RESTORATION ECOLOGY
The Journal of the Society for Ecological Restoration

SER SOCIETY FOR ECOLOGICAL RESTORATION

RESEARCH ARTICLE

Active restoration leads to rapid recovery of aboveground biomass but limited recovery of fish diversity in planted mangrove forests of the North Brazil Shelf

Mark A. Ram[1,2], T. Trevor Caughlin[3], Anand Roopsind[4]

Coastal degradation has spurred active restoration of mangrove ecosystems, from local initiatives to global commitments to increase mangrove forest area by 20% over the next decade. Mangrove restoration projects typically have multiple objectives, including carbon storage, coastal resilience, and fisheries recovery. How planting seedlings, the most common form of active restoration, can promote recovery of mangrove ecosystem functions remains an urgent research need. We quantified multiple ecosystem outcomes of Guyana's national mangrove restoration program, approximately a decade after seedling planting, and compared restoration outcomes with conditions in intact and degraded mangrove forests. Multivariate analyses indicate that intact and restored sites' environmental conditions were similar to each other but different from degraded sites. Aboveground biomass in restored sites (103 Mg ha^{-1}) was 13 and 99% greater than intact (89.4 Mg ha^{-1}) and degraded (0.12 Mg ha^{-1}) sites, respectively. Active restoration successfully increased seedling abundance of both planted and unplanted species, with similar abundance between intact and restored sites. In contrast, fish communities in restored sites remained similar to degraded sites. Restored sites were dominated by a single algivorous fish species, with lower species diversity and commercially valuable fisheries than intact sites. Our results demonstrate that active restoration is a viable option to restore mangrove forest tree biomass and tree species composition in this region. However, even under a best-case scenario for mangrove forest restoration, fisheries did not recover during our study's timespan. Long-term monitoring and controlled experiments will be essential to further understand restoration outcomes for multiple ecosystem services in mangrove forests.

Key words: aboveground tree biomass, active restoration, coastal resilience, fisheries, mangrove ecosystems, natural climate solution

Implications for Practice

- Active restoration of mangrove forests supports rapid recovery of aboveground tree biomass.
- Recovery of fisheries will require longer time or additional restoration interventions beyond planting of mangroves.
- With appropriate site selection protocol, national- scale mangrove-replanting initiatives can successfully reestablish mangrove forest structure.

Introduction

Mangrove forests play an important role in coastal ecosystems with a range of functions that support millions of people (Barbier et al. 2011; Friess et al. 2019). These mangrove ecosystem services include coastal protection from storms, climate mitigation through carbon storage and sequestration (Donato et al. 2011; Alongi 2014), and supporting functions to fisheries (Aburto-Oropeza et al. 2008; Barbier et al. 2011). Intense resource pressure on mangrove forests over the past century has resulted in significant declines in the global mangrove forest extent (Gorman 2018; Friess et al. 2019). The protection and restoration of mangrove forests are also considered important actions for climate change mitigation based on the high-carbon density per area of mangrove forest cover (Griscom et al. 2017, 2020). In response to the importance of mangrove forests as a natural climate solution, international agencies and

Author contributions: MR designed the study and collected field data; AR, TTC analyzed the data; MR, AR, TTC wrote and edited the manuscript.

[1]Department of Biology, University of Guyana, Turkeyen Campus, Georgetown, Guyana
[2]Address correspondence to M. A. Ram, email mark.ram@uog.edu.gy
[3]Department of Biological Sciences, Boise State University, Boise, Idaho 83725, U.S.A.
[4]Center for Natural Climate Solutions, Conservation International, 2011 Crystal Drive, Suite 600, Arlington, Virginia 22202, U.S.A.

doi: 10.1111/rec.13400
Supporting information at:
http://onlinelibrary.wiley.com/doi/10.1111/rec.13400/suppinfo

national governments have launched ambitious goals to restore mangrove forest cover across degraded estuarine and coastal areas. The United Nations, for example, has set a commitment to restore 20% of mangrove forests by 2030 (Waltham et al. 2020). Achieving these goals will require evaluating the efficacy of different restoration treatments for mangrove ecosystem services (Ellison 2000; Lee et al. 2019).

The most fundamental decision when restoring any ecosystem is whether active restoration is required or whether the ecosystem will be able to recover naturally with minimum human intervention (Holl & Aide 2011). There is ample evidence that natural regeneration of mangrove forests is possible after severe disturbance, including oil spills (Duke et al. 1999), hypersalinization (Twilley et al. 1999), and hurricanes (Imbert 2018). Nevertheless, long-term recovery rates of naturally regenerating mangrove forests are highly variable. They require favorable environmental conditions, including appropriate tidal hydrology (Lewis 2005), fertile soil (Chen & Twilley 1998), and low wave exposure (Duke et al. 1999). Planting mangrove trees, as propagules or as nursery-grown plants, can promote faster recovery, particularly for tree biomass (Bosire et al. 2008; Ferreira et al. 2015; Das 2017; Kodikara et al. 2017). However, project costs of mangrove planting can be prohibitive, particularly over large areas (Lee et al. 2019). In some cases, mangrove planting can even result in worse ecological outcomes than natural regeneration, including decreased seedling abundance (Duke et al. 1999) and lower mangrove species richness (Rovai et al. 2012; Ferreira et al. 2015). These potential functional trade-offs point to the need for studies that evaluate costs and benefits of planting mangroves for multiple restoration outcomes (Lewis 2010).

In addition to forest vegetation regrowth for carbon storage and coastal protection (Menéndez et al. 2020), recovery of fish and invertebrate communities is a critically important restoration outcome. Fisheries recovery after mangrove restoration can translate into major economic benefits; e.g. mangrove restoration contributed nearly half a billion dollars to the fishery sector in the Indian state of Gujarat by increasing commercial fish catch (Das 2017). The supporting functions that mangroves provide to fisheries can also motivate community involvement in mangrove restoration and conservation projects (Walton et al. 2006). An underlying assumption of many mangrove-replanting projects that seek to increase fish stocks is that animals will return once habitat structure recovers, an example of a "field of dreams" strategy for faunal communities during restoration (sensu Hilderbrand et al. 2005).

However, the successful restoration of mangrove forest structure and environmental factors does not always lead to fish biodiversity recovery. Several studies have found divergent patterns of macrofaunal abundance in restored mangrove sites relative to intact forested mangrove habitats (Al-Khayat & Jones 1999; Huxham et al. 2004). Fish utilization of restored mangrove habitat is also highly context-dependent based on species-specific life stages (Lewis & Gilmore 2007; Sheaves 2017). Given the current debate on when and where active restoration of mangroves is necessary (Lee et al. 2019), comparisons of fish assemblages among intact, degraded, and actively restored mangrove habitats will provide needed insight on ecosystem functions provided by mangrove restoration.

In this study, we evaluate the ecological outcomes of a national- scale mangrove-replanting program in Guyana. As the vast majority of the Guyanese population and economic activities occur along the Atlantic coast, mangrove forests are considered a critical component of its national strategy to mitigate and adapt to climate change impacts, especially sea-level rise (Vaughn 2017). Mangrove forests also provide important supporting functions that benefit the fisheries sector in Guyana. A recent economic analysis indicates that mangrove deforestation has caused significant losses to Guyanese fishing revenue (Millar et al. 2019). The loss of mangrove forests has led to a national-scale restoration program to increase mangrove forest cover with the goals of improved coastal community resilience and restoration of fisheries (Anthony & Gratiot 2012). This study evaluates restoration outcomes in mangrove forests that include the main ecosystem attributes of environmental factors, vegetation structure, and fish biodiversity along the North Brazil Shelf of Guyana. We tested the following hypotheses (H):

H1. Active restoration results in improved recovery of mangrove biomass, mangrove seedling abundance, and environmental conditions.
H2. Conditional on H1, we hypothesized that the fish community in actively restored sites would be more similar to intact mangrove forest sites than to degraded mangrove sites.

