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ONLINE COVER Though the River Nile supports millions of human livelihoods and holds globally important fish biodiversity, it remains under-protected. No basin-wide spatial conservation planning has been attempted to date. Here, [Allan *et al.*](#) put forward a basin-wide conservation prioritization approach. They compare different cross-boundary collaboration scenarios for achieving biodiversity conservation targets, finding that collaborative conservation efforts are crucial for reducing conservation costs—resulting in a 34% savings compared to uncoordinated, business-as-usual scenarios. The researchers also identify priority areas for conservation action. Conservation priority "hotspots" that were consistently selected across all the collaboration scenarios include the Nile Delta in Egypt, Northern Sudan and Southern Egypt, and the East African Great Lakes. The researchers' approach represents a framework for improving conservation at large and complex river systems globally. [CREDIT: J.D. DALLET/AGE FOTOSTOCK/ALAMY STOCK PHOTO]

ENVIRONMENTAL STUDIES

Navigating the complexities of coordinated conservation along the river Nile

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The river Nile flows across 11 African countries, supporting millions of human livelihoods, and holding globally important biodiversity and endemism yet remains underprotected. No basin-wide spatial conservation planning has been attempted to date, and the importance of coordinated conservation planning for the Nile's biodiversity remains unknown. We address these gaps by creating a basin-wide conservation plan for the Nile's freshwater fish. We identify priority areas for conservation action and compare cross-boundary collaboration scenarios for achieving biodiversity conservation targets, accounting for river connectivity. We found that collaborative conservation efforts are crucial for reducing conservation costs, saving 34% of costs compared to an uncoordinated, business-as-usual scenario. While most Nile basin countries benefit from coordinating conservation planning, costs and benefits are unequally distributed. We identify "hot spots" consistently selected as conservation priority areas across all collaboration scenarios, and provide a framework for improving return on conservation investment for large and complex river systems globally.

INTRODUCTION

The river Nile is an iconic feature of the African landscape and the longest river on Earth. It flows 6700 km from the Great Lakes region of Rwanda and Burundi, through Lake Victoria and northward to Egypt and into the Mediterranean Sea. Its basin covers over a 10th of Africa's surface area, and its waters support over 300 million people across 11 countries (1). The Nile is globally important for sustaining freshwater biodiversity and includes multiple areas of outstanding fish richness and endemism (2). This biodiversity is an essential natural, economic and cultural resource, sustaining livelihoods along the whole Nile's extent (3). However, human pressures within the Nile basin are increasingly threatening its supply and quality of freshwater (4, 5). Increases in irrigated lands, human population, urbanization, intensive industrial development, damming, water pollution, and climate change are all leading to further demand for Nile's limited water resources (5–7). As a result, water security along the Nile is currently uncertain for both humans and biodiversity, and only 4.2% of the basin is under protection (Fig. 1) (8). Freshwater ecosystems are some of the most endangered on Earth, experiencing biodiversity declines greater than most terrestrial ecosystems, and key ecosystem services provided to humans by freshwater systems are negatively affected (4, 9). Key threats to freshwater biodiversity in the Nile include overfishing, habitat loss and modification (particularly by excessive water extraction), and pollution leading to eutrophication and hypoxia. All of these threats, when combined with climate change effects and droughts, are expected to intensify in the near future (10, 11). Given the importance of biodiversity conservation in the river Nile, it is alarming that there are currently no basin-wide biodiversity conservation plans in place (12).

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International cross-boundary collaboration can have positive impacts on the outcomes of conservation of biodiversity and ecosystems (13). These impacts include increased efficiency of conservation plans and reduced costs required to achieve defined biodiversity conservation targets (14, 15). However, while there has been substantial focus on the cross-boundary management of river waters as a resource for human use, as far as we are aware, the benefits of coordinated conservation planning have not been quantified for the full extent of the Nile or most other large river systems globally. This highlights a major gap in our ability to prioritize action for river conservation at large scales. Coordinating collaborative actions at a regional and continental scale must include not only biodiversity considerations but also sociopolitical and economic factors, such as cooperation feasibility, equitable distribution of benefits, and multiple competing national priorities (16, 17). Overcoming international politics and national self-interest are regarded as important challenges facing river basins globally (18) and are particularly pertinent for the Nile basin, where conflicts both within and among nations have been a dominant feature over the past 50 years (19).

In the Nile basin, transboundary collaborative efforts, actions, and research focusing on environmental resources have previously centered mostly on water resource use and its equitable sharing (20–22) on agriculture (23) and on the effects of climate change on water availability and agriculture (24). Biodiversity conservation has often been overlooked in collaborative cross-boundary efforts in the Nile basin to date. The current framework for international water resource-related collaboration among nations is structured around the Nile Basin Initiative (NBI). This is a multilateral platform established in 1999, which facilitates all Nile basin countries to deliberate, coordinate decisions, and establish policy on collaboratively conserving and managing water and other resources in the Nile basin. The NBI has assisted member states in preparing over 30 transboundary sustainable development projects amounting to \$6 billion, demonstrating that funds are readily available for multicountry initiatives (25, 26). Moreover, these multicountry initiatives have also leveraged \$10 for every \$1 invested because implementation is easier and cheaper than in unilateral efforts, making them attractive investment options (25, 26). Hence, there is growing interest from

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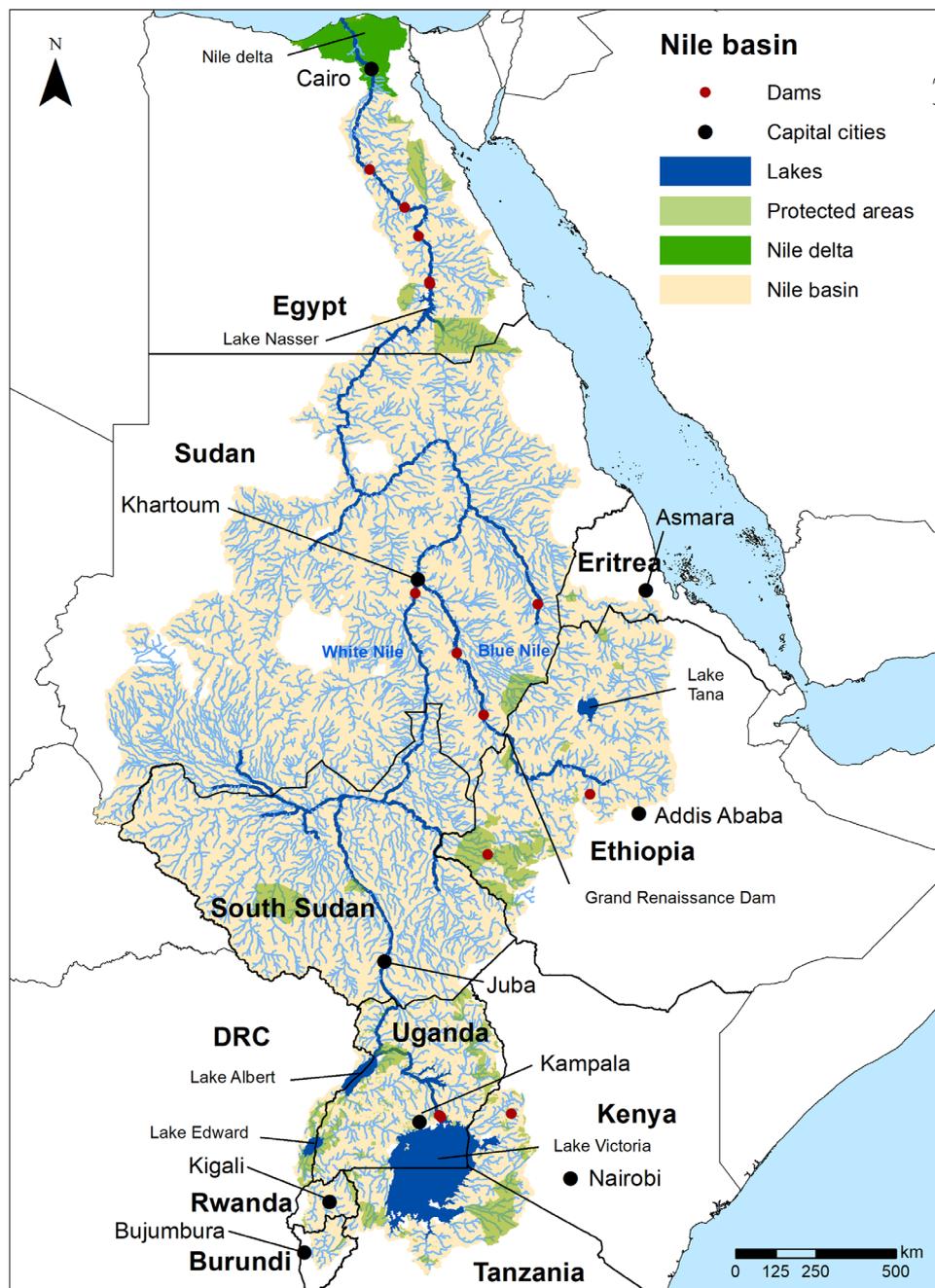


Fig. 1. The Nile River basin, including its 11 countries, capital cities, major lakes, dams, and protected areas. DRC, Democratic Republic of Congo.

development partners including the World Bank, who have contributed 45% of NBI funding since its inception in 1999 (26). In addition, the NBI's goals of energy security, water security, food security, environmental sustainability, climate change, and water governance also directly align with eight of the United Nations Sustainable Development Goals, which have generated over \$7.7 billion of donor funding for Nile basin nations since the year 2000 (27). Funding contributions from member states are limited, but there is interest from major development partners such as the World Bank in funding multilateral and transboundary conservation projects within the Nile basin.

