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Unintended multispecies co-benefits of an Amazonian community-based conservation programme

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Urgent challenges posed by widespread degradation in tropical ecosystems with poor governance require new development pathways to reconcile biodiversity conservation and human welfare. Community-based conservation management has shown potential for integrating socio-economic needs with conservation goals in tropical environments; however, assessing the effectiveness of this approach is often held back by the lack of comprehensive ecological assessments. We conduct a robust ecological evaluation of the largest community-based conservation management initiative in the Brazilian Amazon over the last 40 years. We show that this programme has induced large-scale population recovery of the target giant South American turtle (*Podocnemis expansa*) and other freshwater turtles along a 1,500-km section of a major tributary of the Amazon River. Poaching activity on protected beaches was around 2% compared to 99% on unprotected beaches. We also find positive demographic co-benefits across a wide range of non-target vertebrate and invertebrate taxa. As a result, beaches protected by local communities represent islands of high biodiversity, while unprotected beaches remain 'empty and silent', showing the effectiveness of empowering local conservation action, particularly in countries experiencing shortages in financial and human resources.

Protected areas comprise the most prominent conservation strategy to address overexploited wildlife populations worldwide. Expansion of the global protected area network, with >200,000 now established terrestrial protected areas[1], has moved towards the target of 17% of terrestrial and inland water areas[2]. Meta-analyses investigating protected area effectiveness[3] remain limited by biases in the global distribution of existing protected areas for which interventions and outcomes are known, and comparable data from unprotected areas. In addition, most protected areas 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 demographic outcomes for resource populations remains contentious[5], and the relative conservation performance of exploited and unexploited species within human-occupied protected areas 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, community-based conservation management (CBCM) has shown great potential for integrating socio-economic needs with conservation goals[7,8], particularly in tropical countries where protected areas created on paper are often severely understaffed and underfunded[9], and resource management institutions are frail or non-existent[10]. Some initiatives have demonstrated enhanced livelihoods for resident communities while contributing to biodiversity conservation, even in complex socioecological systems where interactions are dynamic and reciprocal[11,12]. CBCM initiatives may potentially fill this protected area implementation gap by effectively strengthening surveillance systems with full-time physical presence, decentralizing resource stewardship and reducing reserve management costs[13].

Most studies on 'no-take' areas are focused on the population recovery of target species; however, 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 of a target species[14]; however, because unintended indirect interactions can lag behind the direct effects of protection, their quantitative detection is often challenging. Assessing both the 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].

In the current study, we assess the effectiveness of a CBCM programme in the western Brazilian Amazon, targeting the giant South American turtle (*Podocnemis expansa*), yellow-spotted river turtle (*Podocnemis unifilis*) and six-tubercled river turtle (*Podocnemis sextuberculata*). Following severe and long-term population declines caused by historical overexploitation[16], turtle nesting beaches (locally known as *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 programme for adult female

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and hatchling turtles, including a 40-year data set 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 catfish, large-bodied aquatic fauna and terrestrial invertebrates. The spatial design of this multi-taxa assessment allows us to contrast the conservation effectiveness of formal protected areas 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 interview 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 ± s.d.; length = 2,395.1 ± 774.6 m) across the Juruá River increased the number of nests of *P. expansa* by a factor of 11.4 (±12.9, $N=15$) and their hatchlings per beach by 9.7-fold (±8.7, $N=15$) on average (Supplementary Fig. 1). This amounts to a mean of 71,087 (±6,501) more hatchlings released every year on protected beaches. This clear upturn in records of successful turtle nests and hatchlings is supported by widespread reports of recovery in adult turtle populations by local people. In all 52 villages sampled near protected beaches, experienced fishers reinforced reports that the *P. expansa* population had rapidly increased over the last 15 years (2000–2015). In contrast, all 19 local communities reporting population declines were located far from protected beaches (Fig. 1).

