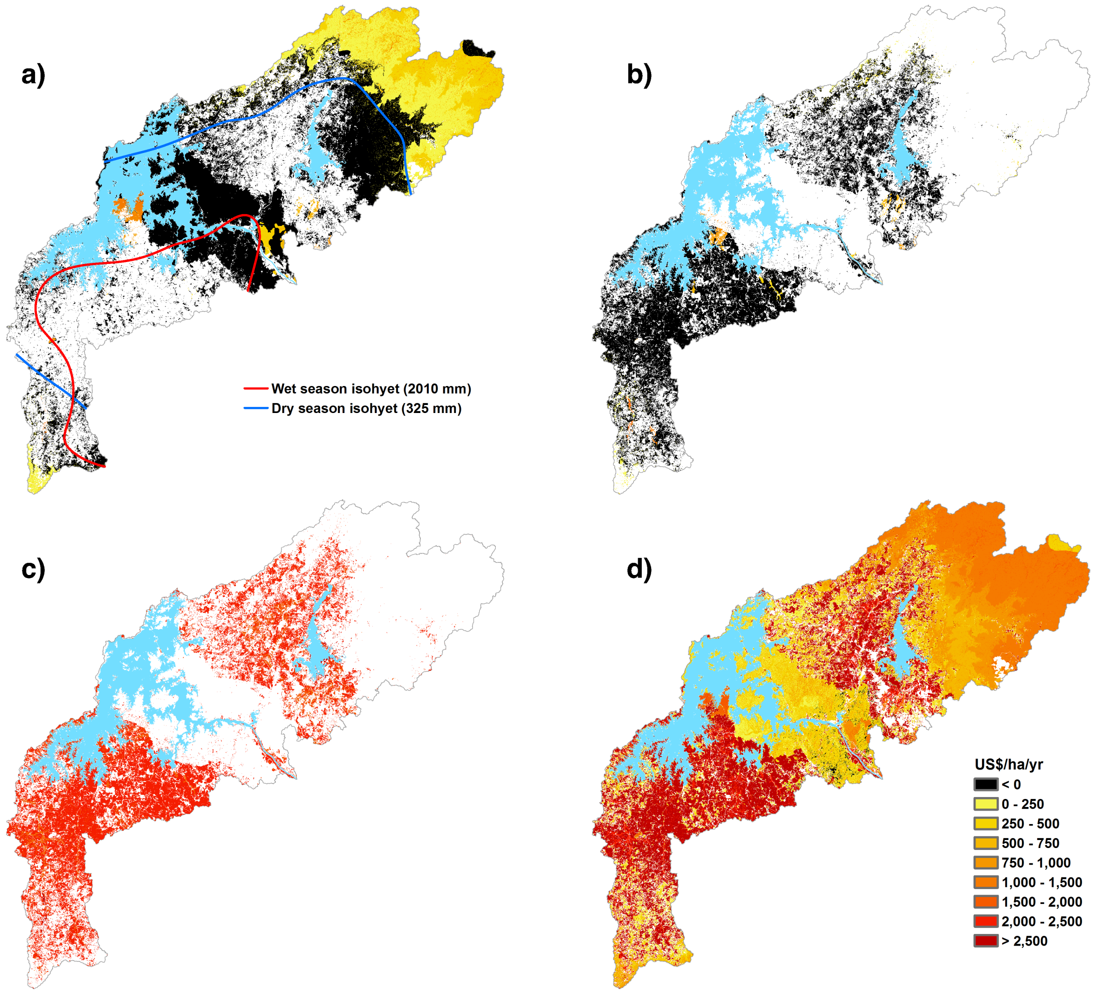
	Water regulation and Opportunity cost of land	Water regulation	Water regulation, Carbon storage and Opportunity cost of land	Water regulation and Carbon storage	Water regulation, Timber production and Opportunity cost of land	Water regulation, Timber production, Carbon storage, and Opportunity cost of land
Natural forest	2.4	4.3	59.6	96.9	-	-
Teak	0	0	40.9	73.0	100	100

Fig.1. Land use land cover in the Panama Canal watershed (year 2008).



Source: Autoridad del Canal de Panamà (ACP).

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 (LULC other than teak plantation and forest are shown in white color).

Source: Authors' calculations. Marginal value of dry-season flows using a value of 0.44 US\$ m^{-3}. Marginal value of sequestered carbon at 4 US\$ t^{-1} C taken from (48). Marginal value of forgone livestock production from grassland conversion using a value of 249 US\$ ha^{-1} yr^{-1} calculated from production data in (61) and assuming livestock density of 1 cattle per hectare. Marginal value of commercial teak plantation derived from sustainable extraction rates reported in (62) and based on stumpage price of 280 US\$ m^{-3} from (63).

SUPPLEMENTARY ON-LINE MATERIAL

SI Text S1: Predicted hydrological impact of current forest cover

In a baseline exercise we estimated the hydrological impact of current forest cover using two conversion scenarios. The first conversion scenario involved deforestation of the remaining area of forest cover. Specifically, we assumed that all remaining forest was converted to grassland. The second conversion scenario involved deforestation only of areas where the impact of forest cover on dry-season flows is currently positive (i.e. only the 37% of the existing forest with the soil, slope and precipitation conditions for a positive effect on total dry-season flow, Fig.2a). The implications of these conversion scenarios for hydrological flows in the Madden and Gatun basins are reported in Tab.S1 for the three cases: (a) current land cover scenario, (b) all forest converted to grassland, (c) only forest in areas of appropriate slope, soil type and precipitation converted to grassland.

Under the first scenario, conversion of remaining forest to grassland would decrease dry-season flow relative to the current state by 4.7% in the Madden basin, but would *increase* it by 13.0% in the Gatun basin. The difference in the impact of deforestation in the two basins is explained by the difference in dry-season rainfall. The lower dry-season rainfall in Gatun is associated with greater soil moisture deficiency. In fact, in most of the Gatun basin we found other land covers to dominate forest in the regulation of water flows. Under the second scenario, conversion only of land satisfying the slope, soil and rainfall conditions associated with positive effects of forest on dry-season flows not surprisingly reduces dry-season water flows in both basins. Specifically, we found that deforestation of beneficial lands reduces dry-season flows by 3.8% in Gatun basin, and by 9% in Madden basin.

SI Text S2: Runoff estimation

Surface runoff is estimated using the SCS Curve Number method (1). At the core of the approach is a phenomenological model of hydrologic abstraction of storm rainfall (2). The method suits our purpose since it directly addresses the relation between land use and runoff. Although the approach was originally developed to address a single storm event, the method has been used in several long-term hydrologic simulation models (3-5). In our case we use a monthly time step and generated a Curve Number index for each pixel, thus generating a spatially distributed model of excess rainfall. Applying the Curve Number method to monthly input data requires a transformation of the original SCS-CN equation (6) which includes measures both of runoff depth arising from rainfall and storage:

$$Q_{it} = \frac{\left(R_{it} - \lambda S_i\right)^2}{R_{it} + \left(1-\lambda\right) S_i}, R_{it} \geq \lambda S_i \qquad \textbf{[s1]}$$

where Q_{it} is the mean surface runoff depth (mm) at the i^{th} spatial unit during month t; R_{it} is mean rainfall depth (mm); S_i is a storage index; and λ is a coefficient expressing the initial abstraction assumption (I_i). This assumption implies that runoff will occur only when $R_{it} \geq I_t = \lambda S_i$ and no runoff takes places if $R_{it} < \lambda S_i$. In the original SCS-CN equation initial abstraction is defined by $\lambda = 0.2$. However, the universality of this value has been questioned (2), and several studies have showed that a λ coefficient locally estimated from field data may improve model fit (3, 7).