Methods

Study Site

We conducted the study along Guyana's Atlantic coast, part of the North Brazil Shelf (Fig. 1). Mangrove forests in this region are characterized by the dominance of *Avicennia germinans* (black mangrove), *Rhizophora* spp. (*R. mangle* and *R. racemosa*; red mangrove), *Laguncularia racemosa* (white mangrove), and *Conocarpus erecta* (buttonwood). The understory of these mangrove forests includes two fern species, *Acrostichum aureum* and *Acrostichum danaeifolium*, as well as multiple other herbaceous species (Pastakia 1991). Mangrove forests along the North Brazil Shelf are impacted by cyclic erosion and accretion processes that occur through tidal wave action (Toorman et al. 2018). In addition to these natural processes, mangrove forests are also subject to harvesting pressure for use as firewood (charcoal) and timber poles (Millar et al. 2019).

The mangrove restoration program in Guyana was initiated in 2010 through funding from the European Union under the Global Climate Change Alliance and Guyana's Government (GCCA+ 2018) and implemented by Guyana's National Agricultural Research and Extension Institute (NAREI). The replanting program goal was to increase mangrove forest area and reestablish ecosystem services to support coastal zone protection and sustainable livelihood opportunities for coastal communities. Restoration of mangrove forests in Guyana is considered a main climate adaptation strategy for expected sea-level rise,

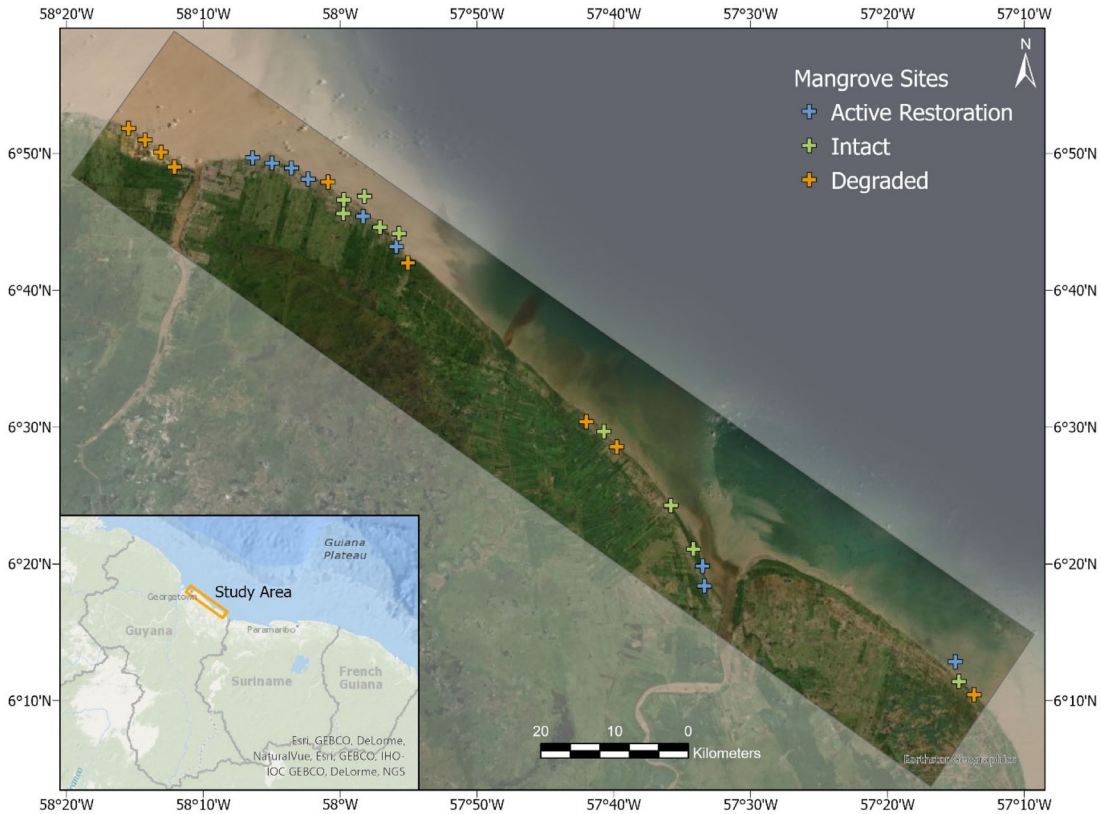

Figure 1. Location of mangrove sites included in study (n = 27). Inset map highlights study area on the North Brazil Shelf coastal region. Points indicating location of mangrove sites are offset to avoid overlap.

Table 1. Average stem density (ha^{-1}) of mangrove species by size class (seedlings, including propagules with leaves to <1.5 cm diameter; saplings 1.5–3.8 cm diameter, trees >3.8 cm diameter) and mangrove habitat classification (intact, degraded, and active restoration). Density of dead trees was also recorded.

Mangrove Site	*Size Class*	Avicennia germinans*: Average Stem Density (ha^{-1} ± SE)*	Laguncularia racemosa*: Average Stem Density (ha^{-1} ± SE)*	Rhizophora *spp.: Average Stem Density (ha^{-1} ± SE)*	*Dead Trees: Average Stem Density (ha^{-1} ± SE)*
Intact	Seedlings	8,522.22 (±3,238.60)	14,166.66 (±6,346.59)	77.78 (±27.78)	—
	Saplings	2,555.56 (±1,008.31)	511.11 (±165.37)	77.78 (±40.06)	—
	Trees	2,077.78 (±511.20)	244.44 (±101.53)	66.67 (±47.14)	1,088.89 (±349.38)
Degraded	Seedlings	8.78 (±5.25)	3.67 (±2.11)	1.89 (±1.89)	—
	Saplings	2.67 (±1.75)	1.33 (±0.90)	0.33 (±0.33)	—
	Trees	1.33 (±0.50)	1.00 (±0.44)	0.22 (±0.22)	20.78 (±3.13)
Active restoration	Seedlings	16,422.22 (±7,772.08)	2,666.67 (±983.90)	166.67 (±79.93)	—
	Saplings	644.44 (±444.76)	88.88 (±61.11)	0.00 (±0.00)	—
	Trees	1,788.88 (±326.36)	111.11 (±99.23)	0.00 (±0.00)	2,477.78 (±793.51)

with the added co-benefits of climate mitigation through carbon sequestration and storage and livelihood support connected to the fisheries sector (NAREI 2015).

The mangrove restoration program resulted in an estimated 500,000 *A. germinans* seedlings planted across 16 coastal communities between 2010 and 2016 (NAREI 2014). Early in the mangrove restoration program, failures occurred due to poor site selection. Building on these lessons, the mangrove restoration program adopted the principles of ecological mangrove restoration (Lewis 2005). Areas targeted for replanting were selected based on the presence of muddy substrate accumulation on the shore (elevation of sling mud: 2.3–2.7 m above water level-chart datum), low levels of tidal inundation, and the presence of waterways and canals (estuarine systems) (Landell Mills Limited 2013). Sites were deemed unsuitable for the replanting program if there was low mud elevation (<2.3 m), strong wave

action, high salinity levels (>12 ppt), and continued human disturbance (NAREI 2014). All the sites selected were planted at an intensity of 1,000 seedlings ha^{-1} of mudflat with *A. germinans* seedlings, sourced from community-owned greenhouses. The average height of out-planted mangrove seedlings was approximately 36 cm.

Data Collection

We randomly selected 27 sites, representing nine replicates for each of the following site classifications: intact, degraded, and actively restored. Intact mangrove sites did not have any anthropogenic impacts and had mature (reproductive) mangrove individuals with a forest canopy >70% and more than 1 ha of contiguous mangrove forest. The degraded mangrove forests had canopy cover that was greatly reduced either from natural processes (e.g. erosions, storms) or human activities (e.g. construction of ripraps, pollution, mangrove harvesting, fires). We determined the presence of historical mangrove forests at five of the degraded sites by interviewing local people from nearby coastal communities. For the other four degraded sites, we were able to obtain this information from the government agency responsible for the national mangrove restoration program. All degraded sites represent areas where there is an opportunity for natural mangrove colonization. At the time of the study, degraded sites were exposed to natural coastal erosion and accretion processes, lacked mature mangroves, and were not subject to any interventions related to coastal engineering to increase rates of accretion, reduce anthropogenic impacts or active replanting of mangrove seedlings. Data collection for environmental variables and fish sampling was done at all 27 sites once during the dry season (July–September 2017) and once during the wet season (January–March 2018).