Collateral benefits for non-target species. Our multi-taxa surveys on protected and unprotected beaches also revealed the strong positive effects of beach guarding for other vertebrate and invertebrate species (Fig. 2). All terrestrial and aquatic taxa surveyed exhibited higher abundance on protected beaches, as emphasized by visual and acoustic cues (Supplementary Fig. 2 and Supplementary Video 1). The impact on the abundance of terrestrial biodiversity was impressive. Protected beaches hosted a much higher number of all avian taxa (Supplementary Fig. 3). Population sizes of the migratory black skimmer (*Rynchops niger*), for example, were 80-fold higher on protected beaches, compared to unprotected beaches (protected beach: 3.3 ± 2.4 individuals ha^{-1}; unprotected beach: 0.04 ± 2.2 individuals ha^{-1}; paired *t*-test: $t=5.2$, $P<0.05$). This mirrored other migratory bird species, including the large-billed tern (*Phaetusa simplex*; protected beach: 5 ± 4.8 individuals ha^{-1}; unprotected beach: 0.17 ± 4.6 individuals ha^{-1}; $t=4.3$, $P<0.05$) and the sand-coloured nighthawk (*Chordeiles rupestris*; protected beach: 3.2 ± 2.9 individuals ha^{-1}; unprotected beach: 0.3 ± 2.7 individuals ha^{-1}; $t=4.5$, $P<0.05$). Considering nest counts, protected beaches hosted 8,700 nests of migratory bird species (black skimmer and large-billed tern), compared to only 371 nests on unprotected beaches. The same pattern was found for sand-coloured nighthawk, which show almost fourfold more nests on protected beaches. These differences extended to green iguanas (*Iguana iguana*; Supplementary Fig. 3), whose nests were almost seven times more abundant on protected beaches (protected beach: 0.8 ± 0.5 nests ha^{-1}; unprotected beach: 0.1 ± 0.5 nests ha^{-1}; $t=8.1$, $P<0.001$). Model averaging of generalized linear models (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 Fig. 4). Pitfall surveys of terrestrial arthropods (yielding 4,401 individuals, representing 11 orders) showed that total abundance was almost twofold higher on protected (196.2 ± 9.86 individuals $trap^{-1}$) than unprotected beaches (116.6 ± 9.84 individuals $trap^{-1}$; $t=3.3$, $P<0.05$). Orthopterans comprised the most abundant order of insects (3,307 individuals; 13.1 ± 9.8 individuals $trap^{-1}$), followed by coleopterans (649 individuals; 3.6 ± 9.8 individuals $trap^{-1}$).

For aquatic taxa, higher abundance of the large-bodied black caiman (*Melanosuchus niger*) similarly was found on protected beaches (protected beach: 12.1 ± 5.2 individuals km^{-1}; unprotected beach: 7.4 ± 18.0 individuals km^{-1}; $t=4.25$, $P<0.05$). The average biomass of large catfish (order Siluriformes, Supplementary Fig. 5) in the river channel was sixfold higher next to protected (mean ± s.d.; 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. (For a full list of species, see Supplementary Table 1.) The only exception was for aquatic megafauna, where sonar detection surveys showed no significant differences between protected (0.97 ± 0.5 individuals m^{-1}) and unprotected beaches (0.65 ± 0.5 individuals m^{-1}; $t=1.82$, $P=0.09$). However, in our multivariate model, years of beach protection had a significantly positive effect on the abundance of aquatic megafauna detected by sonar surveys (Supplementary Fig. 4).

Conservation effectiveness of CBCM. Community-based protection strongly ensures the reproductive success of *P. expansa*, representing 58 times more nests on protected beaches (protected beaches: 584 nests; unprotected beaches: 10; $t=2.20$, $P<0.05$). *P. unifilis* and *P. sextuberculata* also benefited 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 ($\beta=1.4\pm0.14$), followed by the declivity of the beach terrain ($\beta=-0.71\pm0.14$) and non-linear distance to the nearest human village ($\beta=-0.31\pm0.13$), 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.

Socio-economic dimension of CBCM. A total of 40 interviewed beach guards reported positive dividends from beach protection, but also expressed genuine concerns over the sustainability of this CBCM programme in the long term (Supplementary Table 2). Positive outcomes included the population recovery of turtle species that represent an important subsistence food resource, and the strengthening of sociocultural identity. Conversely, informants were concerned about: (1) the failing of the CBCM programme to generate a source of tangible financial return; (2) insufficient support from government agencies, including shortages of basic equipment and material investments; and (3) 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 confronting recalcitrant poachers. The main reason 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.