The retention or storage parameter varies spatially due to changes in soils, land use, management and slope. We applied the equation:

$$S_i = 25.4\left(\frac{1000}{CN_i} - 10\right) \qquad \textbf{[s2]}$$

where CN_i denotes the Curve Number, a dimensionless index, associated with the i^{th} spatial unit. Theoretically $0 \leq CN \leq 100$, however empirically the CN index varies from a minimum value of 25, generally for land under forest cover, to a maximum of 100 for areas covered by water. In the typical Curve Number application a *CN* value is associated with each hydrological unit, generally small sub-basins within the main watershed. However, since we are interested in modeling spatially explicit dynamics and water infiltration at the lowest possible scale, we express the *CN* index at the spatial unit of each pixel. Curve Numbers are normally assigned using established tables relating specific land covers under standard moisture conditions and average 5% slope, to four different soil groups classified according to their hydrological characteristics (1): high infiltration rate (A); moderate infiltration rates (B); low infiltration rates (C); and very low infiltration rates (D).

We enter the caveat that the data on soil characteristics for the region derive from a coarse map (Fig.S1a) from a dated soil survey (8). A shift in the classification from one hydrological soil group to another implies a considerable change in estimated runoff with implications for groundwater recharge and low flow response. One concern is that even if the soil map was initially accurate, shifts between hydrological soil groups due to long term effects of land use change are possible. Deforestation may have a positive impact on dry-season flows only if soil surface characteristics are maintained sufficiently to allow enough rainfall infiltration. In some cases reduced evapotranspiration associated with forest clearance is associated with increased dry-season flow. However, continued exposure of bare soil to intense rainfall, rapid oxidation of soil organic matter, the gradual disappearance of soil faunal activity, and compaction by livestock may all change soil permeability potential. This can lead to a lower dry-season flow despite the reduced evapotranspiration associated with the removal of forest (9).

Forests in tropical environments are expected to differ substantially from similar land cover at more temperate latitudes for which the *CN* tables have been calibrated. Handbook-defined *CN* values are most successfully estimated for traditional agricultural watersheds while forested watersheds are the least successful (10). We estimated the *CN* index for forest cover from a dataset on runoff and precipitation built for the Candelaria basin within the Panama Canal watershed. The sub-basin of 144 Km^2 upstream the Candelaria gauge station has a uniform hydrological soil group (C) and is almost entirely covered (98.5%) by forest. Following (11) an average retention coefficient for each precipitation event (t) can be estimated from observed river flow, $\bar{Q}_t$, and average rainfall, $\bar{R}_t$, for the upstream basin, both expressed in terms of depth:

$$\bar{S}_t = 5\left[\bar{R}_t + 2\bar{Q}_t - \left(4\bar{Q}_t^2 + 5\bar{R}_t\bar{Q}_t\right)^{1/2}\right] \qquad \textbf{[s3]}$$

Thus, any $\bar{R}_t$ and $\bar{Q}_t$ pair yields a solution for $\bar{S}_t$ and, via eq. [**s1**], a CN_t index. Given as many estimated CN_t indexes as observed t events, it has been shown that the curve number asymptotically approaches a constant value with increasing rainfall (10). It follows that we can solve for the asymptotic curve number (CN_∞) using:

$$CN_t(\bar{R}) = CN_\infty + \left(100 - CN_\infty\right)e^{-h\bar{R}_t} \qquad \textbf{[s4]}$$

where h is an empirical constant. The equation may be fitted by a least-squares procedure for CN_∞ and h. The asymptotic constant value is then used in identifying the average CN index for the basin.

We used daily observations (ACP) for the Candelaria basin in year 2008. The total direct runoff was obtained by separating the river baseflow from the total hydrographs measured on Candelaria gauge and considering only daily precipitation events above 10 mm since the relationship between precipitation and runoff becomes evident only above that threshold. The set of estimated CN values associated with each daily event were then used to fit the asymptotic relationship for CN_∞ by a least-squares procedure. The estimated value was CN_∞=75.25 (P_value=0.000; R^2=0.996; n=111) which is in line with the CN=75 value estimated for the confining sub-basin of the upper Chagres River (12). This has similar land cover conditions to the Candelaria basin, with 96.7% of the area covered by primary forest. The estimated value was then recalibrated at CN=73.42 by minimizing the sum of square differences between observed and predicted runoff. Since the average slope of Candelaria basin is 29.29%, the estimated CN index, has to be converted to the standard 5% slope condition using the relationship developed by Sharpley and Williams (13):

$$CN_{\alpha} = CN + \frac{CN_F - CN}{3}\left(1 - 2e^{-13.86\alpha}\right) \qquad \textbf{[s5]}$$

where CN_{α} is the slope adjusted curve number at average percent slope α, the latter expressed in decimals; CN is the standard handbook curve number at 5% slope and average moisture conditions; and CN_F is the curve number at 5% slope and wet moisture conditions (i.e. at field capacity) which is determined by a defined empirical relationship (14). Thus, from the estimated *CN*=73.42 we obtain a standardize value of *CN*=68.57 at 5% slope and hydrological soil group 'C'. Applying the curve number aligner set of equations (15) we obtained the *CN* index values for forest cover on the remaining hydrological soil groups.

The complete set of estimated *CN* values for natural forest is shown in Tab.S2. We selected values for other land cover classes in the Panama Canal watershed from the most updated handbook values (16). Values for bareland were taken from *CN* for fallow conditions in Puerto Rico; residential areas were assumed to comprise 65% impervious surface; agricultural *CN* numbers were taken from row crop values assuming 'raw' and 'good' management practices; values for grasslands were taken from Puerto Rico; shrubland vegetation was assumed to be equivalent to woods/forest under poor conditions since 'rastrojo' land cover is usually associated with secondary forest in recovery or degraded; values for plantation forests were taken from the *CN* numbers for wood/forest in 'fair' condition.

Applying the coefficients of Tab.S2, we estimated the *CN* index for each pixel using the 2008 land cover map by ACP (Fig.1) and a hydrological soil group map (Fig.S1a) obtained from a soil survey (8). The spatially-distributed *CN* values were then corrected for pixels with slope above the standard 5% value using a digital elevation model (Fig.S1b) and applying the equation proposed by (13). The slope-adjusted *CN* map is shown in Fig.S1c. Following eq. [**s1**] and eq. [**s2**], the *CN* distribution and precipitation maps—the latter obtained from spatial interpolation of long-term averages from 24 ACP meteorological stations—were then used for predicting wet-season runoff making the initial assumption that λ=0.2. The average wet-season monthly precipitation was used in this calculation and the predicted runoff was then multiplied by the number of wet-season months to get the total seasonal runoff.

Predicted runoff during the wet season was compared (Tab.S3a) against long-term (1998-2009) observed values for 6 sub-basins across the watershed. In recent years, land cover has been reasonably constant except for the Ciento sub-basin in which there was a 10% shift from shrubland to grassland between 2003 and 2008. Thus, we compared runoff predictions for this sub-basin against a LULC map for 2003, while for all the others we applied the LULC map for 2008. At the initial value λ=0.2 the models all overestimated runoff against the observed long-term wet-season values (Tab.S3a). This is an expected result since we applied the original event-based Curve Number approach to predict monthly runoff from monthly average rainfall data. In the SCS-CN equation the relationship of runoff (Q) to rainfall (R) is nonlinear, with Q increasing faster with increasing values of R especially at low *CN* values. Thus, using monthly average rainfall would produce a higher runoff than the estimates obtained by adding up all the single storms runoffs in the month. Other authors (6) have overcome this by modifying the original equation using regression analysis and U.S. data. Instead, we scale-up the original event-based approach to a monthly time step by recalibrating the value of the initial abstraction coefficient and assuming near-uniform rainfall-runoff proportions at all amounts, durations, and frequencies of precipitation (6). We re-estimated λ by minimizing the sum of squared residuals between the observed and the predicted monthly runoffs for all 6 sub-basins, to give λ=0.7. The wet-season runoff distribution map after calibration is shown in (Fig.S2a). After calibration, under/over estimation of wet seasonal runoff was reduced to within -4.4% and +9.4% (Tab.S3a). The sum of predicted wet-season runoff for all 6 sub-basins was 2,093 million m^3, a +0.3% over-prediction if compared with the observed value. Thus, even though the margin of error in predicting total runoff from the basin is minimal, prediction errors vary according to the spatial scale considered.

