

Unintended multi-species co-benefits of an Amazonian community-based conservation program

João V. Campos-Silva^{1,2,3*}, Joseph E. Hawes^{3,4,5}, Paulo C. M. Andrade⁶ & Carlos A. Peres³

1. Instituto de Ciências Biológicas e da Saúde, Universidade Federal de Alagoas, Maceió, 57072-900, AL, Brazil

2. Departamento de Ecologia, Centro de Biociências, Universidade Federal do Rio Grande do Norte, Natal, 59072-970, RN, Brazil

3. School of Environmental Sciences, University of East Anglia, Norwich, NR4 7TJ, UK

4. Biotecnologia e Recursos Naturais da Amazônia, Universidade do Estado do Amazonas, Manaus, 69065-001, AM, Brazil

5. Applied Ecology Research Group, Department of Biology, Anglia Ruskin University, Cambridge, CB1 1PT, UK

6. Departamento de Produção Animal e Vegetal, Laboratório de Animais Silvestres, Universidade Federal do Amazonas, Manaus, 69077-000, AM, Brazil

* Corresponding author: João Vitor Campos-Silva

Address: Instituto de Ciências Biológicas e da Saúde, Universidade Federal de Alagoas, Av. Lourival Melo Mota, s/n, Tabuleiro do Martins, Maceió, 57072-900, AL, Brazil

Email address: jvpiedade@gmail.com

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Abstract

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Urgent challenges posed by widespread degradation of low-governance tropical ecosystems require new development pathways that can reconcile biodiversity conservation and human welfare. Community-based conservation management (CBCM) has shown potential for integrating socio-economic needs with conservation goals in tropical environments but assessing the effectiveness of this approach is often held back by the lack of comprehensive ecological assessments. Here we show a robust ecological evaluation of the largest CBCM initiative in the Brazilian Amazon. Over 40 years, this program has induced the large-scale recovery of Giant South American Turtle (*Podocnemis expansa*) populations and other freshwater turtles along a 1,500-km segment of a major tributary of the Amazon River. Poaching activity on “no-take” beaches was around 2% compared to 99% on unprotected beaches. We also show positive demographic co-benefits across a wide range of non-target vertebrate and invertebrate taxa. Beaches protected by local communities represent islands of high biodiversity, while unprotected beaches remain “empty and silent”, reinforcing the effectiveness of empowering local conservation action, particularly in tropical countries often experiencing shortages in financial and human resources.

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50 Protected areas (PAs) comprise the most prominent conservation strategy to address
overexploited wildlife populations worldwide. Expansion of the global PA network, with
>200,000 now established terrestrial PAs (1), has moved towards the target of 17% of
terrestrial and inland water areas (2). Meta-analyses investigating PA effectiveness (3)
remain limited by biases in the global distribution of existing PAs for which
55 interventions and outcomes are known, and comparable data from unprotected areas.
In addition, most PAs are legally settled and managed *de facto* or *de jure* by local
communities, particularly in tropical countries with high levels of biodiversity, where
strict “no-take” reserves account for only ~2% of the total protected acreage (4). Yet
the degree to which management by local stakeholders can determine positive
60 demographic outcomes for resource populations remains contentious (5), and the
relative conservation performance of exploited and unexploited species within human-
occupied PAs remains poorly understood.

Local people are often considered to be more concerned about immediate economic
returns, rather than the long-term persistence of resource populations (6). However,
65 community-based conservation management (hereafter, CBCM) has shown great
potential for integrating socio-economic needs with conservation goals (7,8),
particularly in tropical countries where PAs created on paper are often severely
understaffed and underfunded (9), and resource management institutions are frail or
nonexistent (10). Some initiatives have demonstrated enhanced livelihoods for
70 resident communities while contributing to biodiversity conservation, even in complex
socio-ecological systems in which interactions are dynamic and reciprocal (11,12).
CBCM initiatives may potentially fill this PA implementation gap by effectively
strengthening surveillance systems with full-time physical presence, decentralizing
resource stewardship, and reducing reserve management costs (13).

75 Most studies on “no-take” areas are focused on the population recovery of target
species but indirect effects resulting from the protection of target species, including
trophic cascades and other ecosystem dynamics, may also yield positive collateral
outcomes for non-target species. Indeed, substantial shifts in the entire trophic
organization of a community can result from either the overexploitation or protection
80 of a target species (14) but, because unintended indirect interactions can lag behind
the direct effects of protection, their quantitative detection is often challenging.

Assessing both direct and indirect effects of protection is critical to properly understand the ecological consequences of CBCM initiatives. This information is particularly urgent for aquatic environments including poorly known tropical wetlands, considering their vulnerability to future changes and their global importance for both biodiversity and human societies (15).

Here, we assess the effectiveness of a CBCM program in the western Brazilian Amazon, targeting the Giant South American Turtle (*Podocnemis expansa*), Yellow-spotted River Turtle (*P. unifilis*) and Six-tubercled River Turtle (*P. sextuberculata*). Following severe and long-term population declines caused by historical overexploitation (16), turtle nesting beaches (locally, *tabuleiros*) have been systematically protected from adult and egg harvesting by informal guards from local communities, and subsequently monitored for nesting success, especially for *P. expansa*, a sand-dependent high-value species. We show the long-term performance of this program for adult female and hatchling turtles, including a 40-year dataset on participatory monitoring and the local perception of the wider population status of target taxa through semi-structured interviews in villages both inside and outside sustainable-use reserves. We also evaluate the cascading effects of site protection for non-target vertebrate and invertebrate taxa, using a paired design of adjacent protected and unprotected fluvial beaches, under comparable social and economic conditions. In addition to beach-nesting turtles, we sampled beach-nesting birds, caimans, iguanas, large catfishes, large-bodied aquatic fauna, and terrestrial invertebrates. The spatial design of this multi-taxa assessment allows us to contrast the conservation effectiveness of formal PAs and small-scale CBCM initiatives and provides a unique perspective on the potential role of target turtles as umbrella species for a wide range of non-target terrestrial and aquatic taxa. Finally, we interviewed beach guards to include their perception on the success of this initiative, in terms of economic and social factors.

