



Bird rookery nutrient over-enrichment as a potential accelerant of mangrove cay decline in Belize

L. T. Simpson^{1,2} · S. W. J. Canty^{3,4} · J. R. Cissell^{3,5} · M. K. Steinberg¹ · J. A. Cherry¹ · I. C. Feller⁶

Received: 11 January 2021 / Accepted: 28 September 2021
© The Author(s), under exclusive licence to Springer-Verlag GmbH Germany, part of Springer Nature 2021

Abstract

Coastal eutrophication is an issue of serious global concern and although nutrient subsidies can enhance primary productivity of coastal wetlands, they can be detrimental to their long-term maintenance. By supplying nutrients to coastal ecosystems at levels comparable to intensive agriculture practices, roosting colonial waterbirds provide a natural experimental design to examine the impacts of anthropogenic nutrient enrichment in these systems. We tested the hypothesis that long-term nutrient enrichment from bird guano deposition is linked to declines in island size, which may subsequently decrease the stability and resilience of mangrove cays in Belize. We combined remote sensing analysis with field- and lab-based measurements of forest structure, sediment nutrients, and porewater nutrients on three pairs of rookery and control cays in northern, central, and southern Belize. Our results indicate that rookery cays are disappearing approximately 13 times faster than cays without seasonal or resident seabird populations. Rookery cays were associated with a significantly higher concentration of nitrogen (N) in mangrove leaves and greater aboveground biomass, suggesting that eutrophication from bird guano contributes to increased aboveground productivity. Sediments of rookery cays also had lower percentages of soil organic matter and total N and carbon (C) than control islands, which suggests that eutrophication accelerates organic matter decomposition resulting in lower total C stocks on rookery cays. Our results indicate that coastal eutrophication can reduce ecosystem stability by contributing to accelerated cay loss, with potential consequences for mangrove resilience to environmental variability under contemporary and future climatic scenarios.

Keywords Rookeries · Nutrient enrichment · Cay disappearance · C stocks · Global climate change

Introduction

Coastal eutrophication is an issue of serious global concern, as an accelerated global nitrogen (N) cycle (Galloway et al. 2008; Canfield et al. 2010) has greatly increased the flow of reactive N (primarily as NO_3^-) from land to coastal marine ecosystems, causing degradation and decreased resilience to coastal habitats. Coral reefs, seagrass beds, salt marshes and mangroves are sensitive to eutrophication, with detrimental consequences to biodiversity, nutrient cycling, carbon (C) storage, and habitat provisioning (e.g., Hughes et al. 2003; Burkholder et al. 2007; Feller et al. 2010; Deegan et al. 2012). Although nutrient subsidies enhance primary productivity of coastal wetlands, nutrient enrichment experiments have shown that excess nutrients can be detrimental to the long-term maintenance of coastal ecosystems (Koop et al. 2001; Verhoeven et al. 2006; Reef et al. 2010; Deegan et al. 2012; Cabaço et al. 2013). As nutrient loading increases, coastal vegetated habitats can reach tipping points beyond

Communicated by Seth Newsome.

✉ L. T. Simpson
lsimpson@floridaocean.org

¹ University of Alabama, Tuscaloosa, AL 35487, USA

² Florida Oceanographic Society, 890 NE Ocean Blvd, Stuart, FL 34996, USA

³ Smithsonian Marine Station, Fort Pierce, FL 34949, USA

⁴ Working Land and Seascapes, Conservation Commons, Smithsonian Institution, District of Columbia, USA

⁵ Samford University, Birmingham, AL 35229, USA

⁶ Smithsonian Environmental Research Center, Edgewater, MD 21037, USA

which habitat stability decreases and the potential for recovery is reduced (Dakos et al. 2018). Trajectory towards such tipping points can be accelerated with anthropogenic change and/or large-scale stochastic disturbances (e.g., tropical storms), making it difficult to tease apart major drivers of habitat loss (Moore 2018). As such, spatially explicit information is needed to identify the prevalence and variety of stressors driving forest vulnerability at local scales.