SI Text S3: Groundwater recharge

Groundwater recharge occurs during the wet season. In the dry season most of the relatively small amount of precipitation infiltrating the soil is lost through evapotranspiration. Groundwater recharge at the i^{th} pixel was estimated as a residual of wet-season precipitation, R_i^w, minus seasonal runoff, Q_i^w, and evapotranspiration, E_i^w, using a water balance approach (i.e. $G_i = R_i^w - Q_i^w - E_i^w$). Net dry-season baseflow was modeled as a function of groundwater recharge, G_i, dry season evapotranspiration, E_i^d, and rainfall infiltration over the same period, ($R_i^d - Q_i^d$). Water balance implies that potential baseflow in the dry season is equivalent to the groundwater recharge in the wet season. In vegetated areas this is also influenced by evapotranspiration. Vegetation uses the available soil moisture, which we define as the difference between dry-season rainfall and surface runoff. If this is less then 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 (i.e. we assume there is no groundwater uptake from adjacent pixels). Thus the net baseflow contribution from the i^{th} pixel will be lower than the potential baseflow (i.e. $B_i < G_i$) but not negative:

$$B_i = G_i - \left[E_i^d - \left(R_i^d - Q_i^d \right) \right] \geq 0 \qquad \textbf{[s6]}$$

The term in square brackets represents the soil moisture deficiency that diminishes the potential dry season baseflow, forest and grassland being assumed to have the effects described in SI Text S4. For the i^{th} spatial unit, land cover of type *j* is denoted Z_{ij}, with natural forest, Z_{i1} production forest under teak, Z_{i2}, and grassland, Z_{i3}. If land cover type *j* is forest or teak, given their relatively lower runoff compared to grassland

$(Q_i(Z_{i1})<Q_i(Z_{i2})<Q_i(Z_{i3}))$, it will have a more strongly negative impact on dry-season flow if condition [**s6**] is binding such that:

$$G_i(Z_{i3})+Q_i^d(Z_{i3})>G_i(Z_{i1,i2})-\left[E_i^d(Z_{i1,i2})-\left(R_i^d-Q_i^d(Z_{i1,i2})\right)\right]+Q_i^d(Z_{i1,i2})=Q_i^d(Z_{i1,i2}) \quad [\mathbf{s7}]$$

Otherwise, if condition [**s6**] is not binding or $E_i^d(Z_{i1,i2})<\left(R_i^d-Q_i^d(Z_{i1,i2})\right)$, it follows that:

$$G_i(Z_{i3})+Q_i^d(Z_{i3})\gtrless G_i(Z_{i1,i2})-E_i^d(Z_{i1,i2})+R_i^d \quad [\mathbf{s8}]$$

From [**s8**] it can be seen that an increase in average dry season rainfall R_i^d increases the probability that forests or teak plantations will have a positive hydrological effect, since—under the SCS Curve Number approach we used for estimating runoff—the variation in $Q_i^d(Z_{i3})$ will always be less than the variation in R_i^d. A decrease in dry season rainfall has the opposite effect. Rainfall distribution across the watershed therefore determines the hydrological advantage/disadvantage of forest against alternative land covers. In areas with high precipitation (e.g. the Madden basin), forest/plantation is more likely to have a positive impact on dry-season flow than in the areas with low precipitation (e.g. the Gatun basin).

Evapotranspiration (Fig.S2b) was estimated as actual evapotranspiration (E_i) from an input map of potential evapotranspiration (P_i) provided by Etesa. Following (17), this was obtained by multiplying potential evapotranspiration by a leaf area index coefficient ($k_i = l_i/3$, with $0 \le k_i \le 1$). The leaf area index (l_i) distribution across the basin is derived from the LULC map, assuming $l_i = 3$ for all i under natural forest or teak plantations; $l_i = 2.5$ for shrubland vegetation and $l_i = 2.3$ for grassland. These values fall within a range of published estimates for specific land covers (18, 19). All other LULC categories, i,e. non-vegetated areas or water, were evaluated at their potential evapotranspiration level (i.e. $k_i = 1$). Given observed precipitation during wet season, the estimated groundwater recharge map is shown in Fig.S2c.

Direct runoff was estimated using the SCS Curve Number approach (1). When it is applied to individual rainfall events, direct runoff estimated using this methodology includes both infiltration excess, representing overland flow and any subsurface flow that reaches the basin outlet within the time frame of the storm hydrograph. On a monthly time frame the subsurface component, accounted for in the *CN* estimation as direct runoff, would also embed monthly baseflow rather than just representing the sum of event-based quick flows. Since we are calibrating our model on a monthly time frame using observations on river discharges monthly averages, our direct runoff includes the contribution of monthly precipitation on monthly baseflow. It follows that the wet-season recharge estimated in our model only contributes to dry-season baseflow.

SI Text S4: Assumptions on the hydrological effects of different LULCs

We assume that only forest vegetation and teak have the potential to uptake groundwater under soil moisture deficiency conditions, and that uptake cannot exceed groundwater recharge at the i^{th} pixel, as specified in eq. [**s6**]. In other words, there is no negative contribution to net baseflow by the i^{th} spatial unit. Access to groundwater is limited by advection through capillary rise into the upper soil layers when there is a moisture deficiency. This process is similar to other models describing water movement from the shallow aquifer to the soil profile, and ultimately being lost to the atmosphere by evaporation through plant root uptake (20). Under this constraint, if the soil moisture deficiency potentially exceeds recharge and condition [**s6**] is binding, we assume that evapotranspiration is limited and that natural forest and teak plantation would temporarily adjust their water consumption. For other vegetation categories, such as grassland, potential soil moisture deficiency is assumed to limit evapotranspiration directly without generating any groundwater uptake. In other words, grassland does not have any impact on potential dry season baseflow (G_i) since the deeper wet-season storage is out of the reach of grassland roots. Thus, we assume that its dry-season evapotranspiration is limited by dry-season infiltration alone and the following condition $\left[E_i^d(Z_{i3})-\left(R_i^d-Q_i^d(Z_{i3})\right)\right]=0$ is satisfied. This is consistent with the evidence that most shallow-rooted grasslands dry out during the dry season. For this land cover category and for other vegetated and non-vegetated areas (i.e. shrubland, bareland and residential areas) we assumed that $B_i = G_i$. It follows that eq. [**1**] is then reduced to:

$$D_i^d = G_i + Q_i^d \qquad [\mathbf{s9}]$$

Following eq. [**1**], eq. [**s9**] and under the condition expressed in eq. [**s6**], we predicted the spatial distribution of hydrological discharge during the dry season (Fig.S2d). As for the wet season, our dry season predictions were tested against the observed long-term values (Tab.S3b). The predicted water volume discharge during the dry season was found to range from -4.0% for the Chico basin to +8.5% for the Ciento basin. Overall, the sum of predicted water flows across the 6 sub-basins was 381.78 million m^3, within -0.6% of the observed value.

SI Text S5: Carbon sequestration by natural forest and teak plantation

To calculate the carbon storage potential in natural forest, we started with estimates by Heckadon-Moreno *et al.* (21) who measured aboveground biomass carbon storage in trees from 39 plots scattered across the Panama Canal basin. They reported an average value of 177 t C ha^{-1} for mature primary forest and 100 t C ha^{-1} for secondary forest. Using correlations with aboveground biomass, a well-established methodology for estimating carbon stocks in other pools (22), we augmented these estimates by 20% to account for roots (23-26), by 10% to account for litter (23, 25, 27), and by 2% for understory (28). These adjustments yielded values of 234 t C ha^{-1} and 132 t C ha^{-1} for primary and secondary forest respectively. We did not separately account for soil carbon stocks. Preliminary research results from the Agua Salud project site indicates that changes in land cover have little effect on soil carbon stocks, at least over a period of decades. Although soil carbon stocks under mature natural forest (43.0 ± 7.9 t C ha^{-1}) were found to be significantly higher than the carbon stocks under converted pastures (24.8 ± 2.9 t C ha^{-1}), there was no accumulation of soil carbon stocks observed over the first fifteen years of secondary succession (29).