Results

Population recovery of target species. In the last 40 years CBCM of 15 large fluvial beaches (mean \pm SD length = 2,395.1 \pm 774.6 m) across the Juruá River increased the number of nests of *Podocnemis expansa* by a factor of 11.4 (\pm 12.9, $N = 15$) and their hatchlings per beach by 9.7 fold (\pm 8.7, $N = 15$) on average (Supplementary Figure 1). This amounts to a mean of 71,087 (\pm 6,501) more hatchlings released every

115 year on protected beaches. This clear upturn in records of successful turtle nests and hatchlings was supported by widespread reports of recovery in adult turtle populations by local people. In all 52 villages sampled near protected beaches, experienced fishermen reinforced reports that the *P. expansa* population had rapidly increased over the last 15 years (2000-2015). In contrast, all 19 local communities reporting
120 population declines were located far from protected beaches (Fig. 1).

Collateral benefits for non-target species. Our multi-taxa surveys on protected (PB) and unprotected beaches (UB) also revealed strong positive effects of beach guarding for other vertebrate and invertebrate species (Fig. 2). All terrestrial and aquatic taxa surveyed exhibited higher abundances on protected beaches, as emphasized by
125 visual and acoustic cues (Supplementary Figure 2, Movie S1).

The impact on the abundance of terrestrial biodiversity was impressive. Protected beaches hosted a much higher number of all avian taxa (Supplementary Figure 3). Population sizes of the migratory Black Skimmer (*Rynchops niger*), for instance, were 80-fold higher on protected beaches, compared to unprotected beaches (PB: 3.3 ± 2.4
130 ind. ha^{-1} ; UB: 0.04 ± 2.2 ; paired t-test: $t = 5.2$, $p < 0.05$). This mirrored other migratory bird species, including the Large-Billed Tern (*Phaetusa simplex*; PB: $5 \pm 4.8 \text{ ind. ha}^{-1}$; UB: 0.17 ± 4.6 ; $t = 4.3$, $p < 0.05$), and the Sand-colored Nighthawk (*Chordeiles rupestris*; PB: $3.2 \pm 2.9 \text{ ind. ha}^{-1}$; UB: 0.3 ± 2.7 ; $t = 4.5$, $p < 0.05$). Considering nest counts, protected beaches hosted 8,700 nests of migratory bird species (Black
135 Skimmer and Large-Billed Tern), compared to only 371 nests on unprotected beaches. The same pattern was found for Sand-colored Nighthawk which show almost four-fold more nests on protected beaches. These differences extended to Green Iguanas (*Iguana iguana*; Supplementary Figure 3), whose nests were almost seven times more abundant on protected beaches (PB: $0.8 \pm 0.5 \text{ nests. ha}^{-1}$; UB: 0.1 ± 0.5 ; $t = 8.1$, $p <$
140 0.001). Model averaging of GLMs revealed that the time lag (number of years) since the onset of community protection was the only significant predictor of nest abundance for these non-target vertebrate taxa (Supplementary Figure 4). Pitfall surveys of terrestrial arthropods (yielding 4,401 individuals, representing 11 orders) showed that total abundance was almost two-fold higher on protected ($196.2 \pm 9.86 \text{ ind. trap}^{-1}$)
145 than on unprotected beaches (116.6 ± 9.84 ; $t = 3.3$, $p < 0.05$). Orthopterans comprised the most abundant order of insects ($3,307$ individuals; $13.1 \pm 9.8 \text{ ind. trap}^{-1}$), followed by Coleopterans (649 individuals; $3.6 \pm 9.8 \text{ ind. trap}^{-1}$).

For aquatic taxa, higher abundance of the large-bodied Black Caiman (*Melanosuchus niger*) similarly was found on protected beaches (PB: 12.1 ± 5.2 individuals/km; UB: 7.4 ± 18.0 ; $t = 4.25$, $p < 0.05$). The average biomass of large catfishes (Order Siluriformes, Supplementary Figure 5) in the river channel was six-fold higher next to protected (mean \pm SD = 23.4 ± 19.5 kg) compared to unprotected beaches (3.6 ± 18.9 kg; $t = 3.1$, $p < 0.01$). In terms of species richness, we identified 25 catfish species along the river segment adjacent to protected beaches, while only eight species were found along unprotected beaches (see full list of species in Supplementary Table 1). The only exception was for aquatic megafauna, where sonar detection surveys showed no significant differences between protected (0.97 ± 0.5 ind./m) and unprotected beaches (0.65 ± 0.5 ; $t = 1.82$, $p = 0.09$). In our multivariate model, however, years of beach protection had a significantly positive effect on the abundance of aquatic megafauna detected by sonar surveys (Supplementary Figure 4).

Conservation effectiveness of CBCM. Community-based protection strongly ensure the reproductive success of *P. expansa*, representing 58 times more nests on protected beaches (PB: 584 nests; UB: 10; $t = 2.20$, $p < 0.05$). *P. unifilis* and *P. sextuberculata*, also benefitted from beach protection showing marked increases in nesting success. For these turtle species, we recorded 786 nests on protected beaches and only 161 on unprotected beaches (Supplementary Table 1).

Beyond the clear binary effect of protection, our GLMs showed that the number of years a beach had been protected was the strongest predictor of nesting success in freshwater turtles ($\beta = 1.4 \pm 0.14$), followed by the declivity of the beach terrain ($\beta = -0.71 \pm 0.14$) and nonlinear distance to the nearest human village ($\beta = -0.31 \pm 0.13$), which showed a negative effect on the number of nests censused (Fig. 3).

We also confirmed that beach protection dramatically suppressed illegal activity from poachers on nests of all three *Podocnemis* turtle species. On protected beaches, we monitored 521 *P. expansa* nests, 371 *P. unifilis* nests, and 1,467 *P. sextuberculata* nests. Of all 2,359 *Podocnemis* nests surveyed on protected beaches, only 2.1% were harvested by poachers. On the other hand, 99% of the 202 nests monitored on all unprotected beaches (4 *P. expansa*, 42 *P. unifilis*, and 156 *P. sextuberculata*) were raided by poachers.