Lying at the interface between water and land, mangroves are generally considered oligotrophic ecosystems adapted to low-nutrient conditions (Hutchings and Saenger 1987; Lugo 1989), making them sensitive to nutrient enrichment of coastal waters. These systems have been shown to increase productivity when nutrient limitation is alleviated (Feller 1995; Feller et al. 2003; Lovelock et al. 2004), and as nutrient availability increases, plants may invest less in belowground biomass and more in aboveground shoots (Grime 1979; Tilman 1990; Reef et al. 2010). Additionally, increased availability of nutrients via anthropogenic sources increases rates of microbial-mediated nutrient sequestration and mineralization (Rivera-Monroy and Twilley 1996; Alongi et al. 2005; Norris et al. 2013). Hence, a decrease in dense, bank-stabilizing belowground biomass, coupled with an increase in microbial decomposition of organic matter, will eventually undermine the structural integrity of a shoreline, leading to collapse (Deegan et al. 2012). Consequently, increased nutrient availability may have detrimental effects to mangrove health and maintenance. Enriched mangroves have also been shown to experience reduced resilience and recovery when exposed to other environmental stressors and extreme events (Lovelock et al. 2009; Feller et al. 2015), which can be further exacerbated by global climate change variables, (i.e., sea-level rise, increased storm intensity and duration)(Goldberg et al. 2020). Profound changes in ecosystem dynamics, due to nutrient enrichment, are likely to influence the maintenance and longevity of mangrove systems, as well as the provision of associated ecosystem services.

Mangroves provide habitat for many bird species (Nagelkerken et al. 2008) and support permanent and migrant bird colonies globally (Lefebvre and Poulin 1996). Bird colonies (rookeries) act as important nutrient vectors and subsidies in many coastal ecosystems (Anderson and Polis 1999; Whelan et al. 2008); birds forage and return to rookeries where they deposit nutrients to the system in the form of guano (Ellis 2005), which is rich in N, phosphate and potassium. Consequently, rookeries can significantly increase nutrient loading to mangrove systems, leading to increased primary production (Onuf et al. 1977), herbivory (Onuf et al. 1977), sediment nutrients, and foliar leaf concentrations (Adame et al. 2015; McFadden et al. 2016), which has implications for biological connectivity in coastal habitats (Buelow and Sheaves 2015). McFadden and others (2016) observed that nutrient input from bird guano in Honduran mangroves

exceeded nutrient inputs typical of USA corn production fertilizer rates, which translated into rookery sediments having “seven times more plant available phosphorus, eight times more nitrate, and two times more ammonium” than control cay sediments. Mangroves exposed to high nutrient availability alter their energy distribution by increasing canopy growth at the expense of root network development (Grime 1979; Tilman 1990). Therefore, plants exposed to high levels of nutrient availability may have greater susceptibility to environmental stressors and extreme events (e.g., sea-level rise, tropical storms), which require larger investment in roots for tree stability and maintenance. Because colonial waterbirds significantly influence nutrient dynamics of mangroves at the local scale, rookeries provide a unique opportunity to study the effects of anthropogenic nutrient enrichment on mangrove cay maintenance and resilience.

The Mesoamerican reef (MAR) ecoregion is a trans-boundary marine ecosystem, comprised of coral reefs, sea-grass beds and mangroves that support the livelihoods and well-being of over two million people (Kramer and Kramer 2002). Across the four countries of the MAR ecoregion, there was an estimated 239,176 ha of mangroves in 2010, having declined by ~30% since 1990. Approximately one-third (74,684 ha) of the region’s current mangrove systems are located in Belize, distributed along the mainland and across a network of islands and cays (Canty et al. 2018). Mangroves in the MAR provide a number of ecosystem services to the coastal communities of Belize. However, due to a number of anthropogenic and climatic threats, the MAR was officially declared a critically endangered ecosystem by the International Union for Conservation of Nature in 2017 (Bland et al. 2017). Land-use change and poorly managed natural resources contribute to alterations in nutrient loading to coastal ecosystems, and can indirectly accelerate mangrove loss in the MAR. Nutrient loading from shrimp aquaculture (Ledwin 2010), agriculture (Burke and Sugg 2006; Buck et al. 2019), and unregulated municipal waste (Wells et al. 2019) has been shown to increase nutrient levels to Belizean coastlines, which can be transported from the lagoon to reef and cays during periods of high rainfall and low winds (Koltes and Opishinski 2009).