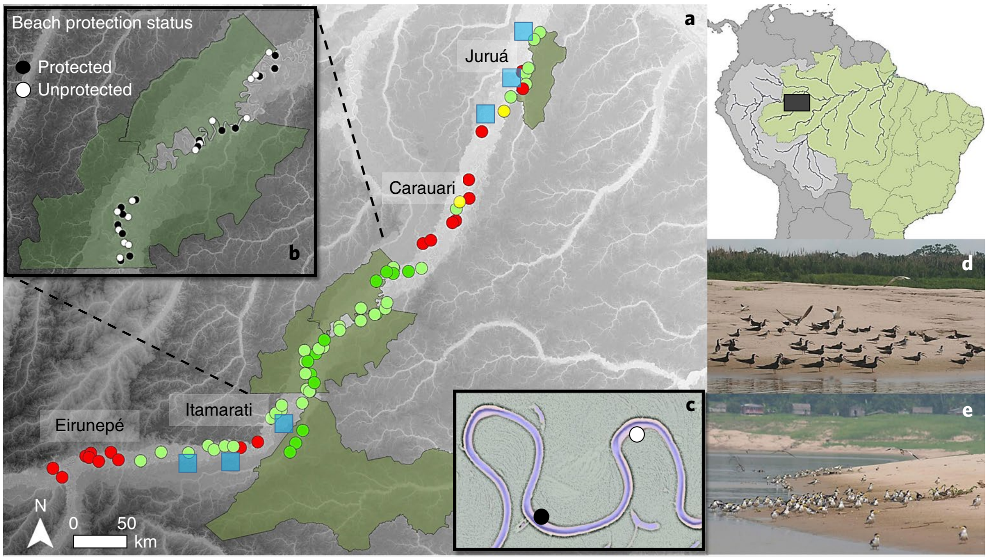

Fig. 1 | Map of the study region in the western Brazilian Amazon region. a, Local ecological perceptions from highly experienced fishers at 73 human settlements along ~1,500 km of the Juruá River regarding the population recovery of giant South American turtles. The red, and light and dark green, circles represent the communities for which local informants perceive either a decline, an increase or a large increase in population sizes over the last 15 years, respectively. The yellow circles represent stable populations that had not appreciably changed over time. The blue squares indicate protected beaches that were not sampled in this study. The green polygons represent the boundaries of the four protected areas. **b**, Inset showing the location of the 28 study beaches. **c**, Inset showing the representation of the paired sampling design. The black and white circles indicate paired protected and unprotected beaches, respectively. **d**,**e**, Examples of protected beaches.

Discussion

The challenge of conserving tropical environments is often exacerbated by limited 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 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 (1) these benefits are not ensured inside protected areas without CBCM initiatives and (2) that they are coupled with unintended benefits for multiple non-target taxa, which are 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 programmes.

Freshwater turtles are one of the most threatened vertebrate taxa[21], following long-term exploitation, from pre-Columbian indigenous people to the contemporary Amazonian dwellers of mixed indigenous and European descent[22,23]. After the Brazilian Fauna Protection Law was brought into effect in 1967, followed by the ratification of CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) in 1975 and the Rio Convention on Biological Diversity in 1992, many 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 because the accessibility of fluvial habitats makes them much more vulnerable to human pressure, which is invariably concentrated along Amazonian rivers[25].

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 Fig. 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 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]; similarly, CBCM has also become a strong opportunity to protect overharvested freshwater turtles[20].

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 neighbourhood 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 contribute to collective surveillance. The same pattern was detected for *Arapaima gigas* (*pirarucu*) 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 centred in small towns near protected areas can exert substantial additional pressure on turtle populations[28].

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 protected areas. In contrast, the CBCM approach reduced nest raiding to just 2.1% on guarded beaches. While the effects of protection within protected area boundaries are highly 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