Plantations are expected to be cut and replanted over a given rotation length. This means that all the carbon accumulated at the end of the rotation cannot be counted as a carbon benefit because some of it will be emitted during harvesting and processing of the timber. It has been proposed (28) that, in such situations, only the average stock of carbon during the rotation period be counted as new carbon sequestered. Therefore, in our model we apply an average value of carbon obtained from local studies. For teak plantations, Dale *et al.* (30) estimate carbon storage following a study by Kraenzel *et al.* (31) reporting carbon content in above- and belowground biomass at four different locations within the Panama Canal basin based on locally derived allometric regression equations for teak. Considering 25-year rotation periods, they assumed that the average carbon stock would increase over time due to incomplete decomposition of slash and as carbon became sequestered in long-term wood products, whose biomass is reported to be around 30% of the biomass that goes into logs—60% of total biomass (32). Incomplete slash decomposition does not represent an increase in soil carbon pool. In fact teak plantations accumulate little to no soil carbon since the slash does not all decompose during a rotation period, but accumulates over time from one rotation to the next (30) thus being classified as carbon storage from litter accumulation. They found that during the first rotation, the average carbon stock was 82 t C ha^{-1}, which increased to 113 t C ha^{-1} at the end of the second rotation, and to 116 t C ha^{-1} at the end of the third rotation. Over how many rotations this pattern of accumulation would continue is unknown and depends on future site preparation (32). We used the Dale *et al.* (30) estimates for 3 rotations in our calculations.

SI Text S6: Joint production of services

We applied a pixel-specific production function yielding four ecosystem services: dry-season water flow, $Y_{i0} = Y_{i0}(D_i^d)$, and three carbon-product bundles corresponding to each land cover type *j* denoted as Z_{ij}: Z_{i1}, natural forest, Z_{i2}, production forest under teak, and Z_{i3}, grassland. The carbon product bundles were, for natural forest,

$Y_{i1} = Y_{i1}\left(X_{i1}, 0, 0, Z_{i1}\right)$, for production forest, $Y_{i2} = Y_{i2}\left(X_{i1}, X_{i2}, 0, Z_{i2}\right)$ and for grassland, $Y_{i3} = Y_{i3}\left(X_{i1}, 0, X_{i3}, Z_{i3}\right)$, X_{i1} denoting carbon storage, X_{i2} denoting timber (teak) production, and X_{i3} denoting livestock production.

The spatially disaggregated implicit production function for these services,

$$F_i\left(Y_{i0}, Y_{ij}, Z_{ij}\right) = 0 \qquad \textbf{[s10]}$$

defines, for the i^{th} pixel, the output of a set of services comprising dry-season water flows, Y_{i0}, plus the three carbon-product bundles, Y_{ij}, $j = 1,...,3$, and the land covers that generate each bundle. The choice of land cover on each pixel 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 optimal land cover may be obtained from the first order necessary conditions for maximizing the net benefits yielded by this bundle of services:

$$\pi_i\left(Y_{i0}, Y_{ij}, Z_{ij}, V, W\right) = V_0 Y_{i0} + V_j Y_{ij} - W_j Z_{ij} \qquad \textbf{[s11]}$$

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.

The first order necessary conditions for optimization of eq. [**s11**] subject to eq. [**s10**] were obtained by setting the partial derivatives of the Lagrangian function

$$L_i = V_0 Y_{i0} + V_j Y_{ij} - W_j Z_{ij} + \mu_i F_i\left(Y_{i0}, Y_{ij}, Z_{ij}\right) \qquad \textbf{[s12]}$$

with respect to the choice variables (land covers) equal to zero. The multiplier, μ_i, is a measure of the marginal social value of a small variation in watershed outputs and inputs.

These conditions include:

$$\begin{aligned}
&\frac{\partial L}{\partial Y_{i0}} = V_0 + \mu_i \frac{\partial F}{\partial Y_{i0}} = 0 \\
&\frac{\partial L}{\partial Y_{ij}} = V_j + \mu_i \frac{\partial F}{\partial Y_{ij}} = 0 \\
&\frac{\partial L}{\partial Z_{ij}} = W_j + \mu_i \frac{\partial F}{\partial Z_{ij}} = 0 \\
&\frac{\partial L}{\partial \mu_i} = F\left(Y_{i0}, Y_{ij}, Z_{ij}\right) = 0
\end{aligned} \qquad [\mathbf{s13}]$$

for all land cover types and associated carbon-product bundles. It follows that for all *j*

$$\frac{V_0}{V_j} = -\frac{\partial Y_{ij}}{\partial Y_{i0}} = \frac{\partial F / \partial Y_{i0}}{\partial F / \partial Y_{ij}} \qquad [\mathbf{s14}]$$

The rate of transformation between ecosystem services is the rate at which one service has to be given up to obtain the other, measured in eq. [**s14**] by $-\partial Y_{ij} / \partial Y_{i0}$. Efficiency in joint production requires that the rate of transformation between any pair of services (the rate at which they are substituted in production) is equal to the ratio between the marginal values of each service. So eq. [**s14**] states that the rate of transformation between dry-season water flow and carbon-product bundle associated with land cover *j* should be equal to the ratio of their marginal values. Eq. [**s13**] also implies that:

$$W_j = V_0 \frac{\partial Y_{i0}}{\partial Z_{ij}} \qquad [\mathbf{s15}]$$

That is, the cost of land cover *j* should be equal to the value of the marginal product of that land cover type with respect to dry-season water flow. The same condition holds for all other ecosystem services.

The marginal value of dry-season flows depends on dry-season water levels in Gatun Lake and the Canal, and is measured in terms of the impact of a unit of flow on the expected transit toll revenue, considering that each lockage uses on average 211,200 m^3 of water (33). One lockage includes both the lifting up of the vessel to the Gatun Lake level and the lowering back to sea level. Since two or more vessels may be included in a chamber for a lockage, lockages and ship transits are not equivalent terms. In 2009 the ACP toll revenue was 1,438 million US$, with 12,641 total lockages, implying an average revenue of 113,776 US$ per lockage.

The marginal impact of dry-season flow on the number of lockages depends on the factors affecting the volume of water in Gatun Lake: precipitation, temperature, infiltration, evapotranspiration, land use and land cover in the watershed. Since there is an upper bound to the volume of usable water in the system (4% of annual precipitation is discharged at the Gatun spillway during the rainy season), hydrological flows above a certain level have no impact on water levels. There is also a lower threshold below which the draft in the locks is reduced, as occurred during the 1982-83 and 1997-98 El Niño droughts. Below this threshold, declining water levels affect both the number of lockages and toll revenue per lockage, since draft restrictions limit access to the Canal to smaller vessels, and tolls increase with the size of the vessel. Above this threshold additional water flow continues to increase the number of lockages possible, but the marginal impact of flow on the number of possible lockages decreases, falling to zero at the point where additional flow has no effect on water levels (when water levels are at the upper bound).