Sea-level rise is also of particular concern for mangroves; increases in sea-level rise are associated with erosion of the mangrove seaward fringe and inland migration of the mangrove system (Gilman et al. 2007, 2008). However, land availability on mangrove islands and cays is finite, and mangroves face submergence over time if unable to migrate to higher land or increase elevation through vertical accretion (McKee et al. 2007). Simultaneous increases in nutrient loading and sea-level rise may result in synergistic loss of mangrove cays at rates exceeding those of either stressor alone, highlighting the importance of understanding local-scale nutrient-enrichment impacts. There is increasing

momentum within the MAR ecoregion to promote local, national and regional efforts to strengthen the management, conservation, restoration and monitoring of mangrove ecosystems (Rivas et al. 2020), and understanding the threats to mangroves will be critical in supporting management efforts and prioritizing conservation actions.

In the current study, we investigated differences in mangrove cay size and C and N stocks in sediments and biomass between cays with and without roosting colonial waterbirds to determine if changes in mangrove cay area were related to the presence of rookeries and their resulting nutrient input. The rookeries provided a unique opportunity to study the effects of naturally occurring nutrient enrichment from bird guano as a proxy for human-mediated coastal eutrophication and its potential impacts to coastal habitats. Researchers have measured the effects of avian nutrient enrichment in mangroves (Onuf et al. 1977; Adame et al. 2015; McFadden et al. 2016), and despite the strong connection between birds utilizing healthy mangrove habitats (Holguin et al. 2006), this is the first study to examine mangrove cay disappearance coupled with rookery presence and their associated nutrient enrichment in the context of anthropogenic nutrient loading. We hypothesized that (1) rookeries result in greater N-enriched aboveground biomass with less C stored in sediments than on control cays, and (2) the presence of rookeries is accelerating the shoreline retreat of mangrove cays by destabilizing the soils, making them more vulnerable to erosion. Our hypotheses are based on the premise that mangroves exposed to high nutrient availability, alter biomass ratios (Grime 1979; Tilman 1990), and will be more prone to shoreline erosion and degradation (Deegan et al. 2012), especially under environmental stress and extreme events, such as sea-level rise, drought and hurricane damage (Lovelock et al. 2009; Deegan et al. 2012; Feller et al. 2015). By coupling remote sensing-based analysis to document historical mangrove cay changes with current nutrient stocks and biomass measurements, we investigated mangrove cay area loss in conjunction with seabird rookery nutrient inputs. This work informs our understanding of anthropogenic nutrient loading impacts on mangrove cay ecosystem structure, function and resilience.

Methods

Site selection and characteristics

Sites were selected from cays along the coast of Belize, with rookeries identified in consultation with local fishermen who possessed extensive traditional knowledge of the area. After developing a preliminary set of five candidate cays, we conducted reconnaissance trips to identify rookery cays that met the following criteria: mangroves were the

dominant species, seabirds were actively roosting or there was evidence of nesting, and the cay was not inhabited by humans. Out of the five rookeries surveyed, three cays met our criteria. Control (non-rookery) cays were selected from adjacent islands, which were at least 6 km apart from its associated rookery, in an effort to minimize the potential impact of avian nutrient inputs from adjacent rookery cays. The three sets of rookery and control island pairs provide a latitudinal gradient with sets defined as northern, central and southern (Fig. 1).

In the Northern region, cays sampled were approximately 2.4 km off the coast of Belize City. The rookery cay of Snapper Cay (SC) (17.622°N, - 88.278°W) was sampled in August 2019 and had previous season's nests on it; *Fregata magnificens* (magnificent frigate bird), *Ardea herodias* (Great blue heron) and *Phalacrocorax brasilianus* (neotropic cormorant) are known to nest on the cay