Environmental Variables

Water depth and turbidity were measured in mm to the nearest one decimal place using a graduated rope and Secchi disk, respectively. Temperature was measured in °C with a handheld thermometer probe to the nearest one decimal place. Dissolved oxygen was measured with a digital dissolved oxygen meter to the nearest 0.1 mg/L. Electrical conductivity was recorded in microsiemens (μs/cm) using a digital electrical conductivity meter. pH was measured to one decimal place with a waterproof pH meter, and salinity was recorded in percent to the nearest one decimal place using a refractometer.

Mangrove Forest Structure and Composition

Within each site, we randomly placed plots to characterize mangrove vegetation. We measured forest structure and aboveground live tree biomass, representing coastal protection and stored carbon, and seedling density, representing longer-term successional trajectories. In intact and restored sites, we established a 0.01 ha plot at each site. Because mangrove density was extremely low in degraded sites, we used larger plots for this treatment, with an area of 1 ha per plot. For all plots, we measured stem density by mangrove species for seedlings (propagules with leaves to <1.5 cm diameter), saplings (1.5–3.8 cm diameter), and trees (>3.8 cm diameter). Stem diameters were recorded for trees >3.8 cm diameter that were alive to estimate aboveground tree biomass (tons of dry organic matter per hectare), and excluded seedlings and saplings. We applied the allometric equation, $\text{biomass} = a_0 \times \text{diameter}^{a_1}$, to estimate aboveground live tree biomass. Parameters a_0 and a_1 are species-specific coefficients established from destructive sampling of mangroves in French Guiana, with tree diameters recorded in cm (Fromard et al. 1998).We also enumerated the density of dead trees, which included standing and fallen dead stems with a diameter >3.8 cm, but these were excluded in the live aboveground biomass estimates. Canopy cover was also measured in each plot as a percent of tree cover to the nearest whole number using a spherical densiometer held approximately 1 m from the ground.

Fish Community Composition

We sampled fish species diversity and abundance during the dry and wet season using a combination of cast nets, dip nets, and gill nets with different dimensions that included (1) 200 m × 1.30 m—50 mm mesh; (2) 200 × 1.30 m—40 mm mesh; and (3) 200 m × 1.30 m—25 mm mesh. Gill nets were set close to the mangrove forest edge along the intact and restored sites. At the degraded sites, which lacked mangrove forests, gill nets were placed in open areas at a distance of 100 m from the shore. The gill nets were deployed before the onset of the high tide and were checked hourly for 3 hours at all sites. Cast nets were used for 1 hour at all sites along the edge of the mangrove vegetation. We used dip nets during the low tide to capture fishes wherever pools were present on mudflats. All fishes caught were identified to species level with a sub-sample of specimens stored in 10% formalin and 70% ethanol.

Statistical Analyses

Environmental Variables. We used principal component analysis (PCA) to quantify patterns in the environmental variables across sites and seasons. We assessed whether the linear combination of traits along the PCA axis could identify similarities across the mangrove sites based on season (wet vs. dry) and status (intact, degraded, and active restoration). We implemented the PCA analysis with the *vegan* package in R, centering and normalizing the environmental data (Oksanen et al. 2019).

Statistical Models for Mangrove Abundance, Aboveground Tree Biomass, and Fish Species Abundance. To assess differences in mangrove seedling abundance, mangrove tree biomass, and fish species abundance among site treatments, we fit generalized linear mixed-effects models (GLMM) in a Bayesian framework (McElreath 2020). Because plot-level mangrove biomass was a positive continuous variable, biomass models assumed gamma-distributed error. To avoid zero values not

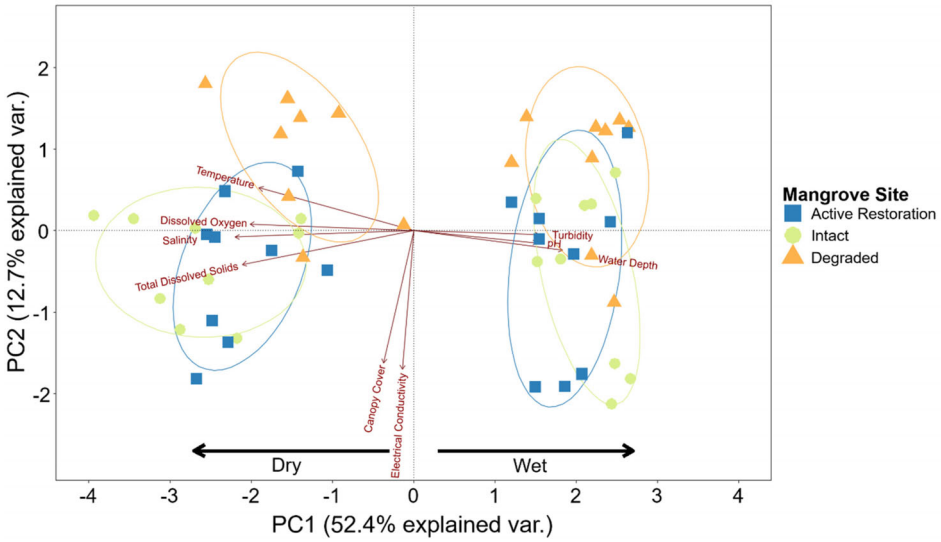

Figure 2. Principal component analysis (PCA) of the 27 mangrove sites across nine environmental variables collected in the dry and wet season. The arrows on the biplot are representative of the eigenvectors (loadings) for the different environmental variables for PC1 and PC2. Ellipses represent 68% confidence intervals based on treatment by season centroids. See Table S1 for summary of values of environmental variables.

supported by gamma regression, we added a small number (0.01) to plots with zero biomass. Because fish species abundance and mangrove seedling abundance were count data, we fit these response variables to a negative binomial model. For both the gamma-distributed biomass model and the negative binomial-distributed count data models, we used a log-link to ensure model predictions were positive. For the mangrove seedling abundance model, we incorporated different plot sizes in our GLMM structure using an offset for plot area (Hilbe 2011). In all models, we treated the community-level parameter of site treatment (intact, degraded, and active restoration) as a fixed effect, representing treatment effects for an average species. To account for the possibility that different fish species responded differently to site treatments we fit species as a random intercept with a random slope for the effect of site treatment. We accounted for non-independence of observations from the same site using a random intercept, with a random slope for the effect of site treatment. Relative to models with different random effects structures, the models with random intercepts and random slopes for site treatment, dependent on both species and site, provided the best fit for all three datasets (fish species abundance, mangrove seedling abundance, and mangrove biomass). While we use treatment as a categorical variable to disentangle the effects of restoration and degradation, an alternate approach would be to predict the rate of ecosystem recovery using a suite of environmental covariates, including a random effect to account for spatial autocorrelation.

All models were fit in *rstanarm* with default priors, including four chains with 2,000 iterations per chain, with a warm-up of a 1,000 iterations (Gabry et al. 2020). We assessed model fit using the Rhat metric, by visually assessing that chains converged, and by checking for a sufficient number of effective samples. To assess uncertainty in our model output, we present 95% credibility intervals, calculated from posterior draws, and the probability of direction (PD) of effects. The PD is an estimate of the probability that an effect is positive or negative, based on the frequency of posterior draws (Makowski et al. 2019). Similar to p values in a frequentist framework, PD represents the amount of evidence for the alternate hypothesis. Unlike p values, PD has a direct interpretation as the probability that a predictor variable has an effect on the response variable.