We estimate the marginal revenue product of dry-season water flows from the Panama Canal watershed via a factor (α) that scales the toll revenue as a function of current water levels at the Gatun Lake relative to the draft restriction level and the level at the spillway. Thus, we assume that total toll revenue is a power function of the current water level in Gatun Lake, with the exponent in the power function, α, itself a function of the current water level relative to the draft restriction level and the level at the spillway:

$$\alpha = \left(\frac{U_s - U_t}{U_s} \right)^{\frac{U_t - U_m}{U_t}} \qquad \textbf{[s16]}$$

where U_s is the spillage level; U_m is the draft restriction level; and U_t is the actual water level at Gatun Lake. This functional form implies that the scaling factor is zero at the spillway, unity at the draft restriction level where the draft of the locks is still at its maximum, and above unity at levels further below the point at which draft restriction is first implemented. Thus, given the average water use (211,200 m^3) and revenue (113,776 US$) per lockage, the marginal value (V_0) of a cubic meter of water added at water level U_t is:

$$V_0 = \alpha \frac{113,776}{211,200} \qquad \textbf{[s17]}$$

For the spilling level (26.67m), the draft restriction level (24.84m), and the long-term average dry-season (January-April) level obtained from daily observations for the period 1995-2009 (26.13m), the mean marginal value of dry-season water in terms of toll revenues was 0.44 US$ m^{-3}. The long-term average dry-season water level reflects water storage in both Madden and Gatun lakes at the beginning of the dry season, plus seasonal water evaporation losses net of direct precipitation on lake surface, and the other water uses (municipal, industrial, hydroelectric) during the dry season. Note that we do not account for within-season flow dynamics.

The value of sequestered carbon was based on a review of prices in the voluntary market. Carbon prices vary widely among regions and projects and over time. Forestry projects, in particular those involving afforestation/reforestation, are amongst the highest priced project types with weighted average prices of 6.8 US$ to 8.2 US$ t^{-1} C across 2006 and 2007 (34). The price for avoided deforestation ranges from 2 US$ to 30 US$ with an average value of 4.80 US$ t^{-1} C (35). Others report that a price for stored carbon of 10 US$ t^{-1} C is more realistic, and could increase over the coming decades (36). However, Neef *et al*. (37) consider that the most reliable price remains that established by the BioCarbon Fund of 4 US$ t^{-1} C. We assumed the value of a ton of sequestered carbon to be 4 US$, based on the lower average bound value reported in (37).

The value of livestock production was calculated as follows. Current livestock density in the basin is around 1 animal per ha of grassland (38), which is in line with the data for the rest of the Country. Animals are usually sold at 28-32 months old, and the average weight of a 2-year old animal, depending on strain, lies in the range 449 kg (Brahman) to 411 kg (Criollo) (39). In the exercise reported in this paper, we assumed that animals were turned over at 2-year intervals. Liveweight prices in Panama in 2009 ranged from 1.00-1.32 US$ kg^{-1}. Assuming an average price of 1.16 US$ kg^{-1} and an average weight of 430 kg, we calculated mean livestock revenues to be 499 US$ ha^{-1} over two years, implying that mean forgone livestock revenue from reforestation was 249 US$ ha^{-1} yr^{-1}.

For teak production, we took the average stumpage price of 280 US$ m^{-3} in 2009, as reported for neighboring Costa Rica's timber market (40). Under the REDD+ programme, timber extraction can be added to carbon storage as complements in production, under Sustainable Forest Management (SFM). This implies a periodic yield of wood whilst maintaining the production potential of the forest. Sustainable timber extraction is based on the growth rate of the timber species based on the mean annual increment, which for teak in Central America has been reported at 10 m^3 ha^{-1} yr^{-1} (41). Thus, we applied a mean (undiscounted) net revenue for teak timber production of 2,800 US$ ha^{-1} yr^{-1}. Since we analyze a steady-state solution with fixed rotation age, we do not discount the stream of net revenues. This implies the additional assumption that teak plantations have an equal area in each age class—what is referred to as a 'normal' forest. Note that since we do not factor in variations in rainfall, slope and soil into estimates of biomass yields, the stumpage value is a first approximation only. Using these values in eq. [**s11**], we estimated the extent of the land area for which condition [**s14**] holds given different bundles of services. The results are reported in Fig.2.

SI Text S7: Sensitivity analysis

We estimated *CN* values for natural forests using the hydrograph of a sub-basin entirely covered by forest in the upper watershed (SI text S2) since there are no values reported for tropical forests in the literature. However, the *CN* values used for other land covers were derived from the literature. We therefore tested the sensitivity of our results to variation in *CN* numbers across the range reported in the literature (1, 16). The range reported for 'woodland' for example, is: 55-66 (soil group B), 70-77 (soil group C), 77-83 (soil group D). For teak forest plantation we used values of 60, 73, 79, being the median values within this range. For grassland we used a study from Puerto Rico reported in (16) that yielded estimates of 70, 80, 84 respectively, the range reported in the literature being: 61-79 (soil group B), 74-86 (soil group C), 80-89 (soil group D). We tested the sensitivity of our results on dry season flows to variations of the Curve Number parameters associated with each land cover type. Dry season flow estimates for the two reforestation scenarios (grassland conversion to natural forest and teak) seem robust to variation in *CN* values (Fig.S4), consistently showing a negative hydrological impact except at parameter values well beyond the range reported in the literature.

Note that parameter variation by 10% (0.9 and 1.1 deflection) can be interpreted as a shift between hydrological soil group categories used to define *CN* values for each land cover type (Tab.S2). Thus, dry season flow predictions are sensitive to the quality of information on soil characteristics as much as they are to the reference values of the *CN* table.

We also tested the spatial sensitivity of grassland conversion to the hydrological parameters used in the Curve Number approach given the marginal value associated with different bundles of ecosystem services (Fig.S5). We found higher sensitivity to low *CN* values for both teak and natural forest. Nevertheless, our results referring to the full bundle of ecosystem services (Fig.S5e.1) and to water regulation alone (Fig.S5a.1 and a.2) are not affected by variation in *CN* numbers beyond the range reported in the literature. For grasslands, we found variation in *CN* numbers affected both dry season flow and optimal reforestation. Thus, parameters for grassland should be carefully chosen, possibly following site-specific estimation as for the approach we followed for natural forest (SI Text S2).

Our estimates of the marginal value of the different ecosystem services are first approximations. They are potentially affected by a number of exogenous trends, and they assume steady state values for the carbon-product bundles associated with different land-cover types. We therefore also tested the sensitivity of the proportion of grassland conversion to variation in the price parameters (Fig.S6). Important sources of uncertainty about the marginal value of ecosystem services include the effect of the Panama Canal expansion on aggregate freshwater usage, the effect of current developments in the global market for carbon, and attempts to link carbon, biodiversity conservation and watershed protection in the REDD+ scheme. In addition, differences in the time it takes for various land cover types to converge on the steady state may affect their relative value. We therefore evaluated the sensitivity of our results on grassland conversion into both natural forest and commercial teak plantation to variation in ecosystem services 'prices' relative to our base case: i.e. water at 0.44 US\$ m^{-3}, carbon at 4 US\$ t^{-1} C, the stumpage price of teak at 280 US\$ m^{-3} and livestock production at 249 US\$ ha^{-1}.

We found grassland conversion into natural forest to be highly sensitive to changes in ecosystem service prices (Fig.S6a). In our base case, hydrological flow regulation and carbon sequestration services together justify a 59.6% conversion of grassland area in the watershed after accounting for the opportunity cost of forgone livestock production. Since 95.7% of existing grassland, if converted to natural forest, would produce a negative impact on dry-season hydrological flows in the watershed, an increase in water price would increase this externality, thus reducing the percentage of efficient grassland conversion. The opposite happens with a decrease in water price. The effect of water price variation stabilizes at around 10% conversion of the most "hydrologically-suitable" lands.

We found reforestation to be more sensitive to changes in the value of land for livestock production, stabilizing at around 5% of grasslands. It is most sensitive to variations in carbon price, the optimal extent of reforestation ranging 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 C would justify 100% grassland conversion to natural forest.

When we considered grassland conversion to commercial teak plantations, we found much less sensitivity to changes in the marginal value of ecosystem services (Fig.S6b). The base case results hold for variations in both carbon prices and livestock production. Timber price variations impact the optimal extent of grassland conversion only below 56

US$ m^{-3}. Since commercial plantations are likely to offer few habitat benefits, and since they perform worse than natural forests in respect of both water regulation and carbon sequestration, we might expect the optimal forest structure to involve a greater mix of natural forest and commercial plantations than in our base case. Mixed forest plantations of local species may therefore represent a valid alternative to the monocultural teak forestry even though their stumpage prices are reported to be considerably lower, ranging from 38.8 US$ m^{-3} for *T. amazonia* to 108.6 US$ m^{-3} for *H. alchorneoides* (42).