Socioeconomic dimension of CBCM. A total of 40 interviewed beach-guards

180 reported positive dividends from beach protection, but also expressed genuine
concerns over the sustainability of this CBCM program in the long-term
(Supplementary Table 2). Positive outcomes included the population recovery of turtle
species that represent an important subsistence food resource, and strengthening of
sociocultural identity. Conversely, informants were concerned about (i) the failing of
185 the CBCM program to generate a source of tangible financial return, (ii) insufficient
support from government agencies, including shortages of basic equipment and
material investments, and (iii) the complete lack of appreciation by government
authorities and society as a whole that failed to adequately recognize the considerable
time and effort allocated to beach surveillance, and personal threats incurred from
190 confronting recalcitrant poachers. The main reasons to persist with beach protection
was often related to a self-imposed moral obligation to provide continuity for the work
that their parents and grandparents had begun.

Discussion

The challenge of conserving tropical environments is often exacerbated by limited
195 human resources or financial and institutional support (9). The CBCM approach is a
timely strategy to empower communities, consolidate institutions in low-governance
environments, and enhance social capital, social learning and conflict resolution (17,
18). Nonetheless, there is a major gap in the literature on the wide ecological outcomes
from these initiatives (19), particularly in tropical wetlands. Our results provide clear
200 evidence on the ecological benefits of a CBCM scheme, which has released more
than 2 million hatchlings of freshwater turtles over the last four decades, driving the
population recovery of a historically overexploited species (20). In particular, we also
show that (i) these benefits are not ensured inside PAs without CBCM initiatives and
(ii) they are coupled with unintended benefits for multiple non-target taxa, which are
205 often obfuscated by restricting assessments to target species responses. Finally, our
results highlight some of the socio-economic considerations that will determine the
future success or failure of this and other similar CBCM programs.

Freshwater turtles are one of the most threatened vertebrate taxa (21), following long-
term exploitation – from pre-Columbian indigenous people to the contemporary
210 Amazonian dwellers of mixed indigenous and European descent (22,23). After the
Brazilian Faunal Protection Law was brought into effect in 1967, followed by ratification
of CITES in 1975 and the Rio Convention on Biological Diversity in 1992, many

215 terrestrial species that succumbed to severe population collapses during the heyday
of 20th Century commercial hunting activity have since experienced clear numerical
recovery (24). However, this has not typically been mirrored in overexploited aquatic
species, as the accessibility of fluvial habitats makes them much more vulnerable to
human pressure, which is invariably concentrated along Amazonian rivers (25).

220 The historical practice of protecting turtle nesting beaches (*tabuleiros*) has since taken
a modern form, initiated by community organizations, managed by local residents, and
now established in an increasing number of sites across the Amazon (Supplementary
Figure 6). Our findings that beach protection by local communities was the overriding
factor driving nest site selection by turtles, coupled with the steady observed
cumulative increase in the number of nests over multiple years of protection, suggest
225 that this initiative could provide a mechanism to ensure successful long-term turtle
reproduction and recovery of wild populations. There is growing evidence that CBCM
of fish stocks in Amazonian oxbow lakes can reverse similar past declines due to
overharvesting (11), and similarly, that CBCM has also become a strong opportunity
to protect overharvested freshwater turtles (20),.

230 Beach protection is highly effective despite high levels of hunting and egg-harvesting
in Amazonian rural communities, including those in extractive reserves (26). Our
finding that nest abundance was negatively influenced by distance to human
settlements supports the idea that greater neighborhood vigilance enhances
protection. Therefore, the effectiveness of local protection was higher at beaches near
local communities, given that a larger number of local residents could actively
235 contribute to collective surveillance. The same pattern was detected for *Arapaima*
gigas in community-protected lakes in our study region (11), but contrary to turtle
nesting sites without CBCM (27). This is particularly important because turtles are a
culinary delicacy in the Amazon and illegal urban trade centered in small towns near
PAs can exert substantial additional pressure on turtle populations (28).

240 Our study strongly challenges any notion that existing sustainable-use reserves
lacking a CBCM can ensure the effective protection of freshwater turtles and other
beach-nesting vertebrates, since the nest harvesting rate on unprotected beaches was
99.0% within PAs. In contrast, the CBCM approach reduced nest raiding to just 2.1%
on guarded beaches. While the effects of protection within PA boundaries are highly
245 variable, depending on the magnitude of local community protection, those effects at

the site scale (CBCM) were remarkably powerful and invariant. Following the long-term systematic overexploitation of freshwater turtles across the Amazon, a CBCM approach clearly shows the potential for population recovery. Existing protected beaches are, however, still patchy and relatively few but are representative of the physical characteristics of hundreds of unprotected beaches throughout the length of the Juruá River (Supplementary Figure 7), indicating that perfectly suitable beaches for turtle nesting are widely available if the CBCM scheme were to be extended. Repeating the warning from marine turtle conservation (29), increasing the scale of protection to cover as many beaches as possible would reduce the risk of focusing on a small number of remaining protected nesting sites.

Beyond the targeted dividends for *P. expansa* and other turtle species, our results reveal unintended effects of beach protection that were overwhelmingly positive for surveyed taxa, including beach-nesting birds, large catfishes and caimans, all of which are invariably harvested within and outside extractive reserves (30). Commercially-valuable fish, such as large-bodied catfish, are hugely important for the local subsistence economy in the Amazon (31,32), and have been severely impacted by overfishing (33). Our results show that protecting turtle nesting grounds extends protection from beaches to the adjacent river channel. The response is similar for crocodylians, which suffered dramatic population declines following the export of 7.5 million caiman skins between 1950 and 1965 (34). The higher caiman abundance near protected beaches is noteworthy because illegal hunting and sales of caiman meat continue across Amazonia (35), despite the ban on the skin trade since 1967 (36). In addition, fishermen often resort to killing caimans at any unprotected site because they raid and damage gillnets and represent a threat to human lives (37).

Although there was a trend for higher sonar detection rates of other aquatic megafauna at protected beaches, compared to adjacent unprotected sites, this was not a significant difference. Given the wide range of large-bodied aquatic species in Amazonian river systems, we were unable to reliably assign species identifications to sonar detections. Despite this methodological limitation, our models showed that the number of years of beach protection had a marked effect on aquatic megafauna. This is likely because uncontrolled commercial fishing boats are permitted to transit throughout major waterways even within PAs, and this pressure is heaviest along unprotected beaches. For turtle hatchling predators such as caiman and catfish, there

is also the annual resource pulse provided by thousands of hatchlings that descend
280 from beaches to the river. This potential ecological cascade exacerbates the critical
role of "no-take" areas in overall community stability, since the species richness and
abundance of apex predators are pivotal contributors to the stability of aquatic
foodwebs (38).