Designing efficient and effective conservation area networks in freshwaters needs to account for the spatial hierarchies of fluvial ecosystems and the necessity to consider different sources of connectivity (28). This is important because disturbances such as pollution, flow alteration, and the spread of introduced species are easily propagated through hydrological networks and seriously affect the biodiversity apparently protected within the reserved area (29). Connectivity is also essential in maintaining some key ecological processes in river-floodplain systems. Longitudinal connectivity allows long- and short-distance migrations of biota through river networks and is important for dispersal, reproduction, and long-term population dynamics of many fish species, for example.

To inform sound and feasible conservation planning in a region as vast and complex as the Nile basin, we must first understand how collaboration potentially affects biodiversity conservation priorities. Here, we create a conservation prioritization and plan for the river Nile and its entire basin and examine the role of collaboration among countries in protecting the Nile's freshwater biodiversity. Using a modified version of the spatial prioritization software Marxan that accounts for river connectivity (30) and the probability of risk to biodiversity (31), we identified the highest-priority Nile River subcatchments to achieve representative freshwater fish conservation in the Nile region while minimizing threats caused by human impact and the cost of conservation actions. We obtained species distribution data for 331 freshwater fish species created by International Union for the Conservation of Nature (IUCN) at the subcatchment resolution (fig. S1) (10, 11). We refined and used the biodiversity-human impact metric (BHM) developed by Kark *et al.* (15) as a surrogate for the cost of conservation action in each subcatchment planning unit (fig. S2). The BHM combines population density and a modified version of land acquisition and management costs, using gridded datasets of population density and gross domestic product (GDP; Materials and Methods). The BHM is a compromise between minimizing land acquisition and management costs and major threats to biodiversity (related to human population density) and proxies for the cost of conservation action in a given subcatchment (15). The quantitative biodiversity conservation targets were set at a minimum of 17% of the geographic range size of the 331 freshwater fish (in line with Target 11 in the Convention on Biological Diversity's 2020 Strategic Plan) while minimizing the cost (BHM) of doing so, maintaining connectivity and ensuring that priority subcatchments identified have a low probability of containing threats to biodiversity (5, 31).

We compared the outcomes of several key collaboration scenarios among Nile basin countries (Table 1). These scenarios ranged from a full collaboration scenario, where all Nile basin countries act together, to a partial collaboration scenario, where some countries within the basin coordinate conservation actions, to a no collaboration, business-as-usual scenario, where countries act individually when planning for the conservation of the Nile's freshwater biodiversity. To determine a realistic partial collaboration scenario, we incorporated the complexities of conflict and collaboration into conservation planning for the Nile basin using the framework developed by Levin *et al.* (16), in combination with a detailed understanding and discussion of the current politics and historical legacies of the Nile basin. This framework allows us to quantify the strength of potential collaboration among countries by examining existing socioeconomic and political links between countries (Fig. 2 and tables S1 and S2). We then analyzed how countries in the Nile would benefit under each of the different collaboration scenarios. We refer to conservation benefits as the avoided conservation costs measured by the BHM and area required for conservation (15, 16).

RESULTS

We found that fully coordinated conservation planning is crucial for the Nile basin's biodiversity as it delivers a substantially less costly conservation outcome than planning for individual African countries without coordination (Table 2). When each of the Nile basin countries acts independently (no collaboration scenario), the total estimated cost of conservation action in the priority subcatchments is

Table 1. The collaboration scenarios among Nile basin countries examined in this study.

Scenarios	Actors
No collaboration scenario	All countries act individually (current situation; business as usual)
Partial collaboration scenario	Egypt and Ethiopia collaborate, the East African community collaborates (Kenya, Tanzania, Uganda, Burundi, and Rwanda), and the remaining countries act individually (Sudan, South Sudan, Eritrea, and DRC)
Full collaboration scenario	Full between-country collaboration across the whole Nile basin

34% more costly than the fully coordinated basin plan that achieves the same biodiversity targets (\$334.4 million and \$249.5 million, respectively, as measured by the BHM). The subcatchments identified in the full collaboration scenario are also preferable for conservation investment to those identified in the no collaboration scenario, having lower threat levels (cumulative biodiversity threat scores of 235.5 for the full collaboration and 259.5 for the no collaboration scenario), and support a smaller human population (16 million people for the full collaboration and 25 million people for the no collaboration scenario). We also found that 108 subcatchments were selected as conservation priorities (in the Marxan best solutions; see Materials and Methods) for both the full and no collaboration scenarios, amounting to 26 and 28% of the total selected subcatchments for each of those scenarios, respectively (Fig. 3). Conservation priority "hot spots" that were consistently selected across all the collaboration scenarios were evident in several subcatchments, including the Nile delta in Egypt, northern Sudan, and southern Egypt and the East African Great Lakes (Fig. 4). Beyond this, there was considerable variation in the spatial location of priority subcatchments across the Nile basin.

Partial collaboration, where some countries act together and others act separately, can sometimes be more practical than full coordination. However, we found that, for the Nile, partial collaboration could also be more costly than full collaboration. While the partial collaboration scenario was substantially less expensive compared with the business-as-usual, uncoordinated scenario, we found that the partially coordinated conservation plan was 6.4% more costly than the fully coordinated plan (by \$16 million as measured by the BHM). This is important because it highlights that countries collaborating bilaterally or in small groups can potentially make a substantial difference to the overall cost of conservation in the Nile basin. We found that, when the East African community alone coordinates its conservation planning and Egypt and Ethiopia collaborate bilaterally, the cost of achieving conservation targets decreases to 21% below the cost of an uncoordinated plan for the basin (a \$68.9 million decrease as measured by the BHM). The greatest cost efficiencies depend on the East African community collaborating with Kenya in particular, which results in a 16% cost savings on an uncoordinated plan (\$55 million as measured by the BHM). This amounts to 80% of the total cost savings of the partially coordinated conservation scenario. When Tanzania and, to a lesser extent, South Sudan