Our base case results are also stable in the face of variations in the marginal value of water flow regulation. Only at prices above 1.76 US$ m^{-3} is there a significant effect on optimal grassland conversion. While we would expect tolls to capture a significant part of the benefit to shipping companies of routing through the Canal, we note that one study reported an average value of water to shipping companies using the Canal up to 1.16 US$ m^{-3} (43). We have also excluded the social benefits of reduced emissions of CO_2, NO_x and SO_2, which would increase the marginal social value of water regulation above our base case.

We also tested the sensitivity of the percentage of current forest cover yielding positive net benefits from the bundling of two services—hydrological flow regulation and carbon sequestration (Fig.S6c). For our base case, 98.4% of existing forest has a positive value for the two aggregated services. We found that our results were not sensitive to variation in the marginal value of water flow regulation. They were, however, sensitive to a decrease in the price of carbon we used in the base case: 4 US$ t^{-1} C.

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Tab.S1. Estimated hydrological flows for the two main sub-basins of the Panama Canal watershed under different LULC scenarios.

	a. Estimated water flows under current land use and land cover		**b. Variation from current flows assuming all forest is converted to grassland**		**c. Variation from current flows assuming conversion of forest only in suitable slope, soil and rainfall conditions**	
	Gatun (m^3*10^6)	Madden (m^3*10^6)	Gatun (%)	Madden (%)	Gatun (%)	Madden (%)
Wet-season runoff	2,514	1,980	+12.3	+18.5	+1.8	+11.5
Groundwater recharge (wet season)	278	269	-60.2	-79.9	-10.9	-51.0
Dry-season ET	900	482	-10.0	-20.2	-1.1	-12.0
Soil moisture deficit (dry season)	170	112	-95.4	-99.6	-10.4	-32.5
Baseflow (dry season)	108	157	-4.7	-65.8	-11.8	-64.4
Dry-season runoff	96	170	+32.9	+51.5	+5.2	+41.9
Dry-season total flow	***204***	***327***	***+13.0***	***-4.7***	***-3.8***	***-9.0***

Source: Authors' calculations.

Tab.S2. Curve numbers table for the Panama Canal basin

	CN(B)	CN(C)	CN(D)
Water bodies	100	100	100
Bareland	86	91	93
Residential areas and roads	85	90	92
Agriculture	75	83	86
Grassland	70	80	84
Shrubland vegetation	66	77	83
Forest plantation	60	73	79
Natural Forest (primary and secondary)	52	69	75

Source: Authors' calculations of CN values for forest. CN values for other LULCs taken from the literature.

Tab.S3. Estimated hydrological flows for gauged sub-basins in the Panama Canal watershed.

a) Wet-season runoff

Sub-basin	Observed runoff volume (m^3*10^6)	Observed runoff depth (mm)	Under/over prediction at λ=0.2 (%)	Under/over prediction at λ=0.7 (%)
Candelaria	373.72	2599	9.3	-4.4
Los Canones	267.47	1359	22.8	4.1
Ciento	181.31	1589	28.3	9.4
Peluca	209.81	2318	10.0	-4.3
Chico	860.77	2125	15.2	-1.2
El Chorro	193.23	1153	28.7	7.2

b) Dry-season flows

Sub-basin	Observed total flow discharge (m^3*10^6)	Predicted potential baseflow (m^3*10^6)	Predicted net baseflow (m^3*10^6)	Predicted surface runoff (m^3*10^6)	Predicted total flow discharge (m^3*10^6)	Under/over prediction of total flow (%)
Candelaria	73.00	47.31	36.33	40.31	76.64	5.0
Los Canones	32.65	24.13	15.39	16.57	31.96	-2.1
Ciento	23.59	21.15	11.22	14.39	25.61	8.5
Peluca	35.91	24.26	17.35	19.93	37.28	3.8
Chico	195.65	127.30	87.05	100.75	187.80	-4.0
El Chorro	23.12	16.43	8.27	14.23	22.50	-2.7

Source: Authors' calculations. Observed flows from river gauge data by ACP

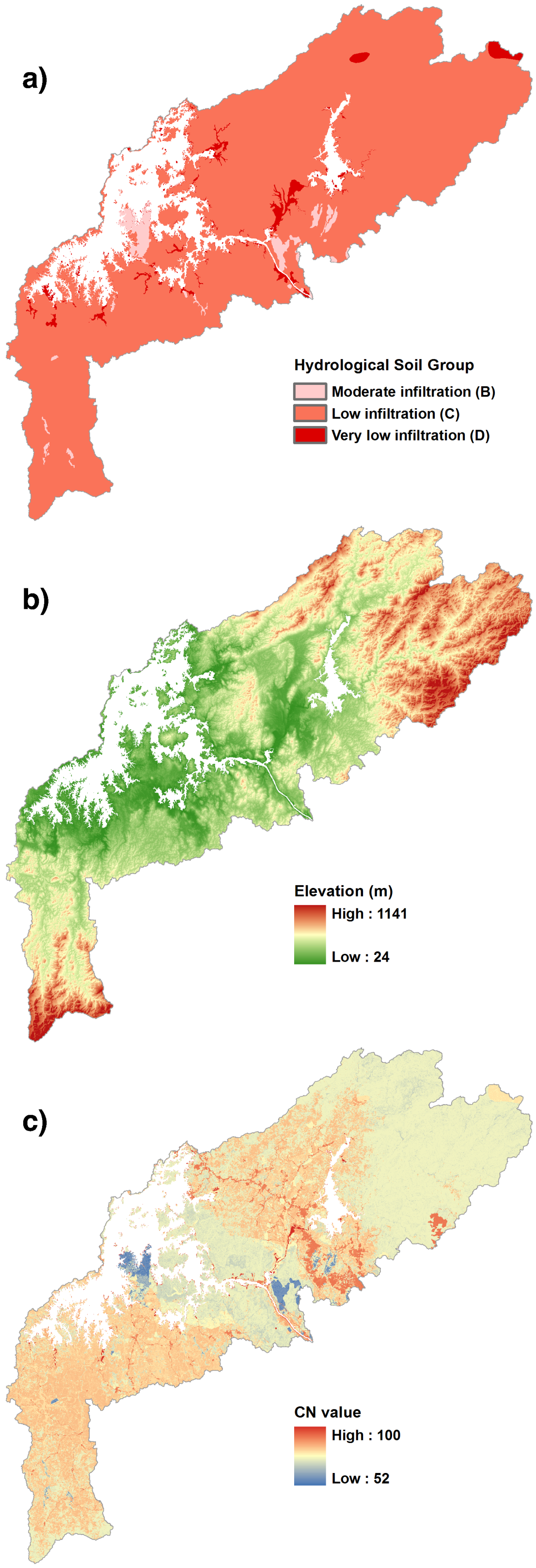
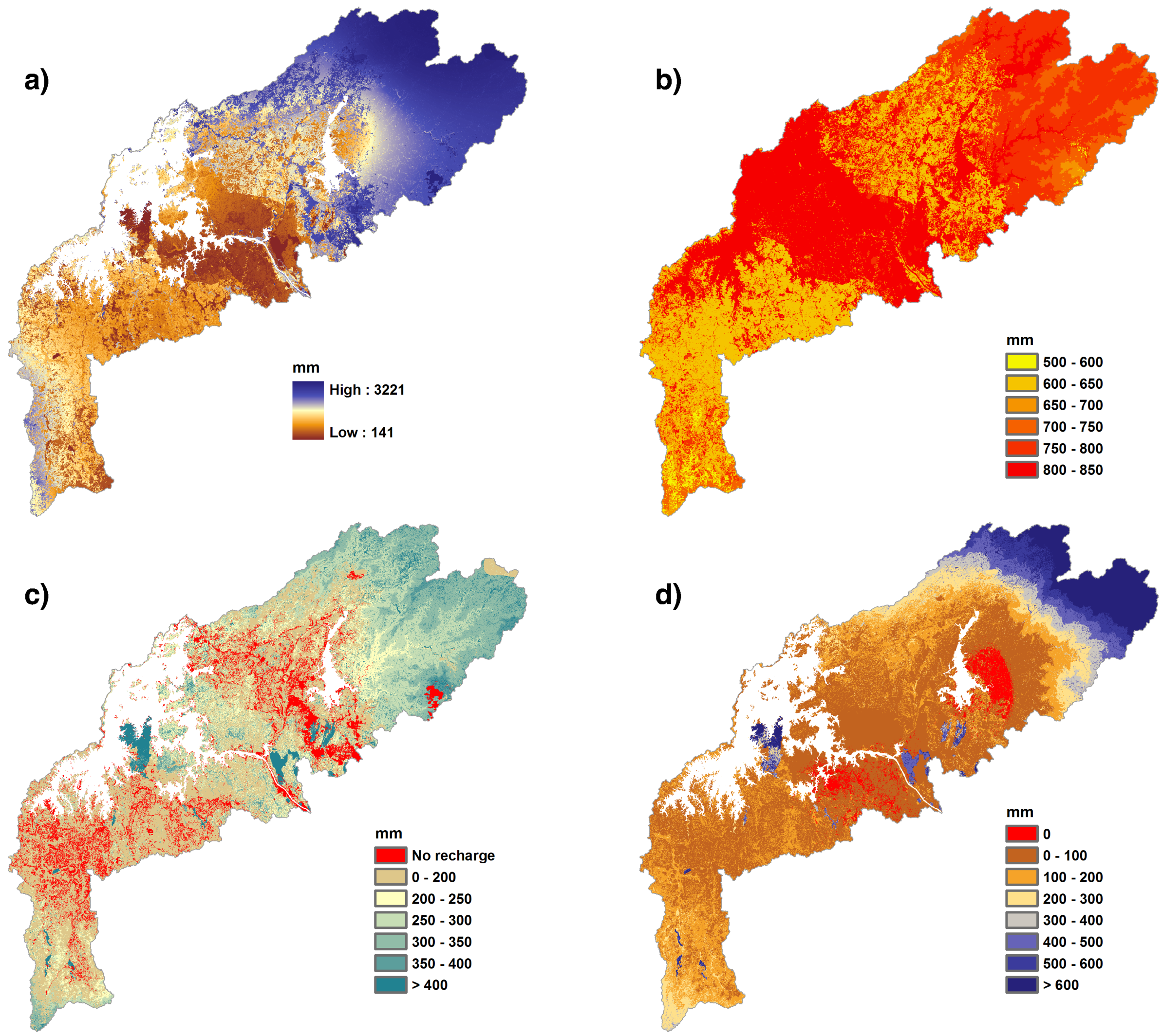