The high concentration of both breeding adults and nests of Black Skimmers, Large-
285 Billed Terns and Sand-colored Nighthawks on protected beaches indicates that
community protection of sand beaches strongly induces the successful breeding of
these colonial bird species, which are generally threatened by egg-collecting and
other anthropogenic activities (39), including agriculture and fishing. Another
290 explanation for the much higher abundance of colonial birds at protected beaches is
the "landscape of fear", whereby selection for low-predation sites is induced by
generally high levels of predation risk (40).

Finally, taxa that are not exploited by people were also markedly more abundant near
protected beaches showing the potential of freshwater turtles in playing a prominent
umbrella species role and sustaining the conservation of many other species.
295 Surprisingly, even terrestrial invertebrates occurred at higher numbers on protected
beaches, dismissing the hypothesis of top-down control due to the higher number of
insectivorous avian species (41). Nutrient deposition from necromass generated by
dead animals, eggs and other carcasses likely indicates a stronger bottom-up effect on
protected beaches (42). Likewise, the occurrence of Green Iguana nests at much
300 higher numbers on protected beaches was unrelated to lower levels of human
exploitation because iguanas (or their nests) are not harvested in our study area,
unlike other regions of Brazil (43).

The monthly maintenance costs of this CBCM scheme are about US\$110 per beach-
guard, which is paid as a food hamper ("*cesta basica*") during the five months of the
305 year comprising the breeding (dry) season. Therefore, over the last five years, each
P. expansa hatchling released cost only US\$0.03 to the Brazilian government and
funding partners, and this figure could be much lower if we included all turtle species.
Considering the wide-ranging ecological benefits combined with minimal
implementation costs, this program represents a high value-for-money conservation
310 tool. In contrast to typical assumptions that rural people are motivated primarily by
economic returns, we report the long-term commitment by beach guards driven by a

sense of moral duty, despite being deprived of monetary compensation for many years.

315 Currently, there are about 390 protected nesting sites maintained through CBCM initiatives in the Brazilian Amazon (Supplementary Figure 6). To ensure the ideal maintenance to all existing CBCM arrangements across the Brazilian Amazon, we would incur an annual cost of approximately US\$833,000 (Projeto Pé de Pincha, unpublished data), which represents a considerable amount of money considering the current funding shortages and lack of political will in the Brazilian Amazon (44).
320 Therefore, we advocate that this program should develop an independent income stream, ensuring its financial viability in long term. This is critical because the widespread dissatisfaction voiced by beach guards, in terms of financial rewards and respectful societal recognition for their often-perilous efforts, means that many of them are now on the brink of giving up on decades of successful beach protection.

325 There is a lively social justice debate about fair payment mechanisms for tropical biodiversity conservation (45). If rural communities cannot be expected to carry the heavy burden of global biodiversity conservation alone, then more expensive effective support would be required from government or non-government sources. A potential solution would be to collect a proportion of the hatchlings from over-exploited turtle
330 species and raise them in semi-natural conditions to be commercialized once they reach full size. The income generated would cover a large part of the outstanding financial demand. This proposal has been discussed for more than 30 years (46), but wildlife regulations in Brazil (and many tropical countries) are extremely bureaucratic, conservative and prohibitive (47).

335 This study brings an important evidence-based reflection on the socioecological implications of CBCM schemes in tropical freshwater environments. Assessing unintended ecological outcomes, as well as the impacts on target populations, makes an important contribution towards a better understanding of the broader effects of CBCM. Multi-taxa surveys such as ours are typically lacking but are critical to
340 understand the cost-benefit ratio of conservation programs, particularly in tropical countries, which urgently require effective and financially viable conservation strategies. The protection of turtle nesting beaches is a clear example of how rural communities can effectively self-organize to promote population recovery of overexploited species. Such empowerment of remote communities should serve as a

345 positive example within underfunded and understaffed 'paper parks' or even areas
outside PAs that are often neglected by conservation and development projects.

Such a positive outlook contradicts the traditional narrative of the conservation crisis,
serving as a timely example of an optimistic success story (48). However, such
optimism is tempered by a word of caution and should not preclude a critical
350 assessment of potential problems. Despite the impressive value-for-money and clear
conservation benefits for target and non-target species, the continuity of this program
is far from guaranteed. Judging the success or failure of conservation initiatives is
challenging; it is vital to incorporate the opinions of multiple stakeholders and consider
the possibilities for simultaneous contrasting verdicts depending on who is making the
355 judgment. While economic considerations should not prevail over other measures,
ensuring the long-term welfare and boosting morale of local beach-guards is essential
to safeguard the success of this management program.

Sustainable-use protected areas cover large areas of suitable habitats for freshwater
turtles in the Amazon (49), but even well-intentioned PA strategies alone are likely
360 insufficient to ensure their basin-wide conservation. Our study shows that community-
based protection of fluvial beaches represent a strong window of opportunity for multi-
taxa conservation in the lowland Amazon, deserving more attention from local and
national governments, especially considering the dearth of financial resources and
bureaucratic hurdles to implement natural resource management. Given committed
365 investments in CBCM strategies, this model could be replicated across Amazonia,
even by communities outside existing PAs, to serve as a focal point for the
conservation of threatened species and habitats in Amazonian floodplains.

Methods

Study Area. Our study landscape is currently inhabited by some 5,000 legal residents
370 distributed across 73 villages (range = 6 - 110 households per village) along ~1,500
km of the Juruá River, a highly productive major white-water tributary of the Amazon.
This section of the Juruá includes four PAs, comprising two extractive reserves
(Reserva Extrativista: ResEx Baixo Juruá, ResEx Médio Juruá), a sustainable
development reserve (Reserva de Desenvolvimento Sustentável: RDS Uacari) and an
375 indigenous territory (Terra Indígena: TI Deni). During the dry season, extensive sandy
beaches form along convex sections of the main meandering river channel, providing

suitable nesting habitat for several taxonomic groups, including freshwater turtles, resident and migrant birds and iguanid lizards. This river segment included ~ 200 fluvial beaches (mean \pm SD; arc length = $1,337 \pm 1,323$ m, area = 28.2 ± 18.3 ha), with comprehensive multi-taxa population surveys conducted at 28 beaches (14 protected under CBCM, 14 unprotected; Fig. 1).