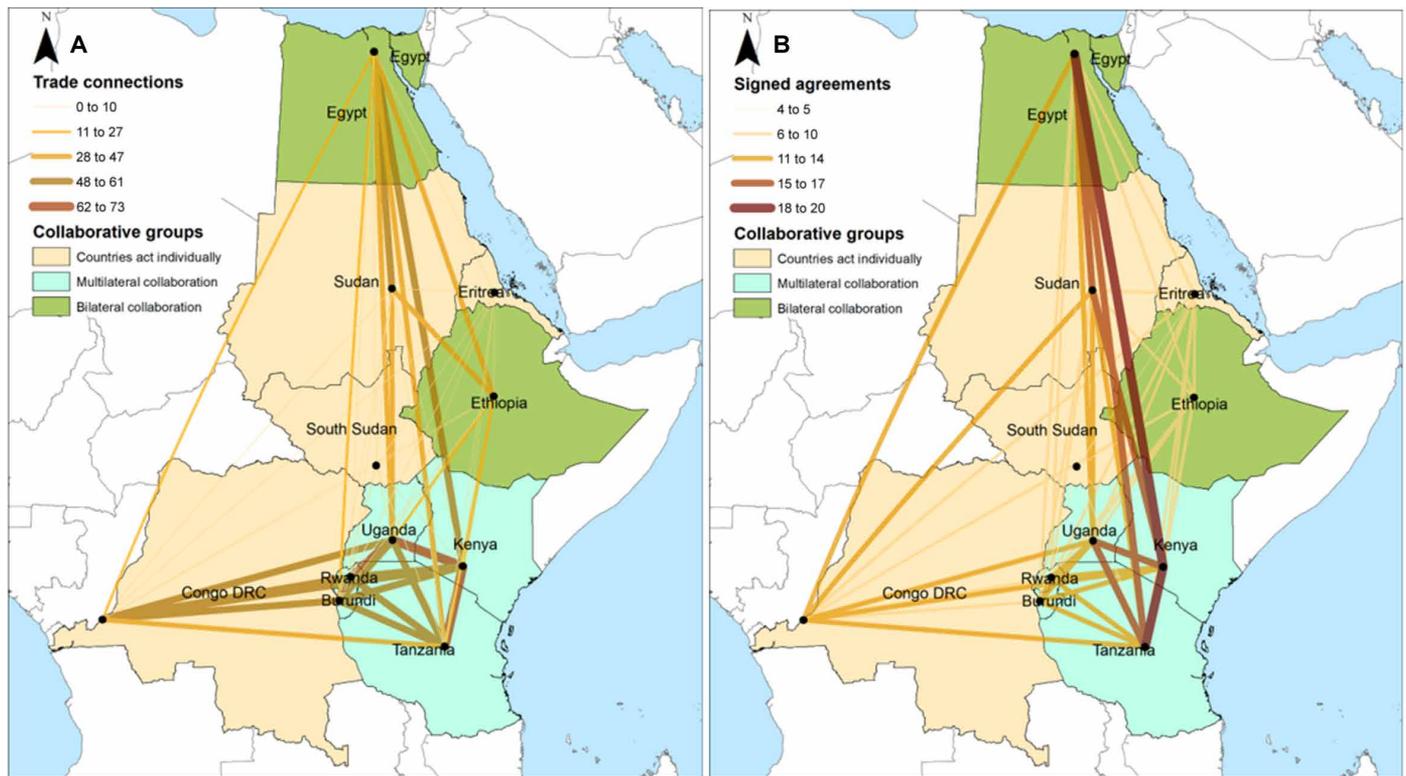


Fig. 2. Network of economic and political links between each pair of Nile basin countries and collaborative groups in the partial collaboration scenario. Between-country connections depicted as lines linking countries. Line width and color represent the strength of the link. (A) The median rank of all variables used to calculate trade connections between countries. (B) The number of shared international environmental agreements.

collaborate with the rest of the Nile basin, conservation costs also decrease. It is possible to meet the conservation targets for a much lower cost in these two countries than in other Nile basin countries such as Kenya, Sudan, or Ethiopia.

We find that countries along the river Nile do not benefit equally from coordinating conservation actions for the river, with some countries benefitting more than others do by collaborating and some having more to lose by not collaborating. Many countries, including Kenya, Burundi, DRC, Eritrea, and South Sudan, would have to pay very little of the total conservation costs of a fully coordinated basin-wide conservation plan, assuming that countries only pay for conservation actions within their boundaries (Table 3). This highlights a key trade-off between the equitable sharing of conservation costs and reduced overall conservation costs through collaboration. For example, when Kenya collaborates with the East African Community countries rather than acting individually, it can save 85% of its conservation costs, but Uganda's proportion of the total costs increases by 7%. However, the overall cost for the East African countries halves (56% decrease; savings of \$55 million as measured by the BHM) when costly subcatchments in Kenya are avoided, suggesting that collaboration could be an attractive scenario whether there is a benefit-sharing platform to balance inequitable distributions of costs. Similarly, Egypt has the highest conservation costs of any country in the Nile basin region regardless of whether it collaborates or not. Moreover, Egypt's proportion of the total costs increases from 58% when it acts alone to 73 and 76% when it partially or fully collaborates, respectively (although the absolute costs for Egypt decrease within the collaboration scenarios). Egypt would need to pay

an inequitable three-quarters of the conservation costs for the entire Nile basin in a fully coordinated scenario, again highlighting the need for a benefit-sharing platform. Nonetheless, as Egypt is the most vulnerable country to be negatively affected by unilateral actions of upstream countries, Egypt has been also found to benefit significantly from collaboration scenarios on the shared use of the Nile's waters (32).

DISCUSSION

International collaboration is acknowledged as key if Nile basin countries aim to conserve important water resources and meet ambitious water security targets such as the "Africa Water Vision" (33) and to achieve national and regional development plans. We have established that international collaboration can play a substantial role in the conservation of African freshwater biodiversity, a resource of global importance on which hundreds of millions of people depend for their livelihoods (1, 3). Whether Nile basin countries coordinate their conservation priorities, even just bilaterally or in subgroups, the Nile's freshwater biodiversity can be conserved more efficiently and for a substantially lower cost than when countries act alone. This is especially important in resource-limited regions, especially for Africa, where biodiversity conservation is just one of many sustainable development challenges. Furthermore, when countries coordinate their actions, conservation affects fewer people and can avoid areas of high biodiversity threat while achieving the same targets of species coverage and representation. This is beneficial since both high levels of biodiversity threats and higher human populations are

Table 2. Total cost (BHM in millions of U.S. dollars), cost as a percentage increase above that of the full collaboration scenario, area (in km²), human population, and cumulative biodiversity threat score of subcatchments selected in the Marxan “best solution” (see Materials and Methods).

Collaboration scenario	Cost (BHM in millions of U.S. dollars)	Cost as % increase above full collaboration	Human population	Cumulative biodiversity threat score	Area (km ²)
No collaboration	334.4	34.0	24,816,395	259.5	328,950.0
Partial collaboration	265.5	6.4	19,943,873	255.7	294,434.0
Full collaboration	249.5	0.0	16,041,420	235.5	260,134.0

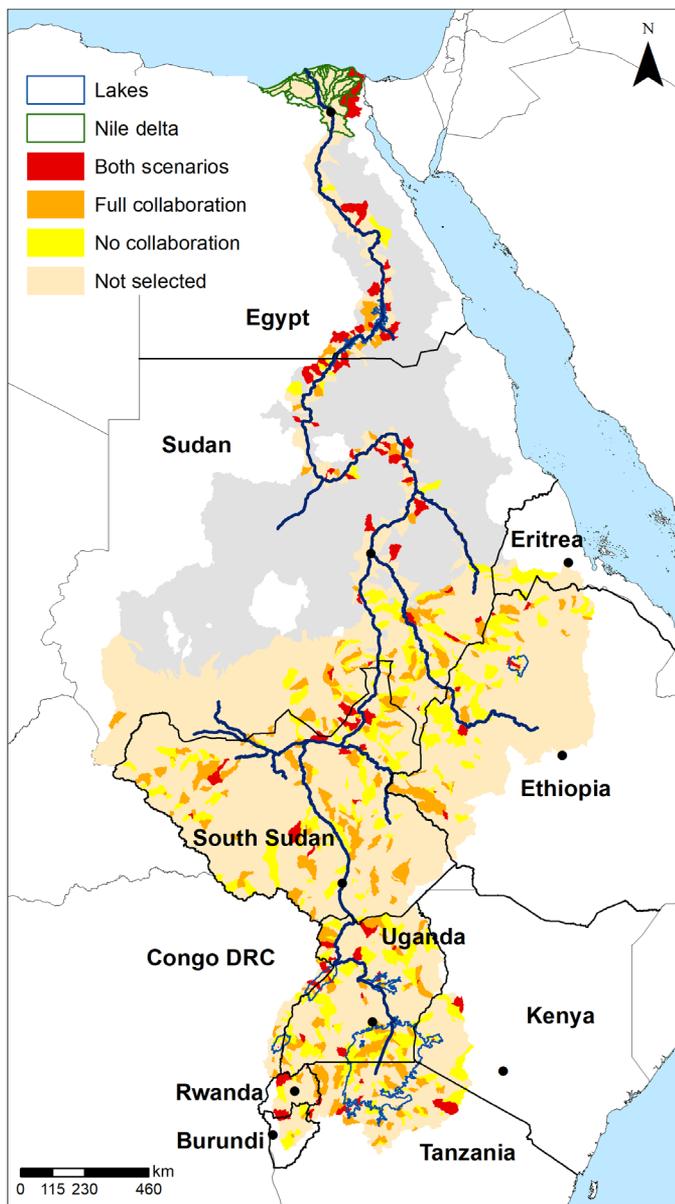


Fig. 3. Conservation priorities in the Nile Basin (subcatchments selected in Marxan’s best solutions) according to the scenario they were selected in. Yellow subcatchments were only selected in the “no collaboration” scenario, red subcatchments were selected in the “full collaboration” scenario, and orange subcatchments were selected in both scenarios.

factors that increase the cost and difficulty of a successful conservation intervention (34).

Our findings complement earlier terrestrial and marine studies outside Africa, proposing that efficiencies can be achieved when planning for conservation at a regional or international scale across all realms (35, 36). In this work, we explicitly accounted for river connectivity when examining the role of cross-boundary collaboration in conservation and analyzed a realistic partial collaboration scenario for the river Nile. The feasibility and outcomes of collaborative efforts are determined by numerous factors, including political will, availability of funding and resources, historical legacies, and perceived costs and benefits among others. Our results demonstrate that substantial savings can be achieved when collaborating in conservation, including when social, economic, and political constraining and enabling factors are accounted for. This is key for the Nile basin, a vast region with very limited monetary resources and can be extended to many other vast river systems worldwide that cross international and political boundaries, such as the Amazon, Mekong, and Colorado rivers.