Fig.S1. Estimated spatial distribution of SCS-Curve Number across the Panama Canal watershed.
(a) Spatial distribution of hydrological soil groups. **(b)** Digital elevation model. **(c)** Spatial distribution of slope-adjusted Curve Number indexes derived from Fig.1, S1a, S1b and Tab.S2, and applying the Sharpley & Williams equation to adjust for slope.

Sources: Author's calculations. Fig.S1a estimated from the Catapan soil characteristics map (8). Digital elevation model (30x30m) by ACP. Sharpley & Williams equation obtained from (13).

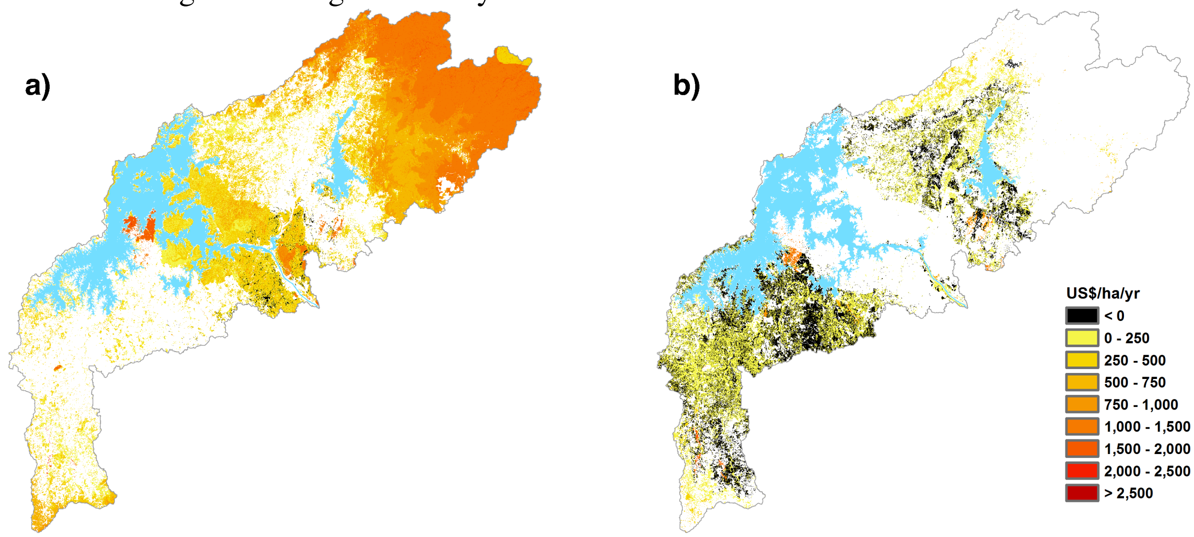
Fig.S2. Estimated spatial distribution of hydrological flows.



(a) Predicted spatial distribution of wet-season runoff obtained from application of the SCS-Curve Number approach, and using the spatially distributed *CN* value (Fig.S1c) as input in equations [s1] and [s2]. **(b)** Wet-season actual evapotranspiration obtained from monthly maps of potential evapotranspiration (PET), and the leaf area coefficient. **(c)** Predicted groundwater recharge calculated trough the water balance approach using wet-season rainfall map, Fig.S2a and S2b. **(d)** Predicted spatial distribution of dry-season hydrological discharge as the sum of surface runoff and groundwater flows.

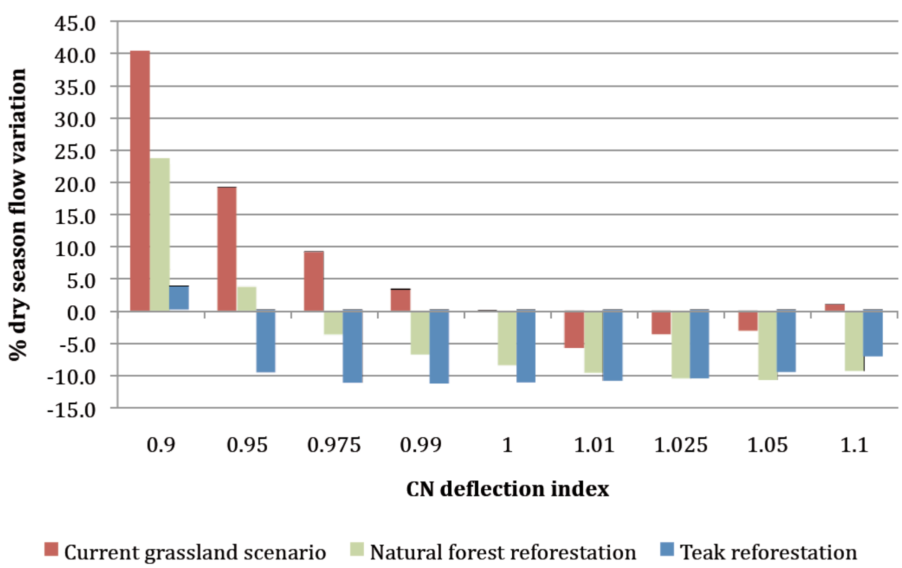
Sources: Author's calculations. Evapotranspiration data from GIS maps of monthly PET provided by ETESA.