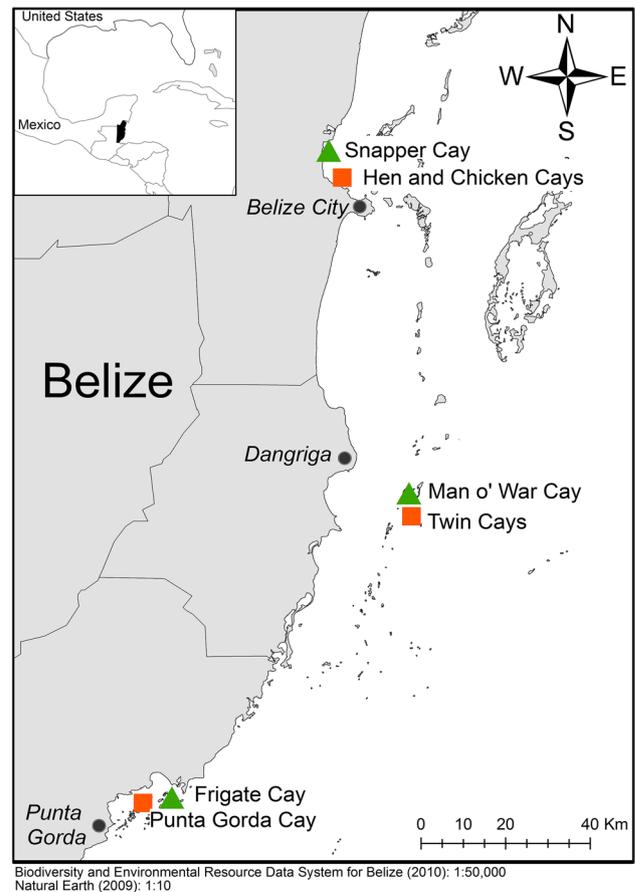


Fig. 1 Location of rookery (green triangle) and control (orange square) cays along a latitudinal gradient off the coast of Belize, Central America. Belize (black) is denoted in corner inset. Northern region cays sampled were Chicken Cay (CC) and Snapper Cay (SC), central region cays were Man o' War Cay (MW) and Twin Cays (TC), and southern region cays were Frigate Cay (FC) and Punta Gorda Cay (PG) (color figure online)

(personal communications Mike Huesner, Belize Audubon Society). Chicken Cay (CC) (of Hen and Chicken Cays) (17.563°N, – 88.249°W) was chosen as the northern control cay (Fig. 1). Both cays were dominated by *Rhizophora mangle* (red mangrove). Central region cays were located approximately 16 km off the coast of Dangriga. Man o' War Cay (MW) (16.884°N, – 88.107°W) was sampled in October 2019 and *F. magnificens* were actively nesting. *Phalacrocorax brasilianus* and *Sula leucogaster* (brown-footed Boobies) were also observed on the cay. The cay was dominated by *R. mangle* and *Avicennia germinans* (black mangrove) with an understory of *Sesuvium portulacastrum* (shoreline purslane). Twin Cays (TC) (16.835°N – 88.102°W), the central control cay, was dominated by *R. mangle* and *A. germinans* with scattered *Laguncularia racemosa* (white mangrove) individuals (Fig. 1). Southern sites were approximately 3.2 km of the coast of Punta Gorda and were sampled in August 2019. The bird rookery, Frigate Cay (FC) (16.230°N, – 88.612°W), was dominated by *R. mangle* and *A. germinans* and did not have any active nests on it at the time. *Fregata magnificens* and *Pelecanus occidentalis* (brown pelicans) are known to nest on the cay (personal communications, Heidi Waters, Toledo Institute for Development and Environment) and remnants of previous year's nests could be seen. The control cay, Punta Gorda Cay (PG) (16.218°N, – 88.673°W) was dominated by dwarf *R. mangle* trees (Fig. 1). The Belizean tidal system is characterized as micro-tidal and of a mixed semidiurnal type, with a mean range of 15 cm (Kjerfve et al. 1982) and the annual precipitation ranges from 1500 to 4000 mm from north to south, respectively (Gischler 2018).

During each trip, ground verification data and a suite of biotic variables were collected to assess effects of seabird presence on mangrove cay size and productivity. The ground verification data collected during each sampling trip informed both our classification of the satellite imagery and our accuracy assessment of the classification results. In total, we recorded the geographic coordinates and land cover type at 160 ground control points with 3 m positional accuracy across all six cays, using a GPSMAP 78sc GPS unit (Garmin, Lenexa, Kansas, USA). Additionally, we collected

hydro-edaphic samples, plant biomass samples and measurements, and canopy cover measurements from each cay. These samples, coupled with land cover change, characterize potential differences between rookery and control cays along the Belize coast and provide a snapshot of potential nutrient loading impacts to mangrove cay structure and function.