Given that the human population in the Nile basin is predicted to rise from 300 million to 500 million by 2030 and that climate change is predicted to affect water availability and biodiversity (7, 37), competition for resources such as water and fish will increase substantially, as will other threats to biodiversity, such as pollution and deforestation of catchments (38, 39). It is therefore imperative that funds are invested and action is taken now to better protect priority areas along the Nile, before the impacts on biodiversity and costs of conservation increase. These investments will need to be supported by international organizations and governments, which can enhance regional cross-boundary collaboration potential.

The results of this analysis can help guide the implementation of conservation interventions, such as the designation of new protected areas with the primary aim of conserving freshwater biodiversity, or the multiple aims of conserving terrestrial and freshwater biodiversity and water security (40). In densely populated regions, such as the Nile delta, where several subcatchments were consistently selected as high priorities for conservation, implementing protective measures such as nature reserves may be challenging and less feasible. Here, specific management actions could be targeted at the key threats to biodiversity in those particular catchments, such as fencing crucial areas of riparian habitat from livestock or controlling fertilizer and pesticide usage. Identifying and spatially mapping the key threats and necessary conservation actions to abate them in priority areas for conservation is an important first step toward this goal but beyond the scope of this study due to the need for detailed mapping, which is not currently possible at the basin scale.

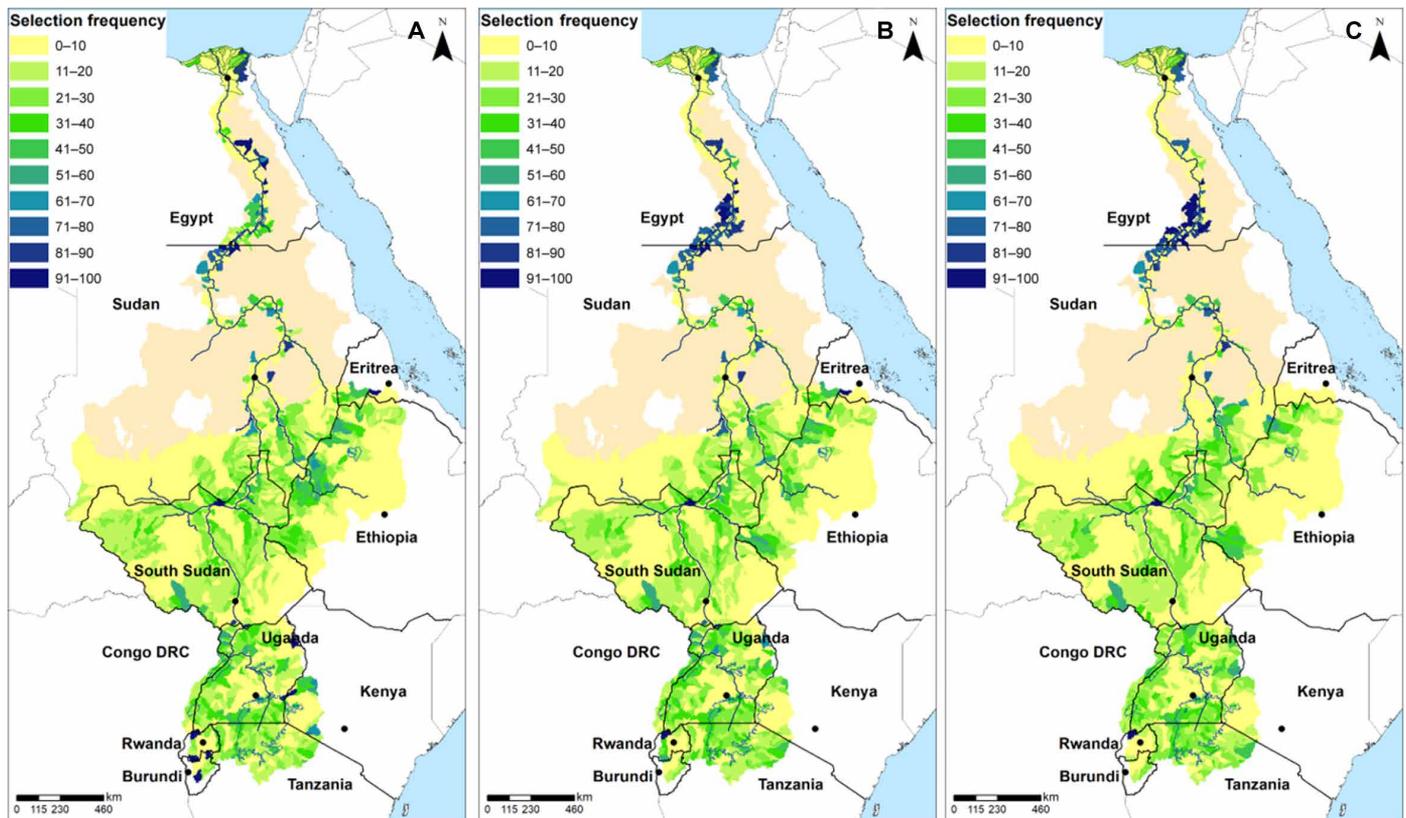


Fig. 4. Selection frequency of Nile basin subcatchments. The number of times each subcatchment was selected as a priority out of 100 Marxan runs for (A) the no collaboration scenario, (B) the partial collaboration scenario, and (C) the full collaboration scenario. Planning units in dark blue were found to be highly irreplaceable for conservation and are therefore conservation priorities; planning units in beige were not included in this analysis.

By identifying conservation priorities under multiple collaboration scenarios, the results of this work serve as an important baseline for decision makers and international organizations in the Nile basin and beyond to start developing and implementing a more detailed basin-wide conservation plan. This quantitative work allows stakeholders to have a strong evidence base for identifying the value and potential of collaboration at the initiation of a planning process, which can lead to improved conservation outcomes (41). There are multiple planning approaches and many possible collaboration scenarios, and ideally stakeholders at both the local and regional scales should be engaged in this process, and their input utilized in conjunction with analyses such as this study (42). The NBI can serve as an excellent platform to facilitate discussions among stakeholders so that all their individual priorities can be integrated into a broader basin-wide plan that incorporates biodiversity in addition to its current focus on other important resources (25, 43). Biodiversity targets and other socioeconomic objectives need to be agreed upon by stakeholders, and decisions made regarding the data, scale, and the types of conservation interventions plausible in priority areas. We constrained our analysis to freshwater fish since they are an important food source in the region for which relatively good data are available at the basin-wide scale. However, spatial conservation priorities can be re-identified with other components of freshwater biodiversity or terrestrial biodiversity when data becomes available at the basin-wide scale.

Equitable sharing of the costs and benefits of conservation is an important factor affecting the success or failure of conservation actions (17, 44). Our work suggests that the costs of implementing a basin-wide conservation plan for the Nile are not equitably distributed. The costs of conservation decrease for all nations in the full collaboration scenario except for Tanzania and South Sudan who would carry an increased cost. This has important implications for national efforts to fund and implement conservation in these countries, especially given the limited funds allocated by them to conservation (26). A platform for cost sharing among countries will almost certainly be required to channel a portion of the much larger cost savings made in the other countries back into Tanzania and South Sudan to ensure that full collaboration results in an overall cost savings or “win-win” for every Nile basin nation (45). Again, the NBI is well established to facilitate equitable sharing of conservation costs and benefits, as well as negotiations about the trade-offs individual countries would have to make (25, 43). Ensuring that basin nations equitably benefit from Nile resources is a key aspect of the NBI’s vision statement (43). The NBI can use the information on the proportion of costs that individual countries pay under different collaboration scenarios (Table 3), when deciding how best to distribute money across the region. The relative share of conservation funds to invest in countries is also of relevance to international funding organizations such as the World Bank, the Global Environmental Facility, or the United Nations Development Program, which distribute funds

Table 3. Total cost of achieving 17% conservation targets and the proportion that each country pays in the three collaboration scenarios (no, partial, and full collaboration), assuming that each country only pays for conservation actions within its own area (cost = BHM in millions of U.S. dollars of the best solution in Marxan).

Country	Cost BHM (millions of U.S. dollars)			Proportion of total cost (%)			Cost savings (millions of U.S. dollars) through collaboration	
	Collaboration scenarios			Collaboration scenarios			Collaboration scenarios	
	No	Partial	Full	No	Partial	Full	Partial	Full
Burundi	7.23	3.66	2.46	2.16	1.38	0.99	-3.57	-4.77
DRC	1.08	0.94	0.54	0.32	0.35	0.22	-0.14	-0.54
Egypt	194.37	192.35	189.56	58.12	72.45	75.97	-2.02	-4.81
Eritrea	0.91	0.93	0.00	0.27	0.35	0.00	0.02	-0.91
Ethiopia	15.49	10.04	7.62	4.63	3.78	3.05	-5.45	-7.87
Kenya	53.07	7.72	1.28	15.87	2.91	0.51	-45.35	-51.79
Rwanda	3.42	2.83	3.21	1.02	1.07	1.29	-0.59	-0.21
South Sudan	2.17	2.50	2.57	0.65	0.94	1.03	0.33	0.40
Sudan	21.71	15.17	6.86	6.49	5.71	2.75	-6.54	-14.85
Tanzania	15.31	8.47	17.72	4.58	3.19	7.10	-6.84	2.41
Uganda	19.61	20.94	17.74	5.86	7.89	7.11	1.33	-1.87

for conservation across the region. There is uncertainty regarding the exact relationship between equity and conservation outcomes (17). However, it is important to consider social equity in both conservation planning and environmental management since it has been shown to improve ecological outcomes (46, 47). There is also the risk that some nations may see collaboration as an opportunity to free-ride, shrinking their conservation commitments and avoiding costs (13, 15). A platform for cost sharing would help avoid these perverse outcomes.