Fig.S3. Estimated steady state annual average values for the bundle of dry season flow regulation and carbon storage services generated by natural forest in the Panama Canal watershed.



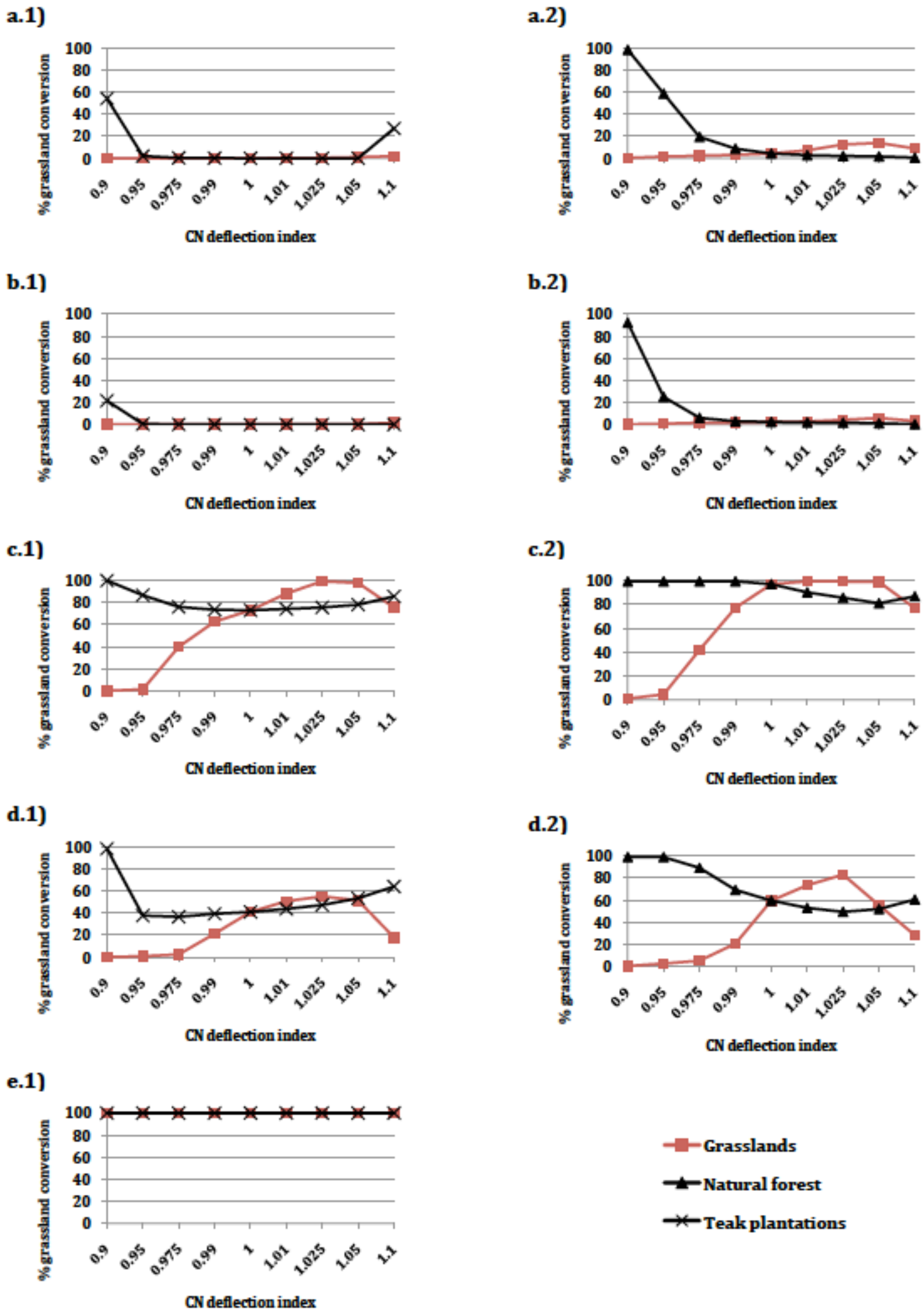
(a) Value of dry-season water flows and sequestered carbon generated by existing forest cover. **(b)** Value of dry-season water flows and sequestered carbon generated by conversion of grassland to 'natural' forest.

Fig.S4. Sensitivity analysis of dry-season flow to *CN* parameter values.



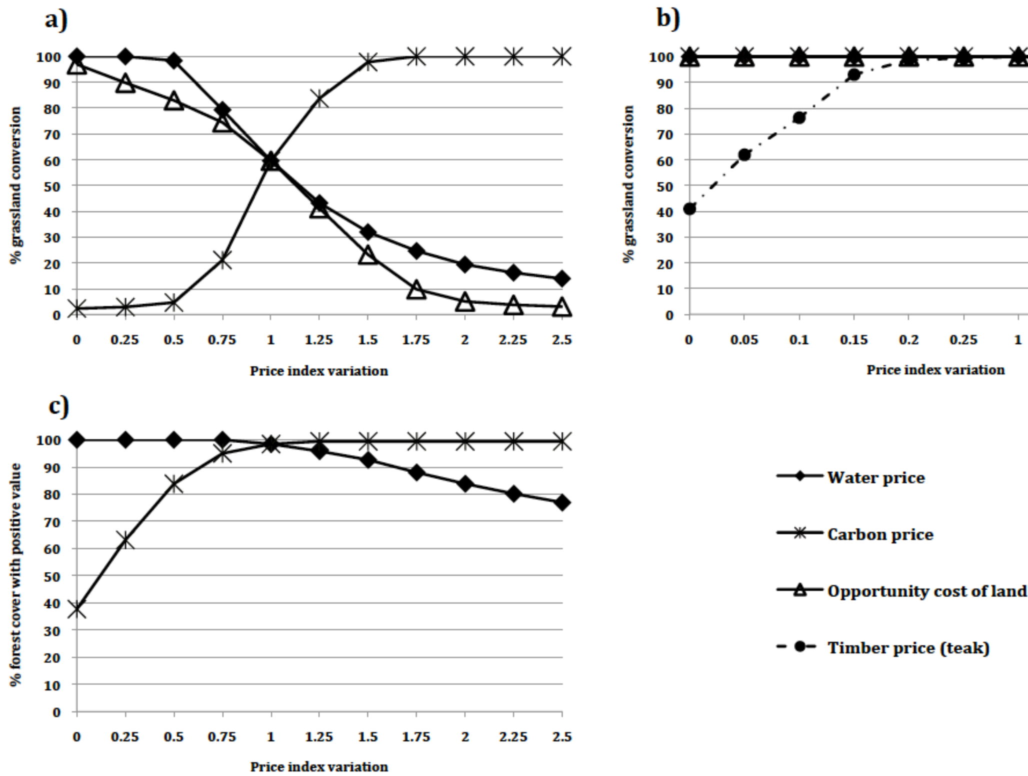
Sensitivity analysis results have been obtained multiplying the *CN* value at each pixel (Fig.S1c) by the deflection index and then summing up the related variation in hydrological flows across all the pixels.

Fig.S5. Sensitivity analysis of grassland conversion to *CN* parameter values.



Grassland conversion to teak plantation for **(a.1)** water regulation; **(b.1)** water regulation and livestock production; **(c.1)** water regulation and carbon sequestration; **(d.1)** water regulation, carbon sequestration and livestock production; **(e.1)** water regulation, carbon sequestration, livestock production and timber. Grassland conversion to natural forest for **(a.2)** water regulation; **(b.2)** water regulation and livestock production; **(c.2)** water regulation and carbon sequestration; **(d.2)** water regulation, carbon sequestration and livestock production.

Fig.S6. Sensitivity analysis to price variations.



(a) Sensitivity analysis of grassland conversion to natural forest. **(b)** Sensitivity analysis of grassland conversion to teak plantations. **(c)** Sensitivity analysis of current forest cover with positive value.