Beaches were not originally protected at random and were likely selected at least in part according to social and economic factors, as well as pre-existing turtle nesting densities along certain section of the Juruá River. To fully account for such biases, we (1) used a paired spatial design that matched adjacent protected and unprotected beaches sharing otherwise identical social and economic conditions in terms of income generation, livelihoods, market access and human population density, and (2) measured a range of environmental variables to clearly demonstrate the ecological suitability of unprotected beaches that are currently underutilized as turtle nesting habitat.

Assessment of freshwater turtle conservation program. The fluvial beach protection along the Juruá river was initiated to supply meat and eggs to powerful rubber barons, and beach protection was only relinquished to local communities with the final collapse of rubber subsidies. The current CBCM program has a mixed approach, whereby government agencies, NGOs, university researchers and local communities work in partnership to boost the population recovery of this overexploited species. Within the adjacent ResEx Médio Juruá and RDS Uacari there are 14 beaches that have been protected by 42 informal beach-guards (2-4 per beach), who take turns occupying a wooden hut placed in front of the beach, while maintaining full-time (24/7) vigilance during all 5-6 dry season months each year. Beach-guards also conduct a participatory evaluation of nesting success, monitoring the number of nests for all three size-graded turtle species (*P. expansa*, *P. unifilis*, and *P. sextuberculata*), any natural predation or illegal harvesting events, and the number of eggs and hatchlings emerging at each nest. However, the population time-series data are only available for *P. expansa*, which has its population monitored since 1977. Beach vigilance is a high-risk activity, due to the high rates of poaching. In compensation, beach-guards receive a monthly allowance in basic food items (*cesta basica*), representing only ~US\$110 from a partnership between government agencies and university projects. Further details on the CBCM program are available in the

410 Supplementary Information (see Supplementary Methods).

We analyzed 40 years of *P. expansa* population data (1977 – 2016) to assess the potential of this community-based conservation arrangement in achieving the main aim of successfully ensuring sustained release of turtle hatchlings (Supplementary Methods). To examine local awareness of population trends, we also performed 73
415 semi-structured interviews at 73 human settlements with at least six households, 34 of which were inside and 39 outside the four focal PAs (Fig. 1). Interviews were restricted to fisherfolk who had accumulated vast experience and had lived full-time in the community over the last 15 years. To select the interviewees, community leaders were asked to indicate the most reputable and experienced fishermen (or women)
420 within that community. The idea of this assessment was to capture the perception of a highly experienced specialist, rather than a more general but lower-quality perception. We quantified the local perception on turtle population status in 2015-2016 [i.e. rapidly increasing population (more than 3-fold larger than that 15 years ago), increasing, stable, or decreasing] for *P. expansa* at beaches that were frequently used by local
425 dwellers, based on the past baseline over the previous 15 years.

Surveys of non-target taxa. To evaluate the incidental population abundance benefits of systematic beach protection, we used individual and nest counts to sample multiple non-target invertebrate and terrestrial and aquatic vertebrate taxa, in addition to compiling beach-guard data on turtles. We sampled 14 pairs of neighboring
430 protected and unprotected beaches ($N = 28$) during the dry season (August-October) of 2014, targeting the reproductive peak of beach-nesting bird species and the activity peak of migratory catfish. Sampled non-target taxa included migratory and resident beach-nesting birds, caimans, iguana, large catfishes, large-bodied aquatic fauna, and terrestrial invertebrates (Supplementary Methods).

Poaching activities and environmental variables. Poaching activities were
435 quantified in protected and unprotected beaches during a 45-day post-egg-laying period, by monitoring the number of nests that had been raided (Supplementary Methods). We also reconstructed a time series including the number of consecutive years each beach had been protected and quantified two landscape variables related
440 to anthropogenic impact using ArcGIS (v. 10.2): (i) fluvial distance to the nearest human settlement, and (ii) fluvial distance to the nearest urban centre. We calculated the total area of sampled beaches using the most extreme geo-referenced points

along the convex river meander and measuring its maximum width. We also quantified physical characteristics of beaches, including beach gradient within 10 m of the river shoreline and particle grain size, which may influence oviposition in *Podocnemis* (Supplementary Methods, Supplementary Table 3).

Socioeconomic dimension of CBCM. We conducted a total of 40 interviews targeting beach-guards to understand their perceptions on beach protection through CBCM. Interviews lasted up to 30 minutes and recorded perceived benefits of CBCM for local livelihoods and any concerns about the future of the program. We also quantified the relative prevalence of given responses (Supplementary Methods).

Data analysis. We performed generalized linear models (GLMs) to evaluate the variation in the number of nests of *P. expansa* in all 28 beaches (14 protected and 14 unprotected) as a function of all potential predictors. Because the proportions of particle-size classes were correlated, we used only the proportion of coarse sand in the models. We combined all possible models, from the constant model to the full model, represented by *Number of nests* ~ *Years of protection* + *Distance to nearest community* + *Distance to nearest town* + *Beach area* + *Beach slope* + *% Coarse sand*.

Secondly, we performed a model selection based on the lowest Akaike Information Criterion, corrected for small sample sizes (AIC_c). ΔAIC_c represents the difference between the AIC_c and the lowest AIC_c of each model, with $\Delta AIC_c < 2$ representing the most likely set of parsimonious models (50). Finally, we performed a model averaging approach, which represents the beta average of all predictors included in the most parsimonious models. This approach allows the comparison of relative effect sizes of all variables using their z-standardized values.

Because of our explicit pairwise design, we also tested for differences in individual adult and nest abundance recorded during surveys for all sampled taxa using paired t-tests. Finally, we performed linear models (LMs) and generalized linear models (GLMs), using different error structures depending on the data distribution, to examine the potential drivers of individual or nest abundance of the sampled taxa. Model selection procedures followed the same steps described above.