Conservation actions along the Nile River are likely to produce multiple benefits for people, such as increased ecosystem service provisioning, supporting cultural services, and improvements in water quality, and can lead to more productive and sustainable fisheries at both national and local levels. Quantifying the costs and benefits of conservation under different collaboration scenarios both at the national and local level is an important avenue for future work, allowing countries to better navigate this complex trade-off. There are several other important trade-offs regarding fully coordinated conservation planning that warrant discussion. All Nile basin nations have committed to achieving biodiversity conservation targets outlined in the Convention for Biological Diversity's Strategic Plan, which require each nation to protect 17% of its area, capturing a representative portion of all species ranges (48). A fully coordinated basin-wide plan that adequately conserved all freshwater fish at the basin scale would not necessarily result in countries meeting their individual national obligations. Full collaboration also means that a smaller area will be conserved overall, which could lead to lower conservation benefits for both biodiversity and people, although it will lead to cost savings, which could be re-invested toward achieving other conservation goals, such as enhancing enforcement within protected areas (49). Given the very small areas currently designated for conservation within this region (4.2% of the Nile basin is protected), an increase in protected areas within a regional collaboration scheme would be highly beneficial and would make a substantial

contribution to averting near-term species extinctions despite not meeting international conservation goals. Another advantage of fully coordinated conservation planning is that it makes it easier to account for ecological connectivity along the river and to consider the propagation of threats into priority areas for conservation. This is key to ensuring the effectiveness of conservation efforts, in addition to cost efficiency. Some species with restricted ranges could be protected within a single country, but collaboration will be crucial for species that migrate and have larger cross-boundary distributions. Nile basin nations will need to consider these trade-offs, along with the cost savings associated with coordinated planning.

One of the biggest challenges in implementing a basin-wide conservation plan for the river Nile is to engage key actors in the discussions and negotiation process, given the complex and often conflictual histories among some of the region's countries. However, many of the issues that make management of the river Nile challenging are the same issues that can open opportunities for new collaborative efforts in conservation and beyond (50). We attempted to capture some of this political detail in our analysis when developing the collaboration scenarios. For example, Egypt has historically had almost unilateral rights to Nile water resources, but the politics of the Nile basin is changing, and countries are increasingly challenging the status quo (19). When Ethiopia began constructing the Grand Ethiopian Renaissance Dam in 2011, which is currently half completed and will become the largest dam in Africa, Egypt objected and came close to conflict (51). However, the two nations have recognized the need for greater collaboration to coordinate operation of both the Grand Renaissance in Ethiopia and Aswan Dams in Egypt to ensure year-round water security and are in the process of negotiating an agreement to better share the Nile waters. Potential cooperation between Egypt and Ethiopia is reflected in the partial collaboration scenario we ran, where the two countries act together in conservation, yet it is just one example of the many concurrent collaboration efforts going on in the Nile basin, which could influence collaboration

in conservation. The broader international community should support this cooperation by providing assurances and trust in agreements and facilitating cooperation among basin nations, as well as leveraging funds invested in the region. The industry, private sector, and non-governmental organizations can also play a crucial role in facilitating transboundary conservation since they can circumvent some of the complexities of domestic and transnational politics while still acting in multiple countries.

This work opens a range of new directions and has identified several caveats to be addressed in future studies. First, conservation planning at the continental spatial scale is only as good as the data available, and finding consistent economic data across a region as vast as the Nile basin is challenging (15). We have attempted to use the best available regionally consistent datasets, which allowed us to compare different collaborative conservation planning scenarios across the region, which was our primary aim. Second, the values of the BHM, our metric that proxies for the cost of conservation, vary widely across the region. These disparities are expected since the Nile delta and western Kenya are very fertile agricultural areas that are densely populated, while other regions (e.g., parts of Sudan in the Sahara Desert where the Nile flows) are largely uninhabited. This explains why these large proportions of the conservation costs in the conservation prioritizations we present are borne by Egypt or Kenya. The BHM (our cost measure) is also a proxy of the cost of conservation management actions and should be interpreted in this context. The absolute costs of conservation in the Nile would differ from our estimates; however, the relative patterns emerging when comparing between scenarios would likely remain similar. If a basin-wide conservation plan for biodiversity is to be implemented for the Nile, then a logical step would be to collate additional, ideally more detailed, accurate and up-to-date regional data on both biodiversity and the cost of conservation intervention.

We quantified the benefits of collaboration in conservation along an entire international river network while accounting for river connectivity and potentially limiting social, political, and economic factors. We demonstrate an approach that can be applied to other large and complex rivers that cross international boundaries, such as the Amazon, Colorado, Mekong, Danube, and others. By planning over an entire river basin, in this case the Nile, outcomes can inform governments in Africa and global organizations and could serve as a useful starting point for a comprehensive planning process that incorporates the regions important biodiversity. There is a clear opportunity for the ongoing NBI to play a central role in bringing actors together to cooperate toward more efficient biodiversity conservation in the region. As the key negotiation platform, we urge the NBI to urgently and explicitly incorporate biodiversity conservation in to their agenda and facilitate the development and implementation of a basin-wide biodiversity conservation plan for the river Nile.

MATERIALS AND METHODS

Quantifying collaboration potential and building scenarios

We compared three collaboration scenarios for the Nile basin. We developed the partial collaboration scenario by quantifying and mapping the strength of potential collaboration among Nile basin countries using a similar framework to Levin *et al.* (16), in combination with a detailed understanding and discussion of the current politics and historical legacies of the Nile basin.

Many factors affect the likelihood of a country collaborating, including socioeconomic factors such as trade, GDP, and political factors such as governance, corruption, and democracy (16). We worked off the assumption that, when countries have strong connections in the above categories, they are more likely to collaborate in conservation. We did not account for the geographical distance between countries because we assume that this is also reflected in the other variables (e.g., trade statistics) that we analyzed.

To estimate the strength of collaboration potential, we constructed matrices quantifying the relative strength of trade connections for all commodity types between Nile basin countries, for marine commodities only, and for environmental agreements signed. Trade statistics (imports and exports) were obtained from the global Trade Map (www.trademap.org/Index.aspx), which is based on the United Nations Commodity Trade Statistics Database (<http://comtrade.un.org>). We collated trade statistics for the year 2012 because this was the most recent year with data available for all countries except for South Sudan and Eritrea for which there was no data on imports and exports within the Nile basin (figs. S3 and S4). We used the trade matrices to examine the economic connections between countries by calculating the relative share of each country's exports and imports to and from each of the other Nile basin countries. We ranked the values in each of the matrices from highest to lowest (e.g., the country importing or exporting the most ranked first) to standardize the matrices and allow comparison between different variables. We then calculated the median rank between each of the 55 possible connections to give a single composite score of trade connections.

The composite trade and environmental agreement matrices were then illustrated spatially as networks; connections were mapped with weighted lines between capital cities to allow for easier visualization (Fig. 3). We used the strength of these connections as a proxy for the likelihood of two countries collaborating in conservation planning (16). These matrices were used to inform and support our decision on the partial collaboration scenario, along with an understanding of the geopolitics.

Spatial prioritization for the Nile basin

We used Marxan software, a decision support tool for conservation planning (52), to evaluate the three different planning scenarios for the Nile basin. Following Hermoso *et al.* (53), we adapted Marxan to account for longitudinal connectivity along the river system. This approach is concordant with ecological theory, as it considers the natural and roughly exponential decay of upstream influences with distance, and is regarded as best practice for freshwater conservation planning (30). We constrained connectivity along the river at a maximum of 1000 km, assuming upstream impacts negligible beyond this distance. We also included major dams as constraints to connectivity in the analysis (53).