To translate fish abundance to community-level metrics, we predicted species-level abundance with posterior draws from our Bayesian GLMMs. We then evaluated community-level metrics, including species richness, Shannon diversity, and abundance of commercially valuable fish species, from each posterior draw. Evaluating these community-level metrics as emergent properties of species-level abundance model outputs enabled us to interpret community patterns in light of individual species abundance and to propagate uncertainty from model estimation to the community- level metrics (Ferrier & Guisan 2006). To facilitate the interpretation of treatment effects, we predicted species abundance at an average site to develop community-level metrics. We drew 4,000 posterior samples for each species at each of the three treatments, resulting in 12,000 samples for each community-level metric.

Results

Environmental Variables

The first and second principal component (PC) axes explained 65.1% of the variation in the environmental data collected across the 27 mangrove sites. The first principal component axis (PC1) is associated with seasonal variations (i.e. wet vs. dry season; Fig. 2). Higher levels of pH, water depth, and turbidity are

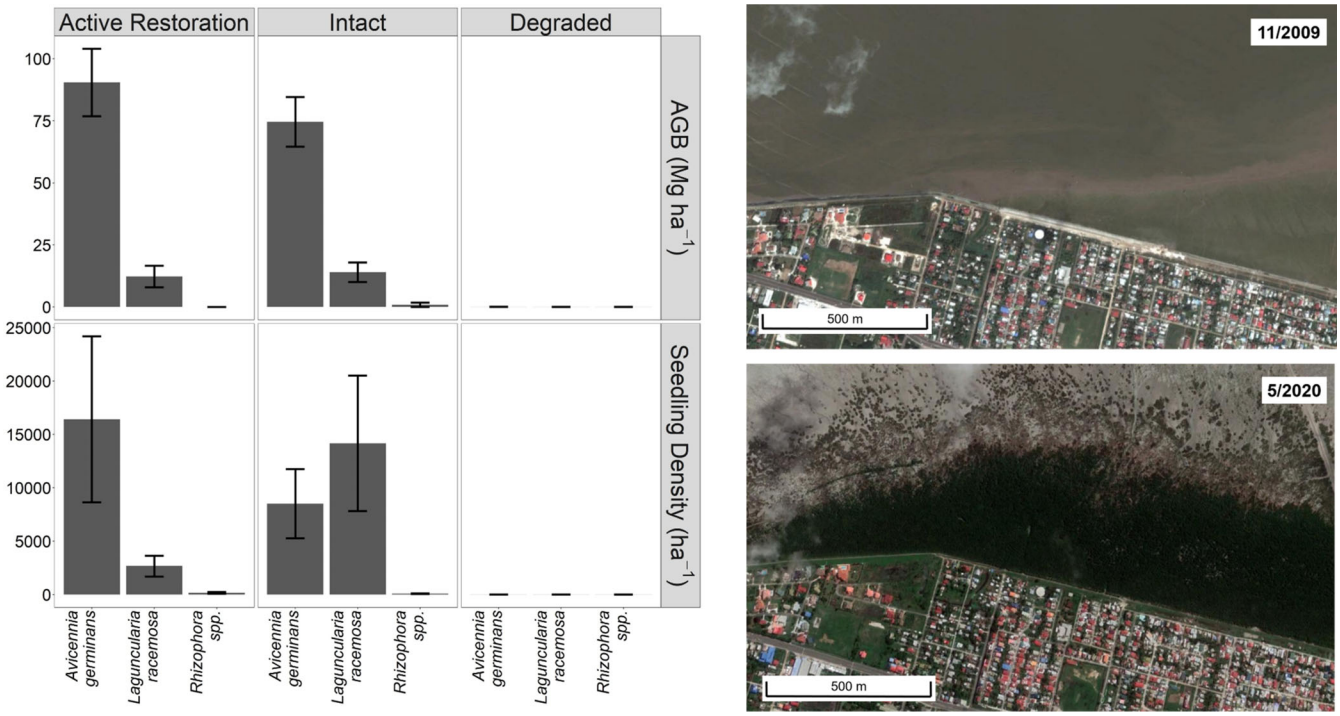

Figure 3. Average aboveground biomass (AGB, Mg ha^{-1}) and stem density (ha^{-1}) by mangrove species and site treatments. Error bars capture ±1SE (left panel). Satellite images show a restored site before replanting in 2009 (upper) and mangrove forest recovery in 2020 (lower) (right panel—images courtesy of Google Earth).

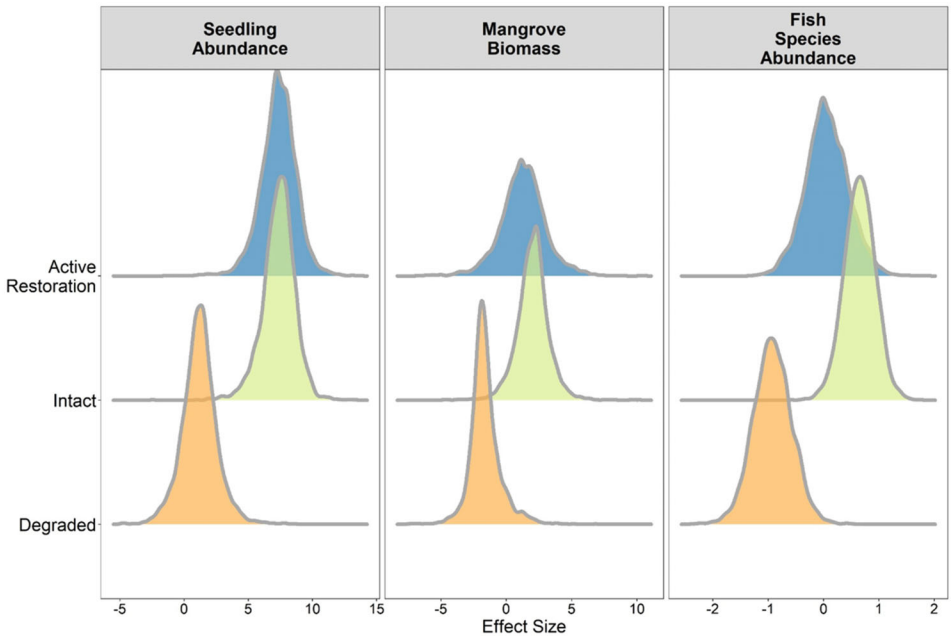

Figure 4. Effects size of mangrove site treatments on mangrove seedling abundance, mangrove biomass, and fish species abundance. These plots show the posterior densities of site treatment effects for an average species in an average site. Posterior draws were extracted from generalized linear mixed models to test statistical effects. Both the posterior density position and the overlap between posterior densities for each treatment indicate statistical certainty.