Data availability

The dataset used in this manuscript and analytical scripts are available in the Supplementary Information. Any additional information is available from the authors

475 upon request.

References

1. UNEP-WCMC and IUCN (2016) *Protected Plant Report 2016* (UNEP-WCMC and IUCN, Cambridge, UK and Gland, Switzerland).
- 480 2. Convention on Biological Diversity (2010) Strategic plan for biodiversity 2011-2020 - COP 10, decision X/2.
3. Geldmann J, et al. (2018) A global analysis of management capacity and ecological outcomes in protected areas. *Conserv Lett*:e12434.
4. Gibson L, et al. (2011) Primary forests are irreplaceable for sustaining tropical
485 biodiversity. *Nature* 478:378–81.
5. Sayer J, et al. (2005) Implications for biodiversity conservation of decentralized forest resources management. *The Politics of Decentralization: Forests, Power and People*, eds Pierce Colfer CJ, Capistrano D (Earthscan, London), pp 121–137.
- 490 6. Terborgh J, Peres CA (2017) Do community-managed forests work? A biodiversity perspective. *Land* 6:22.
7. Berkes F (2007) Community-based conservation in a globalized world. *Proc Natl Acad Sci USA* 104:15188–93.
8. Pailler, S., Naidoo, R., Burgess, N. D., Freeman, O. E., & Fisher, B. (2015).
495 Impacts of community-based natural resource management on wealth, food security and child health in Tanzania. *PloS one*, 10(7).
9. Bruner A, Gullison R, Balmford A (2004) Financial costs and shortfalls of managing and expanding protected-area systems in developing countries. *Bioscience* 54:1119–1126.
- 500 10. de Marques AAB, Schneider M, Peres CA (2016) Human population and socioeconomic modulators of conservation performance in 788 Amazonian and Atlantic Forest reserves. *PeerJ* 4:e2206.
11. Campos-Silva JV, Peres CA (2016) Community-based management induces rapid recovery of a high-value tropical freshwater fishery. *Sci Rep* 6:34745.

- 505 12. Naidoo, R., Weaver, L. C., De Longcamp, M., & Du Plessis, P. (2011) Namibia's community-based natural resource management programme: an unrecognized payments for ecosystem services scheme. *Environ Conserv*, 38(4), 445-453.
13. Somanathan E, Prabhakar R, Singh B (2009) Decentralization for cost effective conservation. *Proc Natl Acad Sci USA* 106:4143–4147.
- 510 14. Dorresteijn I, et al. (2015) Incorporating anthropogenic effects into trophic ecology: predator–prey interactions in a human-dominated landscape. *Proc R Soc B Biol Sci* 282:20151602.
15. Castello L, et al. (2013) The vulnerability of Amazon freshwater ecosystems. *Conserv Lett* 6:217–229.
- 515 16. Schneider L, Ferrara CR, Vogt RC, Burger J (2011) History of turtle exploitation and management techniques to conserve turtles in the Rio Negro basin of the Brazilian Amazon. *Chelonian Conserv Biol* 10:149–157.
17. Berkes F (2009) Evolution of co-management: role of knowledge generation, bridging organizations and social learning. *J Environ Manage* 90:1692–1702.
- 520 18. Barrett CB, Brandon K, Gibson C, Gjertsen H (2001) Conserving tropical biodiversity amid weak institutions. *Bioscience* 51:497–502.
19. Evans L, Cherrett N, Pemsil D (2011) Assessing the impact of fisheries co-management interventions in developing countries: a meta-analysis. *J Environ Manage* 92:1938–1949.
- 525 20. Cantarelli VH, Malvasio A, Verdade LM (2014) Brazil's *Podocnemis expansa* conservation program: retrospective and future directions. *Chelonian Conserv Biol* 13:124–128.
21. Gibbons JW, et al. (2000) The global decline of reptiles, déjà vu amphibians. *Bioscience* 50:653–666.
- 530 22. Van Vliet N, et al. (2015) Ride, shoot, and call: wildlife use among contemporary urban hunters in Três Fronteiras, Brazilian Amazon. *Ecol Soc* 20:8.
23. Prestes-Carneiro G, Béarez P, Bailon S, Py-Daniel AR, Neves EG (2016) Subsistence fishery at Hatahara (750–1230 CE), a pre-Columbian central

- 535 Amazonian village. *J Archaeol Sci Reports* 8:454–462.
24. Antunes AP, et al. (2016) Empty forest or empty rivers? A century of commercial hunting in Amazonia. *Sci Adv* 2:e1600936–e1600936.
25. Peres CA (2000) Effects of Subsistence Hunting on Vertebrate Community Structure in Amazonian Forests. *Conserv Biol* 14:240–253.
- 540 26. Caputo FP, Canestrell D, Boitani L (2005) Conserving the terecay (*Podocnemis unifilis*, Testudines: Pelomedusidae) through a community-based sustainable harvest of its eggs. *Biol Conserv* 126:84–92.
27. Conway-Gómez K (2007) Effects of human settlements on abundance of *Podocnemis unifilis* and *P. expansa* turtles in northeastern Bolivia. *Chelonian Conserv Biol* 6:199–205.
- 545 28. Peñaloza CL, Hernández O, Espín R, Crowder LB, Barreto GR (2013) Harvest of endangered sideneck river turtles (*Podocnemis* spp.) in the Middle Orinoco, Venezuela. *Copeia* 2013:111–120.
29. McClenachan L, Jackson JBC, Newman MJH (2006) Conservation implications of historic turtle beach loss nesting. *Front Ecol Environ* 4:290–296.
- 550 30. Peres CA, Palacios E (2007) Basin-wide effects of game harvest on vertebrate population densities in Amazonian forests: implications for animal-mediated seed dispersal. *Biotropica* 39:304–315.
31. Endo W, Peres CA, Haugaasen T (2016) Flood pulse dynamics affects exploitation of both aquatic and terrestrial prey by Amazonian floodplain settlements. *Biol Conserv* 201:129–136.
- 555 32. Hallwass G, Lopes PF, Juras AA, Silvano RAM (2011) Fishing effort and catch composition of urban market and rural villages in Brazilian Amazon. *Environ Manage* 47:188–200.
- 560 33. Petre M, Barthem RB, Córdoba EA, Gómez BC (2004) Review of the large catfish fisheries in the upper Amazon and the stock depletion of piraíba (*Brachyplatystoma filamentosum* Lichtenstein). *Rev Fish Biol Fish* 14:403–414.
34. Smith NJH (1981) Caimans, capybaras, otters, manatees, and man in Amazonia. *Biol Conserv* 19:177–187.