Marxan uses a simulated annealing algorithm to identify sites that fulfill predetermined quantitative targets for biodiversity features while minimizing cost (52). Our conservation features were the 331 freshwater fish species found in the Nile basin. Distribution range data at the subcatchment scale were obtained from the IUCN (10, 11). For the full collaboration scenario, we set quantitative conservation targets at 17% of each species current estimated geographic range sizes in the Nile basin. We selected 17% because that is the national protection target specified in the Convention on Biological Diversity's 2020 Strategic Plan (48). For the no collaboration

scenario where countries act independently, we set the target at 17% of each species range within that country (15). Under the partial collaboration scenario, some countries act individually, in which case their target was 17% of each species range within that country. However, when countries acted bilaterally or in groups, their target was 17% of the species range within their combined extent. We used 2935 subcatchments of the Nile basin as the planning units, which are a similar spatial resolution to the fish distribution data and are a logical management unit for river conservation. We aimed to only include subcatchments where the river flows consistently and is likely to contain fish species. These were identified based on the following criteria: (i) A lake is present (54), (ii) average rainfall in a subcatchment exceeds 450 mm year⁻¹ (55), (iii) above 50% of a water body in a subcatchment is detectable in most years (56), and (iv) data on threats to freshwater biodiversity exist for that subcatchment (5). Major lakes including Lake Victoria were included as several smaller subcatchments rather than individually.

We used the BHM as a surrogate for the cost of conservation action in a planning unit (subcatchment) because data on the actual costs of conservation action is unavailable for the entire region. The absolute costs of conservation will likely differ from the costs estimated using the BHM; however, relative costs of different conservation plans will likely stay similar. The BHM is a metric developed by Kark *et al.* (15) and combines population density (DENSITY) and land acquisition cost (ACQUISITION). The BHM is an efficient compromise between minimizing land acquisition costs and major threats to biodiversity (15). The BHM was calculated as $(\text{DENSITY} \times \text{ACQUISITION}) / \text{DENSITY}_{\text{NILEBASIN}}$, where $\text{DENSITY}_{\text{NILEBASIN}}$ is the average population density over the entire Nile basin in 2012 (67 people per square kilometer). For DENSITY, we used LandScan population data for 2012 (57), which at a resolution of 1 km² is the finest scale global population distribution data available. Spatial economic data was obtained from the Geographically based Economic (G-Econ) dataset, which contains gridded global economic data at a 1° resolution for the year 2005 and is the most up-to-date data of its kind (58). We used the mean GDP, scaled by purchasing parity power (the local buying power of a U.S. dollar in 2005 divided by the exchange rate) to estimate ACQUISITION. The spatial distribution of the BHM is shown in fig. S2 and is in millions of U.S. dollars.

We ran Marxan 100 times with 1 million iterations for each collaboration scenario with a boundary length modifier (BLM) value of 0.00006. We calibrated the BHM by running Marxan several times with different BHM values and plotting the cost of the best solutions against the connectivity between planning units (59). We selected a BLM value of 0.00006 because it was a good compromise between achieving a well-connected conservation plan without unnecessarily increasing the costs of conservation (BHM). Collaboration scenarios were compared using the Marxan best solution, which is the solution that meets all the biodiversity conservation targets (17% of each species range) for the lowest cost (BHM), while minimizing connectivity penalties for missing connections between planning units where the river flows.

We incorporated data on biodiversity threats into our Marxan analysis by first calculating the average level of biodiversity threat (standardized between 0 and 1) in each Nile basin planning unit using a cumulative map of 23 threats to rivers at 1° resolution globally (5). We then included this as an additional constraint in Marxan so that the best solution had to meet the species coverage targets speci-

fied above and maintain an average threat score below 0.5 across the selected planning units (or receive penalties for exceeding the threshold) (31). The algorithm can still select subcatchments with high human threats whether species ranges are restricted to these areas or whether multiple species co-occur, so the return on conservation investment is high. In these cases, the algorithm will also have to select additional subcatchments with low threats to balance out the overall threat score for the conservation plan. The advantage of this approach is that planning units identified in the best solution are likely (but not necessarily) to be in places with relatively low levels of threats to biodiversity, where conservation action has a better chance of succeeding and is less costly. An alternative philosophy for incorporating threats into planning analyses is to actively target areas of high threat or targeting the sources of threats within rivers (e.g., industrial areas and fertilizers from riparian agriculture). This is especially important for threats such as pollution, where downstream conservation action will confer little conservation benefit. Conservation action in places with high threats and rehabilitating of ecologically degraded areas is often substantially more expensive than proactively protecting less threatened areas. Given that restricted funds are a major constraint for conservation in the Nile basin, we opted for an approach that aims to initially secure the least threatened areas of the basin while still achieving the biodiversity targets.

After identifying best solutions for each scenario, we compared their areas, the human populations residing in them, and their exposure to biodiversity threats. We did not lock current protected areas into our Marxan analysis. Although 4.2% of the Nile basin lies within protected areas, most of these were designated to protect terrestrial biodiversity and only capture rivers incidentally (60). Furthermore, many protected areas in the Nile basin region are ineffective at preventing illegal activities taking place within their boundaries (61). We assessed how well current protected areas are contributing to freshwater fish conservation and found that 61% (202) of the fish species we analyzed had less than 2% of their distribution captured in current protected areas. Only 21% ($n = 73$) of fish species had over 10% of their distributions protected. Therefore, we followed previous conservation planning analyses in Africa (62) and excluded current protected areas from our analysis.

To avoid variable planning unit sizes influencing our results, we treated fish presence in a subcatchment as binary (present/absent). This avoids Marxan favoring large planning units, which the algorithm tends to favor because it can capture large portions of species ranges relative to smaller planning unit. We also followed well-established conservation planning methods to rigorously assess the sensitivity of our results to different cost values (62, 63). We ran Marxan four times for a no collaboration scenario while varying the costs of planning units, holding all conservation targets and other input parameters (e.g., BLM) constant. We first ran a baseline scenario using BHM values as costs. We then ran three additional scenarios where we randomly selected a third of all planning units and increased their cost by 100, 150, or 200% (62, 63). We then used Fleiss' kappa statistic to analyze the degree of overlap between the priority areas selected in the four different Marxan runs. Fleiss' kappa gives a value between 0 and 1, where 1 indicates complete agreement between scenarios and 0 indicates no agreement. We found that the results had a low sensitivity and were robust to changes in cost. The Fleiss' kappa statistic across all scenarios was 0.90, indicating substantial agreement in priority area selection (64).

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/5/4/eaau7668/DC1>

Fig. S1. Freshwater richness for 331 fish species in the river Nile.

Fig. S2. Spatial distribution of the BHM.

Fig. S3. Distribution of economic variables in the Nile basin in 2012.

Fig. S4. The distribution of socioeconomic and political factors in the Nile basin.

Table S1. Demographic and trade data for each Nile basin country (listed in order from north to south).

Table S2. General geographic and protected area statistics for each of the Nile basin countries.

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Supplementary Materials for

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This PDF file includes:

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Supplementary Materials

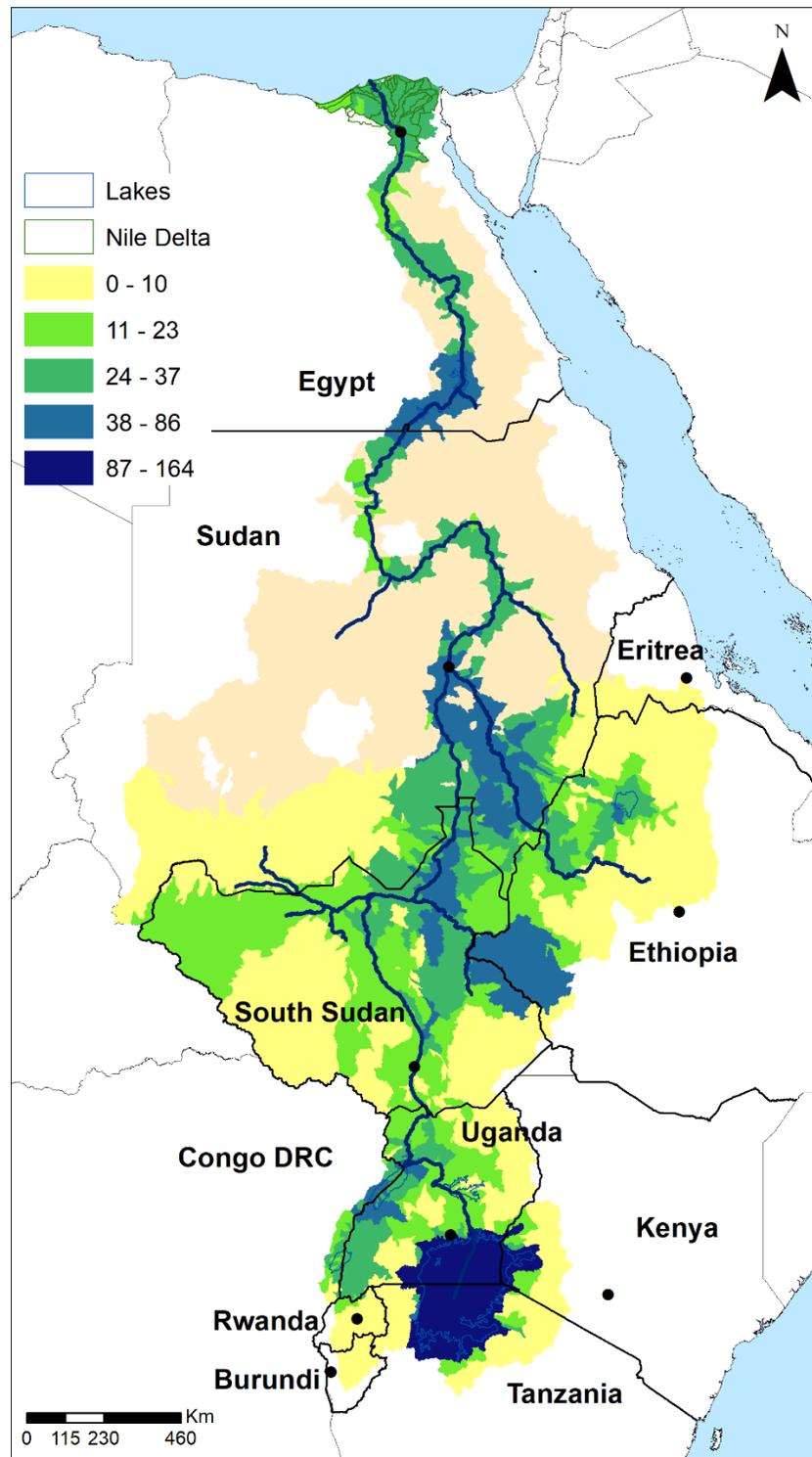


Fig. S1. Freshwater richness for 331 fish species in the River Nile. Spatial data obtained from the International Union for the Conservation of Nature (IUCN).

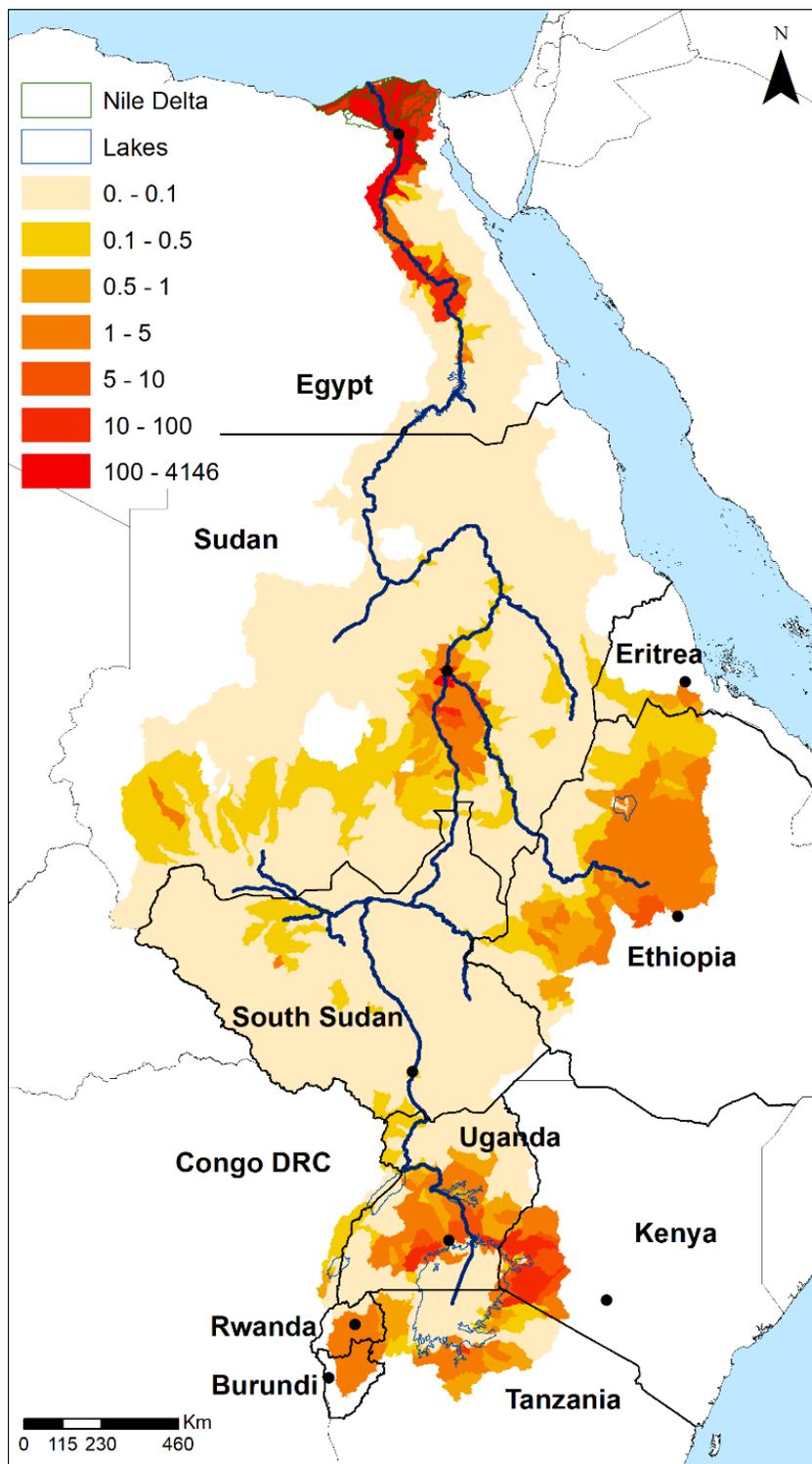


Fig. S2. Spatial distribution of the BHM measured in millions of USD in the Nile Basin.

Table S1. Demographic and trade data for each Nile basin country (listed in order from north to south).

Country	2012 Population (millions)	2012 GDP (USD billions)	2012 GDP per capita (USD)	Purchasing Power Parity (PPP)	Number of Shared borders	Exports			Imports		
						2012 Total exports to world (USD millions)	2012 Total exports to Nile basin (USD millions)	Percentage of exports to Nile basin	2012 Total imports from world (USD millions)	2012 Total imports from Nile basin (USD millions)	Percentage of imports within Nile basin
Egypt	84.0	253.9	3024.2	1.9	3.0	29417.0	1112.1	3.8	69865.6	459.5	0.7
Sudan*	35.3	51.6	1459.8	2.0	7.0	3810.0	98.1	13.3	7511.6	98.1	9.6
Eritrea	5.6	3.1	556.9	6.3	3.0	403.3	no data	no data	383.5	no data	no data
Ethiopia	86.5	39.9	461.3	6.5	6.0	2891.3	33.9	1.2	11912.9	33.9	1.9
South Sudan	10.4	10.4	997.0	1.5	6.0	no data	no data	no data	no data	no data	no data
Uganda	35.6	24.7	693.4	1057.7	5.0	2357.4	788.1	33.4	6044.1	788.1	11.9
Kenya	42.7	40.7	952.2	38.0	5.0	5259.2	1931.2	36.7	15191.5	1931.2	3.3
DRC**	69.6	18.1	260.7	550.8	10.0	5647.4	115.7	2.0	5307.0	724.0	13.6
Rwanda	11.3	6.8	598.9	257.0	4.0	505.7	181.9	36.0	1624.3	181.9	29.6
Burundi	8.7	2.5	282.4	563.5	3.0	242.7	19.5	8.1	1003.1	194.3	19.4
Tanzania	47.7	29.9	628.3	665.6	8.0	5547.2	507.8	1.8	11715.6	507.8	6.5

*Economic data for Sudan includes South Sudan. Trade statistics obtained from: <http://www.trademap.org/>. Population and GDP statistics obtained from UNECA African Statistical Year Book 2013. Purchase Power Parity (PPP) data obtained from the World Bank: data.worldbank.org/indicator and from <http://databank.worldbank.org/data/reports.aspx?source=2&series=PA.NUS.PPP&country>

**Democratic Republic of Congo

Table S2. General geographic and protected area statistics for each of the Nile basin countries. Countries are listed from North to South

Country	Area of Country (km²)	Area of Country in Nile Basin (km²)	Percentage of Country in the Nile Basin	Area Protected in Country (km²)	Percentage of Protected areas in each country (km²)	Area Protected in Nile Basin (km²)	Percentage of protected areas in the Nile Basin
Egypt	987702	239172	24.2	161049	16.3	65333	6.6
Sudan	1880789	1216033	64.7	26476	1.4	26269	1.4
Eritrea	123944	24963	20.1	6602	5.3	918	0.7
Ethiopia	1144968	359265	31.4	229221	20.0	76024	6.6
South Sudan	626505	618680	98.8	16619	2.7	16619	2.7
Uganda	241434	234191	97.0	35976	14.9	35974	14.9
Kenya	597807	49002	8.2	89120	14.9	10411	1.7
Congo DRC	2402901	19145	0.8	242938	10.1	57867	2.4
Rwanda	25370	20854	82.2	2530	10.0	2530	10.0
Burundi	27284	13200	48.4	959	3.5	959	3.5
Tanzania	941829	116442	12.4	300526	31.9	84196	8.9
Totals	9000533	2910945	32.3	1112016	12.4	377100	4.2