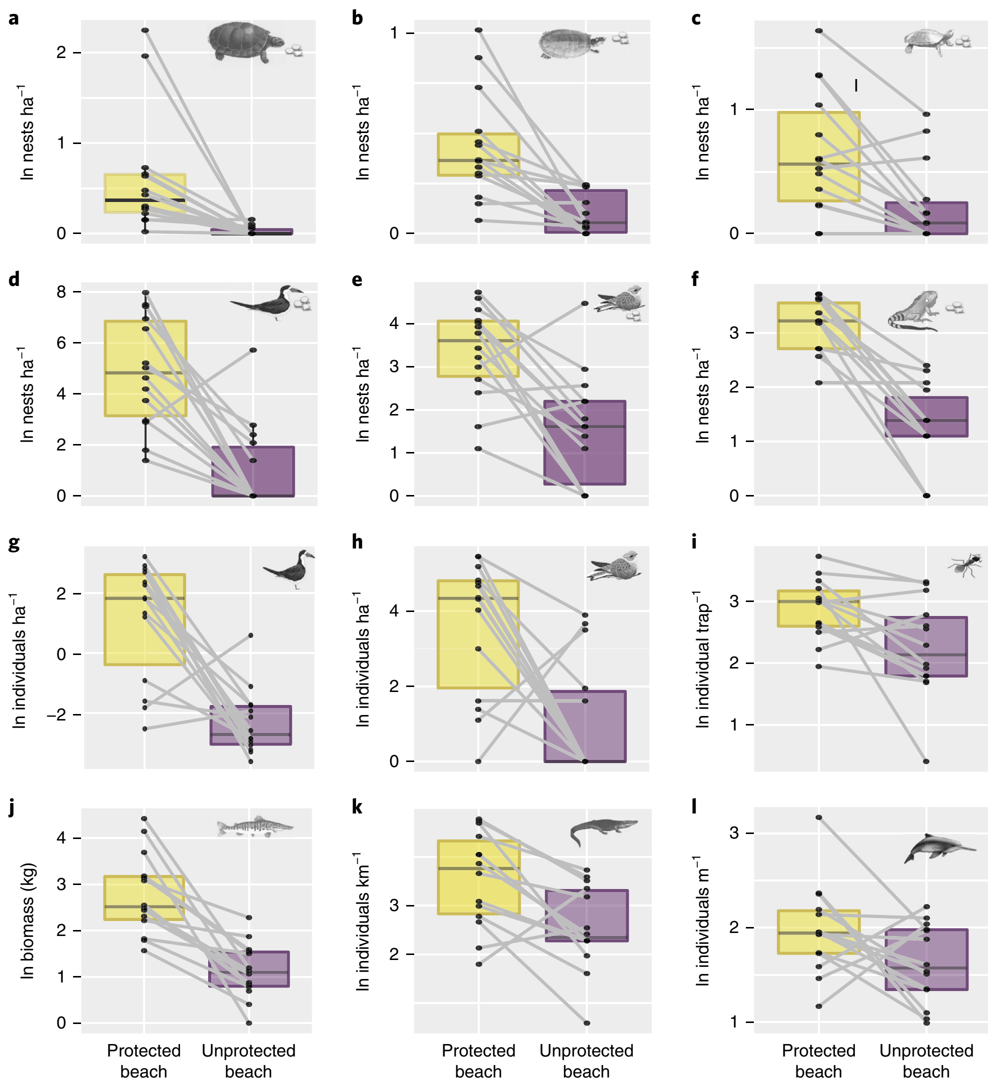

Fig. 2 | Paired nesting and abundance responses for target and non-target taxa. **a**, Giant South American turtle (*P. expansa*) nesting. **b**, Yellow-spotted river turtle (*P. unifilis*) nesting. **c**, Six-tubercled river turtle (*P. sextuberculata*) nesting. **d**, Continental migrant bird nesting. **e**, Sand-coloured nighthawk (*C. rupestris*) nesting. **f**, Green iguana (*I. iguana*) nesting. **g**, Continental migrant birds. **h**, Sand-coloured nighthawk. **i**, Terrestrial invertebrates. **j**, Large catfish. **k**, Black caiman (*M. niger*). **l**, Aquatic megafauna. The yellow and purple boxplots represent protected and unprotected beaches, respectively.

for population recovery. Existing protected beaches are still patchy and relatively few; however, they are representative of the physical characteristics of hundreds of unprotected beaches throughout the length of the Juruá River (Supplementary Fig. 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 catfish 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 crocodilians, 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, fishers often resort to killing caimans at any unprotected site because they raid and damage gill nets 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 could not 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 probably because uncontrolled commercial fishing boats are permitted to transit throughout major waterways even within protected areas, 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 from beaches to the river. This potential ecological cascade exacerbates the critical role of 'no-take'

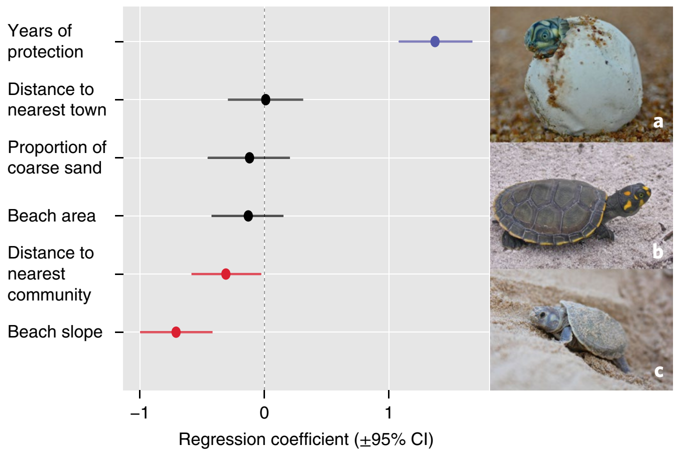

Fig. 3 | Standardized size effect for all predictors of freshwater turtle nests. **a**, Giant South American turtle (*P. expansa*). **b**, Yellow-spotted river turtle (*P. unifilis*). **c**, Six-tubercled river turtle (*P. sextuberculata*). The mean estimates are represented by the dots; the horizontal lines represent the 95% confidence intervals (CIs). For significant variables, the 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.