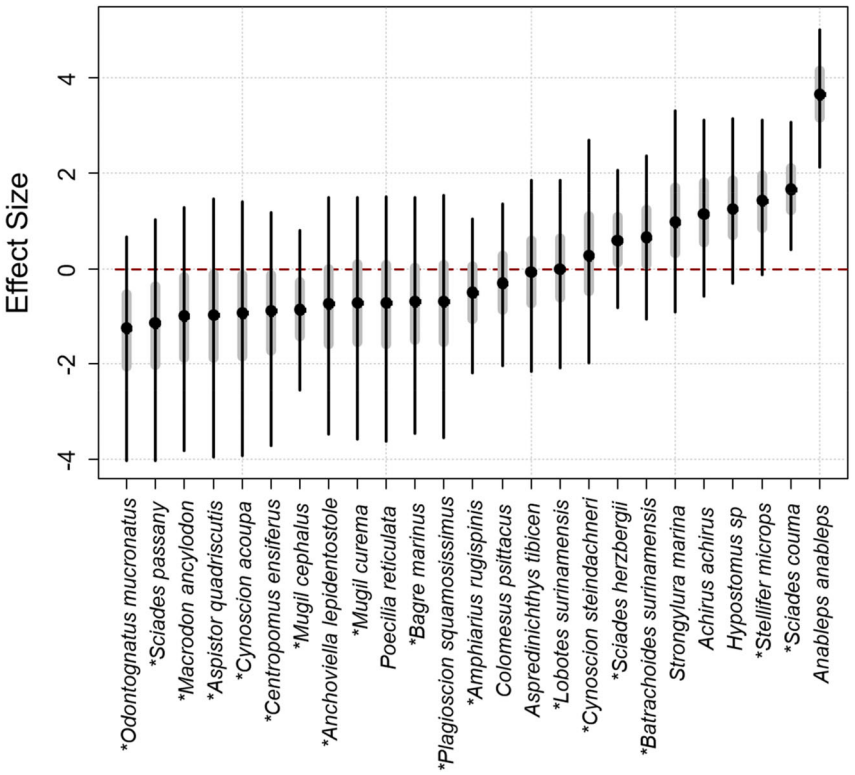

Figure 5. Species-level impacts of active restoration on fish abundance. This coefficient plot indicates the effect of restoration, relative to the intact treatment, on each of the 25 fish species found in our study. Effect size represents posterior draws from the negative binomial generalized linear mixed model. A positive effect size reveals species that benefited from the restoration treatment, while a negative effect size indicates greater abundance in the intact treatment. Overlap with zero indicates uncertainty in effect size estimates. Black dots show the posterior medians, thick gray lines indicate the 50% credibility interval, and thin gray lines indicate the ±95% CI. Starred names along the *x*-axis indicate commercially valuable species.

associated with the wet season. In contrast, higher temperature, salinity, dissolved oxygen, and total dissolved solids (TDS) were measured in the dry season. The second principal component axis captures the different mangrove sites based on their treatment status, with higher levels of canopy cover and electrical conductivity associated with the intact and restored sites relative to degraded sites (Table S1, Supporting Information). While all sites experienced seasonal changes in environmental characteristics, restored and intact sites were more similar to each other in both the wet and dry seasons, relative to the degraded sites.

Mangrove Forest Structure and Composition

We recorded four mangrove species in our study: *A. germinans*, *L. racemosa*, and *Rhizophora* spp. *Avicennia germinans* dominated tree (>3.8 cm) species composition across sites in intact, degraded, and actively restored mangrove habitats, respectively (Table 1). *Laguncularia racemosa* was the second most abundant species, and *Rhizophora* spp. was rare across all sites (Table 1). Aboveground live tree biomass (Mg ha^{-1} dried weight) was 89.4 (SE ± 12.40), 0.12 (SE ± 0.06), and 103.0 (SE ± 12.30) in the intact, degraded, and actively restored mangrove sites, respectively (Fig. 3). Our statistical models suggest that while the overall effect of restoration was nearly indistinguishable from intact treatments, there was a >99% probability that degradation resulted in a significant loss in mangrove biomass (Fig. 4). While the negative effect of degradation was nearly uniform across all species, species-level random effects from our GLMMs reveal species-level differences between intact and restored sites. The most certain species-level effects, relative to the average species in an average site, included a 92.6% probability that *Rhizophora* spp. had lower biomass in restored sites, and an 87.1% probability that *A. germinans* had higher biomass in restored sites (Fig. 3; Fig. S1).

Abundance of Mangrove Seedlings

Across all species and sites, there were nearly three orders of magnitude more seedlings in intact and actively restored sites than degraded sites which had limited regeneration (Table 1 & Fig. 3). The intact treatment had notably higher abundance of *L. racemosa*, while seedling abundance of *A. germinans* was highest in the restored treatment (Fig. 3). Our statistical model also reveals high certainty that degraded sites had lower mangrove seedling abundance than intact sites (Fig. 4), with a probability of >99% that the effect of degradation was negative on seedling recruitment. In contrast, the effect of active restoration on mangrove seedling abundance was centered on zero, with

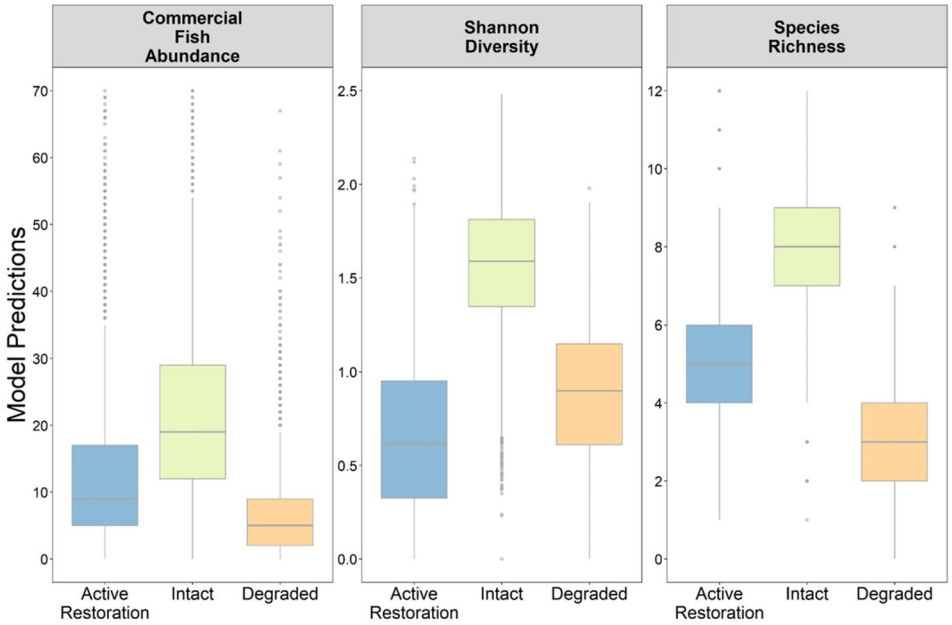

Figure 6. Predicted fish community structure for different treatments at an average site. To avoid extreme values, we only display predicted outliers within the 95% CI indicated by points beyond the upper and lower box whiskers. The 50% quantile (median value) is indicated by the horizontal line within the boxplot.

approximately equal probability of observing higher or lower abundance of seedlings relative to intact sites (Fig. S2).

Avicennia germinans benefited most from active restoration with a predicted median increase in seedling abundance of 37% (95% CI: −22 to 875%) in actively restored sites, compared to intact sites. In contrast, *L. racemosa* had slightly lower seedling abundance in the restored treatment than the intact treatment, although this difference was relatively uncertain (PD = 76%). Degradation had a negative effect on the seedling abundance of all three species, with the strongest impact on *L. racemosa* seedling abundance with a predicted median decrease of 73.5% (95% CI: 98.7% decrease to 43.2% increase) relative to the intact treatment. While *Rhizophora* spp. seedling abundance was generally highest in the actively restored and intact treatments and lowest in the degraded treatment, these differences were very uncertain, likely due to the general scarcity of *Rhizophora* spp. seedlings in our plots.

Fish Species Abundance

Across all sites and seasons, we recorded 1,126 individuals representing 14 families and 25 fish species. The dry season had a higher catch abundance (870) with greater species richness (20) in comparison to the wet season (16 fish species and a total catch of 256). The highest fish abundance was recorded in the actively restored sites (715 individuals) followed by intact (317 individuals) and degraded (94 individuals) mangrove sites (Table S2). The three most abundant fish species were *Anableps anableps* (66.0%), *Sciades couma* (12.1%), and *Mugil cephalus* (7.3%). *Anableps anableps* was the relative dominant species across all sites, with 48% and 25% relative abundance in degraded and intact sites, respectively, and the absolute dominant species in actively restored sites, where it had a relative abundance of 87%. Out of all fish species caught, 72% had some commercial and subsistence fisheries value (Table S2).