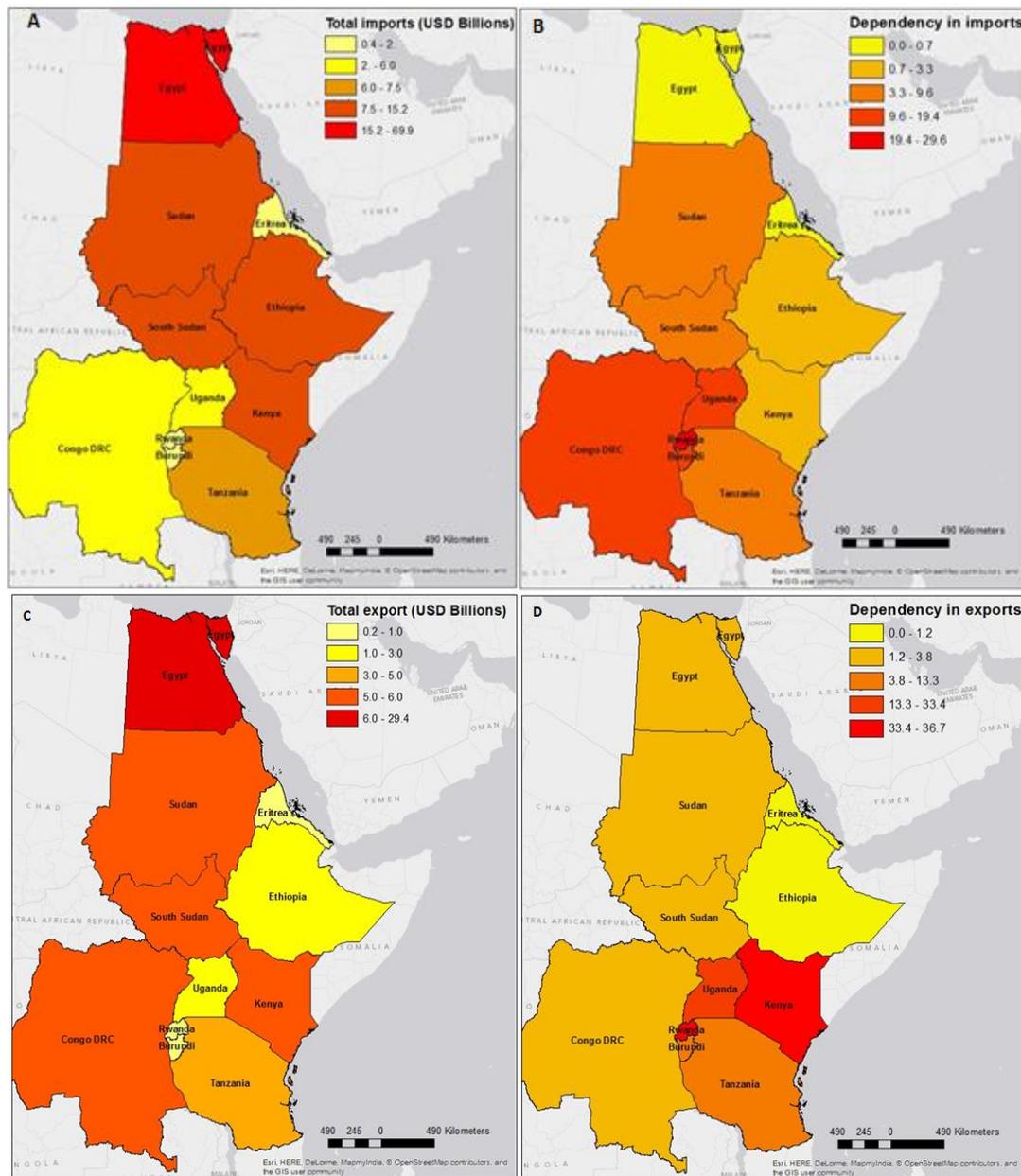


Fig. S3. Distribution of economic variables in the Nile basin in 2012. (A) Total annual imports in billions of US dollars. **(B)** Dependency on imports calculated as the percentage of imports from Nile Basin countries. **(C)** Total annual exports in billions of US dollars. **(D)** Dependency on exports calculated as the percentage of exports sent to Nile Basin countries.

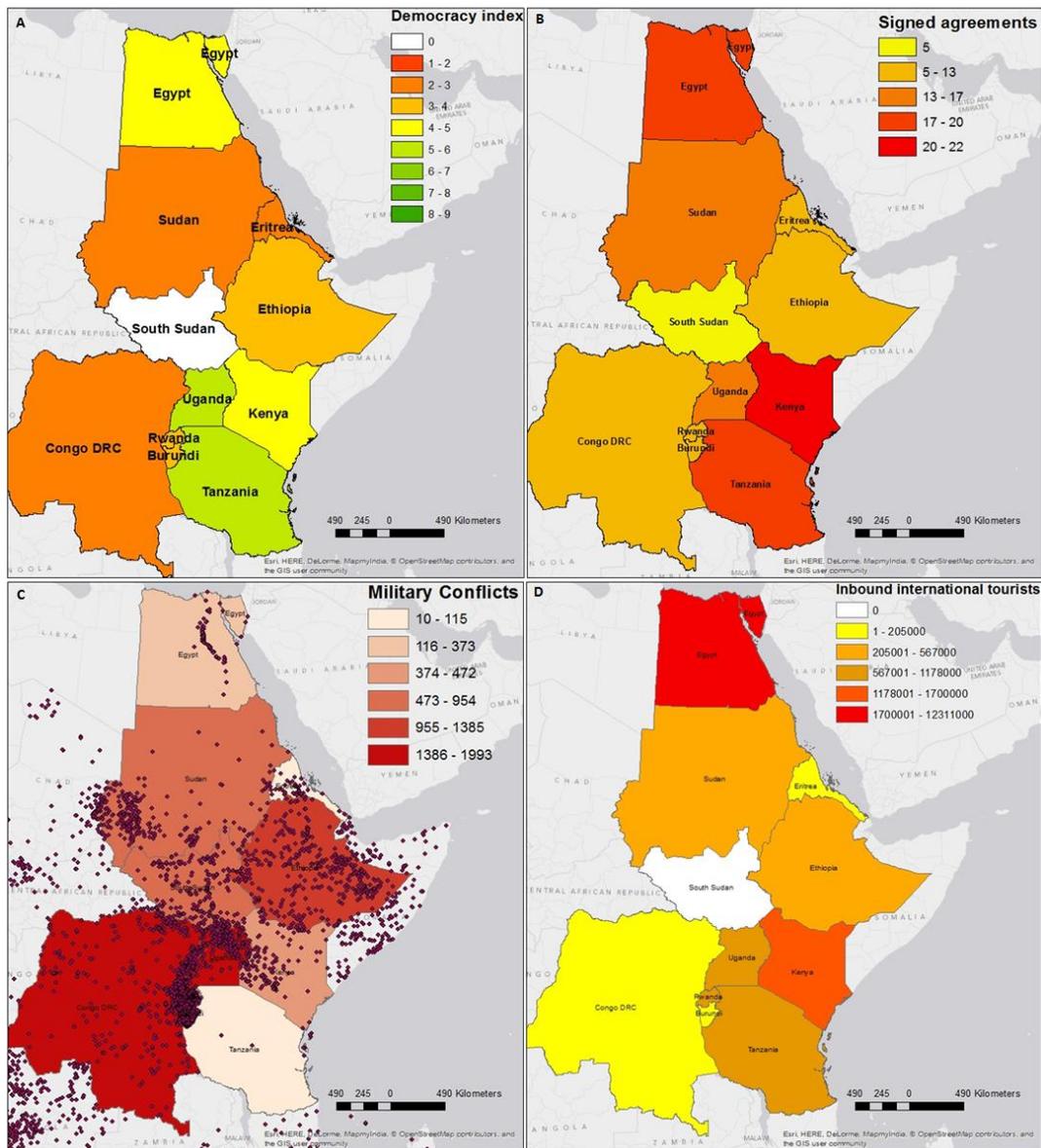


Fig. S4. The distribution of socioeconomic and political factors in the Nile basin. (A)

Democracy index. **(B)** The number of signed international agreements relating to conservation and the environment. **(C)** The number of military conflicts between 1989 and 2010, each point represents an individual conflict. **(D)** Number of inbound international tourists in 2012. We used the Corruption Perceptions Index, derived from the World Resources Institute (<https://www.transparency.org/cpi2013/>) and the Democracy Index 2011 from the Economist Intelligence Unit (www.eiu.com/public/topical_report.aspx?campaignid=DemocracyIndex2011). There was no data available for South Sudan.