- 565 35. Da Silveira R, Thorbjarnarson JB (1999) Conservation implications of commercial junting of black and spectacled caiman in the Mamirauá Sustainable Development Reserve, Brazil. *Biol Conserv* 88:103–109.
- 36 Mendonça WCDS, Marioni B, Thorbjarnarson JB, Magnusson WE, Da Silveira R (2016) Caiman hunting in Central Amazonia, Brazil. *J Wildl Manage* 80:1497–1502.
- 570 37. Peres CA, Carkeek AM (1993) How caimans protect fish stocks in western Brazilian Amazonia - a case for maintaining the ban on caiman hunting. *Oryx* 27:225–230.
38. Downing AL, Brown BL, Leibold MA (2014) Multiple diversity-stability mechanisms enhance population and community stability in aquatic food webs. *Ecology* 95:173–184.
- 575 39. del Viejo AM, Vega X, González MA, Sánchez JM (2004) Disturbance sources, human predation and reproductive success of seabirds in tropical coastal ecosystems of Sinaloa State, Mexico. *Bird Conserv Int* 14:191–202.
- 580 40. Laundré JW, Hernandez L, Ripple WJ (2010) The landscape of fear: ecological implications of being afraid. *Open Ecol J* 3:1–7.
41. Whelan CJ, Wenny DG, Marquis RJ (2008) Ecosystem services provided by birds. *Ann N Y Acad Sci* 1134:25–60.
42. Cederholm CJ, Kunze MD, Murota T, Sibatani A (1999) Pacific salmon carcasses: essential contributions of nutrients and energy for aquatic and terrestrial ecosystems. *Fisheries* 24:6–15.
- 585 43. Alves RRN, et al. (2012) A review on human attitudes towards reptiles in Brazil. *Environ Monit Assess* 184:6877–6901.
- 44 Campos-Silva, J. V., da Fonseca Junior, S. F., & Peres, C. A. D. S. (2015). Policy reversals do not bode well for conservation in Brazilian Amazonia. *Nat Conservacao*, 13(2), 193-195.
- 590 45. Ferraro PJ, Kiss A (2002) Direct payments to conserve biodiversity. *Science* 298:1718–1719.
46. Alho, C. J. (1985). Conservation and management strategies for commonly

- 595 exploited Amazonian turtles. *Biol Cons*, 32(4), 291-298.
47. Campos-Silva, J. V., Peres, C. A., Antunes, A. P., Valsecchi, J., & Pezzuti, J. (2017). Community-based population recovery of overexploited Amazonian wildlife. *PECON*, 15(4), 266-270.
48. Balmford A, Knowlton N (2017) Why Earth Optimism? *Science* 356:225.
- 600 49. Fagundes CK, Vogt RC, De Marco Júnior P (2016) Testing the efficiency of protected areas in the Amazon for conserving freshwater turtles. *Divers Distrib* 22:123–135.
50. Burnham KP, Anderson DR (2002) *Model Selection and Multimodel Inference: a practical information-theoretic approach* (Springer-Verlag, New York).

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Author contributions

J.V.C.S., J.E.H., and C.A.P. designed the study; J.V.C.S, J.E.H., P.C.M.A., and C.A.P. collected the data; J.V.C.S and C.A.P. analyzed the data; J.V.C.S, J.E.H., P.C.M.A and C.A.P. wrote the paper.

Competing interests

The authors declare no competing interests.

Figure legends

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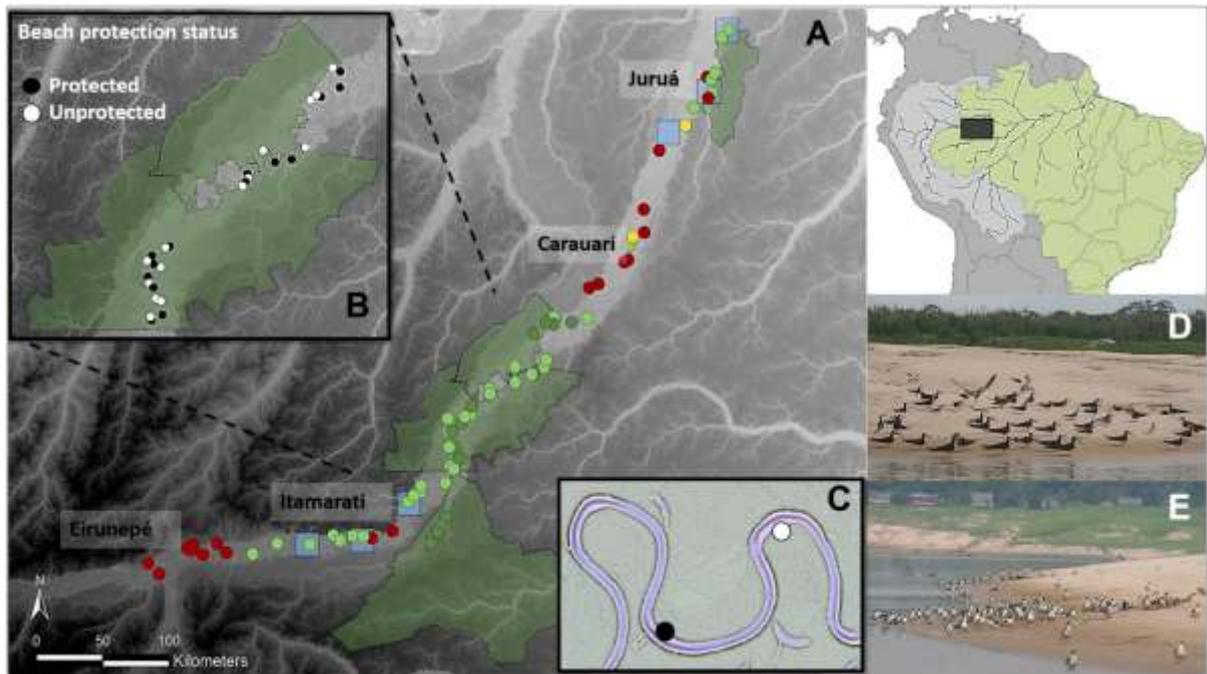
Figure 1. Map of the study region in western Brazilian Amazonia. (a) Local ecological perceptions from highly experienced fishers at 73 human settlements over ~1,500 km of the Juruá River regarding the population recovery of Giant South American Turtles. Red, light and dark green circles represent communities for which local informants perceive either a decline, an increase or a large increase in population sizes over the last 15 years. Yellow circles represent stable populations that had not appreciably changed over time. Blue squares indicate protected beaches that were not sampled in this study. Green polygons represent the boundaries of the four protected areas. Insets show: (b) location of the 28 study beaches, and (c) representation of the paired sampling design. Black and white circles indicate paired protected and unprotected beaches, respectively. Photos (d - e) show two examples of protected beaches.