GLMMs revealed decreased abundance in restoration treatments for an average species, despite a strong positive effect of restoration on *A. anableps*. Overall, across all species and sites, fish species abundance decreased by a median of 45% in actively restored sites, relative to intact sites (95% CI: 82% decrease to 72% increase). We estimated an 86% probability that the average restored site would have lower fish diversity relative to intact sites. The apparent contradiction between the negative effect of restoration on fish species abundance and the raw data, which showed higher overall abundance in restored sites, is due to the hyperabundance of a single species, *A. anableps*, in restoration treatments. As the GLMMs differentiate abundance based on species identity, they reveal decreased abundance in restoration treatments for an average species, despite a strong positive effect of restoration on *A. anableps*. In degraded sites, models predicted a median decrease of fish abundance of 79% (95% CI: 92–45% decrease) relative to intact sites, including a >99% probability that the average degraded site had lower fish species abundance. At the species level, random effects suggest that the restoration treatment had significant benefits for a small number of species, including *A. anableps* and *S. couma* (Fig. 5).

Fish Community Metrics

Fish species richness, Shannon diversity, and abundance of commercially valuable species were much higher in intact sites than either actively restored or degraded sites (Fig. 6). Our models suggest that, relative to intact sites, species richness is

reduced by more than half in degraded sites, with a median loss of eight species. Actively restored sites also had fewer species than intact sites, with a median loss of three species relative to intact sites. For commercially valuable fish species abundance, degraded sites had the lowest fish abundance, but restored sites still had a median of nearly nine fewer fishes than intact sites. Shannon diversity was lower in restored sites than intact sites, with a median diversity value of 0.62 (95% CI: 0.07–1.61) in restored sites compared to a median value of 1.58 (95% CI: 0.77–2.18) in intact sites.

Discussion

Intact mangrove forests provide a suite of ecosystem services, from climate mitigation to fisheries support. Planting mangrove seedlings is a common restoration technique for degraded coastal areas, with the potential for both positive and negative impacts on ecosystem services. We evaluated the outcomes of a large-scale mangrove restoration project in coastal Guyana for biodiversity, aboveground live tree biomass, and commercial fish abundance. Less than a decade after planting, mangrove biomass and seedling abundance were similar between intact and restored sites and depressed in degraded sites. However, restoration did not provide clear benefits for fish communities, including species richness and abundance. As massive mangrove planting projects ramp up to support international goals, including increasing mangrove area by 20% by 2030 (Lee et al. 2019), our results demonstrate how active restoration could provide a route to rapid recovery for some, but not all, ecosystem services.

Mangrove live aboveground tree biomass in restored sites, consisting of both planted species (*A. germinans*) and an unplanted early-successional species (*L. racemosa*), reached levels equivalent to, or higher than, comparable intact sites. In contrast, live tree biomass in degraded sites remained low, indicating limited potential for natural regeneration at these sites most likely due to unsuitable environmental conditions. These biomass results are consistent with others that have shown rapid recovery in aboveground tree biomass to pre-disturbed levels with restoration (Bosire et al. 2008; Kairo et al. 2009; Ferreira et al. 2015; Sasmito et al. 2019), including higher stem density in some actively restored mangrove sites relative to comparable natural mature stands (Bosire et al. 2008). The differences between actively restored and degraded sites in our study are likely due to project managers' expertise in choosing sites for active restoration (e.g. Reid et al. 2018). The expected challenge with maintaining mangrove forests, which may have contributed to the poor recruitment of mangroves at the degraded sites, is the cyclic erosion and deposition process that characterizes mudflats along the North Brazil Shelf (Toorman et al. 2018). While demographic data, including growth and survival of individual mangroves, were not available for our study, collecting and analyzing these data are key to advancing our understanding of vegetation recovery during restoration (e.g. Caughlin et al. 2019).

While live aboveground tree biomass reflects the immediate impacts of active restoration, mangrove seedling composition represents the potential future composition and structure of restored stands. We found evidence that active restoration resulted in comparable mangrove seedling density and diversity to mature mangrove stands (Fromard et al. 1998, 2004). A concern with mangrove planting projects, which most often plant a single species, is that resultant mangrove stands will become monospecific plantations, rather than diverse natural stands (Rovai et al. 2012; Ferreira et al. 2015). This concern seems unwarranted in our study sites, where seedling abundance of an unplanted species (*L. racemosa*), considered a pioneer in coastal and estuarine habitats (Fromard et al. 2004; Jaikishun et al. 2017), also benefited from active restoration. A third taxon, *Rhizophora* spp., which primarily occurs inland along riverbanks where freshwater inputs to the marine ecosystem are present, was generally rare, but seedling density of this genus was also higher on average in restored sites than degraded sites. As these three genera represent the dominant floral composition of the mangrove forests of the North Brazil Shelf (Fromard et al. 1998, 2004), we did not find evidence that planting a single species resulted in forest compositional changes. In contrast, the recruitment of multiple mangrove species appeared to benefit from restoration, potentially a consequence of altered environmental conditions generated by planting *A. germinans*. Nevertheless, the biodiversity costs of single-species mangrove planting may be higher in regions with a higher diversity of mangrove species (e.g. Southeast Asia; Ricklefs & Latham 1992).

The mangrove restoration assessed in this study resulted from an iterative process of trial and error with early failures of mangrove replanting attributed to a lack of local expertise and knowledge on the conditions needed for mangrove growth and development (Vaughn 2017). Following the input of technical experts and training of in-country project staff following the principles of ecological restoration for mangroves (see Lewis 2005), site-level characteristics needed for successful mangrove rehabilitation were quantified (Toorman et al. 2018). These site-level assessments' key outcome was the importance of elevated mudflats in the range of +2.3 to +2.7 m above chart datum (Landell Mills Limited 2013). Thus, our assessment of mangrove restoration outcomes represents a best-case scenario based on the pre-selection of sites characterized by optimal conditions for mangrove growth and recruitment (Lewis 2005). Targeting sites with suitable geomorphic features, particularly high-elevation silt deposits, was likely a key factor in the recovery of aboveground live woody tree biomass (Cameron et al. 2019). Rigorous experiments that control for site-specific conditions will be an important next step in determining the benefits of active restoration versus no restoration actions in sites with favorable conditions for mangrove colonization, such as elevated mudflats (Atkinson & Bonser 2020).

Despite the benefits of active restoration for mangrove forest structure, we did not find strong evidence for fish community recovery in planted sites. For an average fish species, abundance was more similar between degraded and restored sites than between restored and intact sites. Lower species abundance translated into lower species richness and abundance of commercially valuable species in restored sites. These findings are similar to those reported in other studies that indicate fish and

invertebrate diversity remains suppressed for several years post-restoration compared to mature mangrove ecosystems (Al-Khayat & Jones 1999; Iii & Gilmore 2007; Barimo & Serafy 2020). In our sites, faunal recovery, including fish diversity and commercial fish abundance, may require a longer time than our study encompassed.

One explanation for reduced fish diversity in restored sites is the limited structural complexity of newly established mangrove forests (Laegdsgaard & Johnson 1995). As mangrove forests mature, development of fallen debris, aerial roots, and other structural features provide benefits for faunal communities, including refugia from predation, barriers from physical disturbance, and attachment points for sessile invertebrates (Hutchison et al. 2014). A related possibility is that return of the complex food web that underlies old growth mangrove forests may take longer than the initial reestablishment of mangrove stem density. One indicator of low trophic complexity in restored sites is the hyperabundance of a single algivorous species, *A. anableps*. In contrast, the higher abundance of fish species in the invertivore feeding guild at intact mangrove sites suggests a more complex food web structure in those sites (Brenner & Krumme 2007; Corrêa & Uieda 2007; Zvonareva et al. 2015). Longer-term monitoring of faunal communities in restored sites will be necessary to understand whether the diverse fish assemblages in intact sites will gradually return to planted mangrove forests.