areas in overall community stability, since the species richness and abundance of apex predators are pivotal contributors to the stability of aquatic food webs[38].

The high concentration of both breeding adults and nests of black skimmers, large-billed terns and sand-coloured 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 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. 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 the necromass generated by dead animals, eggs and other carcases probably indicates a stronger bottom-up effect on protected beaches[42]. Likewise, the occurrence of green iguana nests at much 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 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; this figure could be much lower if we included all turtle species. Considering the wide-ranging ecological benefits combined with minimal implementation costs, this programme represents a high value-for-money conservation 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.

Currently, there are about 390 protected nesting sites maintained through CBCM initiatives in the Brazilian Amazon (Supplementary Fig. 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]. Therefore, we advocate that this programme should develop an independent income stream, ensuring its financial viability in the 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.

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 governmental or non-governmental sources. A potential solution would be to collect a proportion of the hatchlings from overexploited turtle 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].

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 understand the cost–benefit ratio of conservation programmes, 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 positive example within underfunded and understaffed 'paper parks' or even areas outside protected areas 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 assessment of potential problems. Despite the impressive value for money and clear conservation benefits for target and non-target species, the continuity of this programme 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 judgement. 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 programme.

Sustainable use protected areas cover large areas of suitable habitats for freshwater turtles in the Amazon[49], but even well-intentioned protected area strategies alone are probably insufficient to ensure their basin-wide conservation. Our study shows that community-based protection of fluvial beaches represents 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 investments in CBCM strategies, this model could be replicated across the Amazon region, even by communities outside existing protected areas, to serve as a focal point for the conservation of threatened species and habitats in the Amazonian floodplains.

Methods

Study area. Our study landscape is currently inhabited by some 5,000 legal residents 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 protected areas, comprising two extractive reserves (Reserva Extrativista: RESEX do Baixo Juruá; RESEX do Médio Juruá), a sustainable development reserve (Reserva de Desenvolvimento Sustentável (RDS) Uacari) and an indigenous territory (Terra Indígena 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 ± s.d.; arc length = 1,337 ± 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 probably 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 habitats.

Assessment of freshwater turtle conservation programme. The fluvial beach protection along the Juruá River was initiated to supply meat and eggs to powerful rubber barons; beach protection was only relinquished to local communities with the final collapse of rubber subsidies. The current CBCM programme has a mixed approach, whereby government agencies, non-governmental organizations, university researchers and local communities work in partnership to boost the population recovery of this overexploited species. Within the adjacent RESEX do 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, fisherpopulation time-series data are only available for *P. expansa*, whose population has been monitored since 1977. Beach vigilance is a high-risk activity because of 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 governmental agencies and university projects. Further details on the CBCM programme are available in the Supplementary Information (see Supplementary Methods).

We analysed 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 semi-structured interviews at 73 human settlements with at least six households, 34 of which were inside and 39 outside the four focal protected areas (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 fishers (men or women) 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 (that is, rapidly increasing population (more than threefold larger than that 15 years ago), increasing, stable or decreasing) for *P. expansa* at beaches that were frequently used by local 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 neighbouring 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 catfish, large-bodied aquatic fauna and terrestrial invertebrates (Supplementary Methods).

Poaching activities and environmental variables. Poaching activities were 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 to anthropogenic impact using ArcGIS (v10.2): (1) fluvial distance to the nearest human settlement; and (2) 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 the 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).

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

Data analysis. We performed 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 to the full model, represented by the number of nests (a function of years of protection + distance to nearest community + distance to nearest town + beach area + beach slope + % coarse sand).

Second, we performed a model selection based on the lowest Akaike information criterion (AIC), 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 applied a model averaging approach, which represents the beta average of all predictors included in the most parsimonious models. This approach allows the comparison of the 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 one-tailed *t*-tests. Finally, we performed linear models and 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 earlier.

Data availability

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

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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. analysed 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.

Additional information

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