Figure 2. Paired nesting and abundance responses for target and non-target taxa. (a) Giant South American Turtle (*P. expansa*) nesting, (b) Yellow-spotted River Turtle (*P. unifilis*) nesting, (c) Six-tubercled River Turtle (*P. sextuberculata*) nesting, (d) continental migrant bird nesting, (e) *Chordeiles rupestris* nesting, (f) *Iguana iguana* nesting, (g) continental migrant birds, (h) Sand-colored Nighthawk (*Chordeiles rupestris*), (i) terrestrial invertebrates, (j) large catfishes, (k) Black Caiman (*Melanosuchus niger*), (l) aquatic megafauna. Yellow and purple boxplots represent protected (PB) and unprotected beaches (UB).

Figure 3. Standardized size effect for all predictors of freshwater turtle nests. (a) Giant South American Turtle (*P. expansa*); (b) Yellow-spotted River Turtle (*P. unifilis*) and (c)

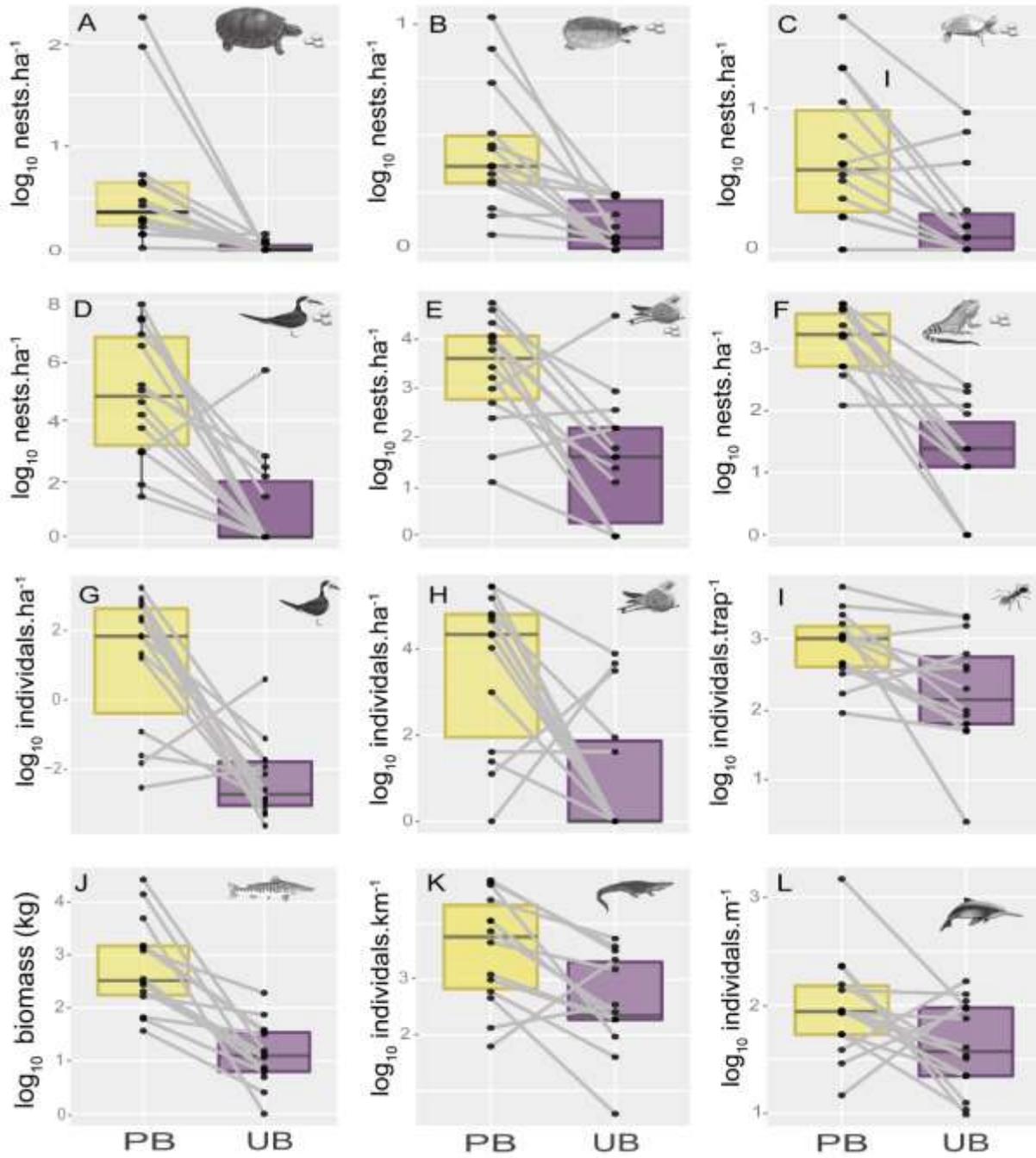
Six-tubercled River Turtle (*P. sextuberculata*). The mean estimates are represented by dots, and horizontal lines represent 95% confidence intervals (CI). For significant variables, CIs do not cross the vertical dotted line at zero. Blue and red estimates indicate significant positive and negative effects, respectively. Photo credit: Camila Ferrara.

Figure 1.



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685 Figure 3.