An alternate explanation for divergent fish community structure between intact and restored sites is that full recovery of aquatic fauna will require restoring hydrological features in addition to vegetation (Lewis & Gilmore 2007). Guyana's coastline has experienced severe alteration from coastal engineering projects, such as coastal walls and channels that have blocked freshwater discharge into oceans and altered tidal flows (Pastakia 1991). Site differences in topography and water currents can override habitat type to influence faunal communities in estuarine habitats (Vance et al. 2002). However, our analysis of environmental conditions, including salinity, turbidity, and water depth, suggests a high degree of overlap between restored and intact sites, with divergent conditions in degraded sites. Furthermore, differences among sites in the dry and wet season were generally larger than the differences between restored and intact sites during the same season. As coastal engineering projects in Guyana increasingly incorporate an ecological perspective (Vaughn 2017), whether restoring natural hydrological regimes could speed up recovery of faunal communities remains an important question. As improving the quality of commercial fisheries is often used to motivate local community involvement in mangrove restoration, our results suggest caution may be warranted to avoid over-promising rapid recovery of fish communities, at least in the Guyana case. Longer term, stakeholder involvement in mangrove restoration could provide an avenue for monitoring the impacts of restoration on fisheries, and ultimately improve restoration outcomes for marine fauna (Datta et al. 2012). Additionally, spatially explicit models for ecosystem recovery will be an important next step to improve our understanding of variability in mangrove restoration outcomes.

Altogether, our results demonstrate the potential for successful mangrove forest restoration along the North Brazil Shelf, including aboveground tree biomass recovery and recruitment of native mangrove species. These successful restoration outcomes may have been aided by engagement with coastal communities to grow mangrove seedlings, indirectly reducing anthropogenic resource use pressures on rehabilitated areas through outreach and education (Walton et al. 2006). Nevertheless, even under a best-case scenario for mangrove forest restoration, fisheries recovery did not occur at the rate of mangrove biomass. Highly divergent recovery times across ecosystem functions may be the norm for planted mangrove forests; for example, recovery of the deep peat layer that characterizes mature mangrove stands may require 45–80 years (Osland et al. 2020). Our study reinforces the likelihood that recovery rates for mangrove ecosystem services vary widely, even when mangrove planting projects are relatively successful.

Acknowledgments

This study was funded through a grant from the World Wildlife Fund-Guianas program, the University of Guyana, the University of Florida, the National Science Foundation under grant #1415297 in the SBE program, and the National Aeronautics and Space Administration Land Cover/Land Use Change program under grant #19-LCLUC19_2-0030. We would like to thank Jimmy Itwaru, who assisted with field data collection, and Donald Taphorn, who assisted in fish species identification. We are also grateful to the Mangrove Department coordinator at the National Agricultural and Research Institute, Kene Moseley, for access to reports on the Guyana mangrove restoration program. The authors have no conflict of interest to report.

LITERATURE CITED

Aburto-Oropeza O, Ezcurra E, Danemann G, Valdez V, Murray J, Sala E (2008) Mangroves in the Gulf of California increase fishery yields. Proceedings of the National Academy of Sciences 105:10456–10459

Al-Khayat JA, Jones DA (1999) A comparison of the macrofauna of natural and replanted mangroves in Qatar. Estuarine, Coastal and Shelf Science 49: 55–63

Alongi DM (2014) Carbon cycling and storage in mangrove forests. Annual Review of Marine Science 6:195–219

Anthony EJ, Gratiot N (2012) Coastal engineering and large-scale mangrove destruction in Guyana, South America: averting an environmental catastrophe in the making. Ecological Engineering 47:268–273

Atkinson J, Bonser SP (2020) 'Active' and 'passive' ecological restoration strategies in meta-analysis. Restoration Ecology 28:1032–1035

Barbier EB, Hacker SD, Kennedy C, Koch EW, Stier AC, Silliman BR (2011) The value of estuarine and coastal ecosystem services. Ecological Monographs 81:169–193

Barimo JF, Serafy JE (2020) Fishes of a restored mangrove habitat on Key Biscayne, Florida. Florida Scientist 66:12–22

Bosire JO, Dahdouh-Guebas F, Walton M, Crona BI, Lewis RR, Field C, Kairo JG, Koedam N (2008) Functionality of restored mangroves: a review. Aquatic Botany 89:251–259

Brenner M, Krumme U (2007) Tidal migration and patterns in feeding of the four-eyed fish *Anableps anableps* L. in a north Brazilian mangrove. Journal of Fish Biology 70:406–427

Cameron C, Hutley LB, Friess DA, Brown B (2019) Community structure dynamics and carbon stock change of rehabilitated mangrove forests in Sulawesi, Indonesia. Ecological Applications 29:e01810

Caughlin TT, de la Peña-Domene M, Martínez-Garza C (2019) Demographic costs and benefits of natural regeneration during tropical forest restoration. Ecology Letters 22:34–44

Chen R, Twilley RR (1998) A gap dynamic model of mangrove forest development along gradients of soil salinity and nutrient resources. Journal of Ecology 86:37–51

Corrêa MdeODA, Uieda VS (2007) Diet of the ichthyofauna associated with marginal vegetation of a mangrove forest in southeastern Brazil. Iheringia. Série Zoologia 97:486–497

Das S (2017) Ecological restoration and livelihood: contribution of planted mangroves as nursery and habitat for artisanal and commercial fishery. World Development 94:492–502

Datta D, Chattopadhyay RN, Guha P (2012) Community based mangrove management: a review on status and sustainability. Journal of Environmental Management 107:84–95

Donato DC, Kauffman JB, Murdiyarso D, Kurnianto S, Stidham M, Kanninen M (2011) Mangroves among the most carbon-rich forests in the tropics. Nature Geoscience 4:293–297

Duke NC, Pinzon ZS, Prada MC (1999) Recovery of tropical mangrove forests following a major oil spill: a study of recruitment and growth, and the benefits of planting. Pages 231–254. In: Yánez-Arancibia A (ed) Ecosistemas de manglar en América Tropical. Instituto de Ecología A.C. México, Veracruz.

Ellison AM (2000) Mangrove restoration: do we know enough? Restoration Ecology 8:219–229

Ferreira AC, Ganade G, Luiz de Attayde J (2015) Restoration versus natural regeneration in a neotropical mangrove: effects on plant biomass and crab communities. Ocean & Coastal Management 110:38–45

Ferrier S, Guisan A (2006) Spatial modelling of biodiversity at the community level. Journal of Applied Ecology 43:393–404

Friess DA, Rogers K, Lovelock CE, Krauss KW, Hamilton SE, Lee SY, Lucas R, Primavera J, Rajkaran A, Shi S (2019) The state of the world's mangrove forests: past, present, and future. Annual Review of Environment and Resources 44:89–115

Fromard F, Puig H, Mougin E, Marty G, Betoulle JL, Cadamuro L (1998) Structure, above-ground biomass and dynamics of mangrove ecosystems: new data from French Guiana. Oecologia 115:39–53

Fromard F, Vega C, Proisy C (2004) Half a century of dynamic coastal change affecting mangrove shorelines of French Guiana. A case study based on remote sensing data analyses and field surveys. Marine Geology 208: 265–280

Gabry J, Ali I, Brilleman S, Novik JB, Zeneca A, Wood S, et al. (2020) rstanarm: Bayesian Applied Regression Modeling via Stan. https://CRAN.R-project.org/package=rstanarm (accessed 5 Aug 2020)

Global Climate Change Alliance+ (GCCA+) (2018) Sustainable coastal zone protection through mangrove management in Guyana | Global Climate Change Alliance+. https://www.gcca.eu/programmes/sustainable-coastal-zone-protection-through-mangrove-management-guyana (accessed 9 Jun 2020)

Gorman D (2018) Historical losses of mangrove systems in South America from human-induced and natural impacts. Pages 155–171. In: Makowski C, Finkl CW (eds) Threats to mangrove forests. Springer International Publishing, Cham, Switzerland

Griscom BW, Adams J, Ellis PW, Richard AH, Lomax G, Miteva AD, et al. (2017) Natural climate solutions. Proceedings of the National Academy of Sciences 114:11645–11650

Griscom BW, Busch J, Cook-Patton S, Ellis PW, Funk J, Leavitt SM, et al. (2020) National mitigation potential from natural climate solutions in the tropics. Philosophical Transactions of the Royal Society B: Biological Sciences 375:20190126

Hilbe JM (2011) Negative binomial regression. Cambridge University Press, Cambridge

Hilderbrand RH, Watts AC, Randle AM (2005) The myths of restoration ecology. Ecology and Society 10:19

Holl KD, Aide TM (2011) When and where to actively restore ecosystems? Forest Ecology and Management 261:1558–1563

Hutchison J, Spalding M, zu Ergmassen P (2014) The role of mangroves in fisheries enhancement. The Nature Conservancy and Wetlands International. Cambridge University, UK.

Huxham M, Kimani E, Augley J (2004) Mangrove fish: a comparison of community structure between forested and cleared habitats. Estuarine, Coastal and Shelf Science 60:637–647

Iii RRL, Gilmore RG (2007) Important considerations to achieve successful mangrove forest restoration with optimum fish habitat. Bulletin of Marine Science 80:15

Imbert D (2018) Hurricane disturbance and forest dynamics in East Caribbean mangroves. Ecosphere 9:e02231

Jaikishun S, Ansari AA, Dasilva P, Hosen A (2017) Carbon storage potential of mangrove forest in Guyana. Bonorowo Wetlands 7:43–54

Kairo JG, Bosire J, Langat J, Kirui B, Koedam N (2009) Allometry and biomass distribution in replanted mangrove plantations at Gazi Bay, Kenya. Aquatic Conservation: Marine and Freshwater Ecosystems 19:S63–S69

Kodikara KAS, Mukherjee N, Jayatissa LP, Dahdouh-Guebas F, Koedam N (2017) Have mangrove restoration projects worked? An in-depth study in Sri Lanka: evaluation of mangrove restoration in Sri Lanka. Restoration Ecology 25:705–716

Laegdsgaard P, Johnson C (1995) Mangrove habitats as nurseries: unique assemblages of juvenile fish in subtropical mangroves in eastern Australia. Marine Ecology Progress Series 126:67–81

Landell Mills Limited (2013) *Technical assistance for mangrove rehabilitation*. Final report/. Government of Guyana, Georgetown

Lee SY, Hamilton S, Barbier EB, Primavera J, Lewis RR (2019) Better restoration policies are needed to conserve mangrove ecosystems. Nature Ecology & Evolution 3:870–872

Lewis RR (2005) Ecological engineering for successful management and restoration of mangrove forests. Ecological Engineering 24:403–418

Lewis RR (2010) Mangrove field of dreams: if we build it, will they come? Wetlands Science and Practice 27:1

Lewis RR, Gilmore RG (2007) Important considerations to achieve successful mangrove forest restoration with optimum fish habitat. Bulletin of Marine Science 80:823–837

Makowski D, Ben-Shachar MS, Chen SHA, Lüdecke D (2019) Indices of effect existence and significance in the bayesian framework. Frontiers in Psychology 10:2767

McElreath R (2020) Statistical rethinking: a bayesian course with examples in R and STAN. CRC Press, Boca Raton, Florida

Menéndez P, Losada IJ, Torres-Ortega S, Narayan S, Beck MW (2020) The global flood protection benefits of mangroves. Scientific Reports 10:1–11

Millar E, Bollini C, Vincent DJ (2019) Economic valuation of mangrove-fishery linkages in Guyana and Suriname. Masters Thesis, Duke University, Durham, North Carolina. https://dukespace.lib.duke.edu/dspace/bitstream/-handle/10161/18395/Bollini.Millar_MP_FINAL.pdf?sequence=1

National Agricultural Research and Extension Institute (NAREI) (2014) Mangrove department annual report. NAREI, Guyana

National Agricultural Research and Extension Institute (NAREI) (2015) Mangrove department annual report. NAREI, Guyana

Oksanen J, Kindt R, O'Hara B (2019) Vegan: Community Ecology Package. https://CRAN.R-project.org/package=vegan (accessed 5 Aug 2020)

Osland M, Feher L, Spivak AC, Nestlerode JA, Almario AE, Cormier Nicole, et al. (2020) Rapid peat development beneath created, maturing mangrove forests: ecosystem changes across a 25-yr chronosequence. Ecological Applications 30:e02085

Pastakia C (1991) A preliminary study of the mangroves of Guyana. Aquatic Biological Consultancy Services Limited. The European Community, Article B 946/89, Contract No 8912. Georgetown, Guyana

Reid JL, Fagan ME, Zahawi RA (2018) Positive site selection bias in meta-analyses comparing natural regeneration to active forest restoration. Science Advances 4:eaas9143

Ricklefs R, Latham R (1992) Global patterns of diversity in mangrove floras. In: Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press, Chicago, USA.

Rovai AS, Soriano-Sierra EJ, Pagliosa PP, Cintrón G, Schaeffer-Novelli Y, Menghini RP, et al. (2012) Secondary succession impairment in restored mangroves. Wetlands Ecology and Management 20:447–459

Sasmito SD, Taillardat P, Clendenning JN, Cameron C, Friess DA, Murdiyarso D, Hutley LB (2019) Effect of land-use and land-cover change on mangrove blue carbon: a systematic review. Global Change Biology 25:4291–4302

Sheaves M (2017) How many fish use mangroves? The 75% rule an ill-defined and poorly validated concept. Fish and Fisheries 18:778–789

Toorman EA, Anthony E, Augustinus PGEF, Gardel A, Gratiot N, Homenauth O, Huybrechts N, Monbaliu J, Moseley K, Naipal S (2018) Interaction of mangroves, coastal hydrodynamics, and morphodynamics along the coastal fringes of the Guianas. Pages 429–473. In: Makowski C, Finkl CW (eds) Threats to mangrove forests. Springer International Publishing, Cham, Switzerland

Twilley RR, Rivera-Monroy VH, Chen R, Botero L (1999) Adapting an ecological mangrove model to simulate trajectories in restoration rcology. Marine Pollution Bulletin 37:404–419

Vance D, Haywood M, Heales D, Kenyon R, Loneragan N, Pendreyne R (2002) Distribution of juvenile penaeid prawns in mangrove forests in a tropical Australian estuary, with particular reference to *Penaeus merguiensis*. Marine Ecology Progress Series 228:165–177

Vaughn SE (2017) Disappearing mangroves: the epistemic politics of climate adaptation in Guyana. Cultural Anthropology 32:242–268

Waltham NJ, Elliott M, Lee SY, Lovelock C, Duarte CM, Buelow C, et al. (2020) UN decade on ecosystem restoration 2021–2030—what chance for success in restoring coastal ecosystems? Frontiers in Marine Science. https://doi.org/10.3389/fmars.2020.00071

Walton MEM, Samonte-Tan GPB, Primavera JH, Edwards-Jones G, Vay LL (2006) Are mangroves worth replanting? The direct economic benefits of a community-based reforestation project. Environmental Conservation 33:335–343

Zvonareva S, Kantor Y, Li X, Britayev T (2015) Long-term monitoring of Gastropoda (Mollusca) fauna in planted mangroves in central Vietnam. Zoological Studies 54:39

Supporting Information

The following information may be found in the online version of this article:

Table S1. Average values (standard errors) for the different environmental variables measured in the intact ($n = 9$), degraded ($n = 9$), and actively restored ($n = 9$) mangrove sites in the dry and wet season.

Table S2. Fish species, average number of individuals captured (SE) by habitat and season and commercial importance (LC, locally consumed; EX, exported; NC, not consumed) and feeding guilds (I: Algivore II: Herbivore, III: Invertivore (mainly crabs), IV: Invertivore (mainly shrimps), V: Piscivore, VI: Zooplanktivore) for fish species.

Figure S1. Species-level effects of site treatment on mangrove biomass.

Figure S2. Species-level effects of site treatment on mangrove seedling abundance.

Coordinating Editor: John Isanhart

Received: 7 September, 2020; First decision: 19 October, 2020; Revised: 17 March, 2021; Accepted: 19 March, 2021