Remote sensing image selection and preprocessing

This study used supervised classification of high spatial resolution satellite imagery to systematically and efficiently map and quantify historical changes on mangrove cays. Remote sensing-based analyses in general, and supervised classifications in particular, are robust and widely used methodologies to document historical mangrove changes (Green et al. 1998; Heumann 2011; Kuenzer et al. 2011; Pham et al. 2019). Using high spatial resolution (≤ 3 m) imagery, our analysis presents highly accurate depictions of how each cay has changed over the past two decades.

One “start-date” image and one “end-date” image was used for each of the six cays, for a total of 12 study images (Table 1). The six start-date images were the earliest suitable high spatial resolution satellite images available for our study cays. Due to the low availability of cloud-free images, we were not able to acquire start-date images that had all been captured during the same year. However, the two start-date images for each rookery-control pair were captured during the same years, allowing for direct comparison of the rates and amounts of island decline between the paired rookery and control cays. The six end-date images were acquired through the Planet Labs Education and Research Program (Planet Team 2017) and all 12 study images were multispectral, with blue, green, red, and near-infrared spectral bands. The six end-date images had spatial resolutions of 3 m, and the six start-date images, which were pansharpened by commercial imagery suppliers, had spatial resolutions of either 1 or 0.6 m. All 12 images had been geometrically and radiometrically corrected by their respective imagery providers. The six end-date images had already been atmospherically corrected, but the six start-date images were not. However, atmospheric correction was not necessary, because our

Table 1 Summary of satellite images used in remote sensing analysis

Cay code	Location	Cay type	Start date			End date		
			Date	Sensor	Spatial res. (m)	Date	Sensor	Spatial res. (m)
SC	Northern	Rookery	11/17/2002	QuickBird	0.6	8/23/2019	PlanetScope	3.0
CC	Northern	Control	9/19/2002	QuickBird	0.6	8/30/2019	PlanetScope	3.0
MW	Central	Rookery	9/13/2001	IKONOS	1.0	10/17/2019	PlanetScope	3.0
TC	Central	Control	9/13/2001	IKONOS	1.0	10/16/2019	PlanetScope	3.0
FC	Southern	Rookery	9/29/2004	QuickBird	0.6	8/30/2019	PlanetScope	3.0
PG	Southern	Control	9/29/2004	QuickBird	0.6	8/21/2019	PlanetScope	3.0

methodology did not directly compare pixel values across images (Young et al. 2017). No cloud cover obscured any parts of the study cays in the 12 images.

Remote sensing image classification

A supervised classification process was used to systematically and efficiently quantify the mangrove extent for each study cay on each study date (Nguyen et al. 2020). The analysis was performed with the Semi-Automatic Classification Plugin (Congedo 2021) in QGIS 3.4, which classifies each study image into two land cover classes (mangrove and non-mangrove) using the following process:

Referencing our field observations and visual examination of each study image (Veerendra and Latha 2014; Ibharim et al. 2015; Viennois et al. 2016), 10–15 training polygons for each land cover class on each study image were manually delineated. The computer collated the spectral properties of the pixels within these training polygons to identify the unique “spectral signature” of each land cover class (Jensen 2015; Sabins and Ellis 2020). Then, using a maximum likelihood algorithm, the computer examined every other pixel in the image and classified it either as mangrove or non-mangrove depending on which spectral signature it more closely matched. The output of the supervised classification was a classified thematic map depicting mangrove and non-mangrove land cover classes for the given study cay at the given study date. This process was repeated for each of the 12 study images to create 12 classified thematic maps (one start-date map and one end-date map for each of the six cays) of mangrove and non-mangrove features. Using a nearest-neighbor algorithm, each of the start-date classified thematic maps were resampled from their original resolution to a spatial resolution of 3-m to allow for direct comparison with the end-date maps (Serra et al. 2003).

Mangrove forested area was then calculated for each map by multiplying the number of mangrove pixels by pixel area (9 m²). Change in mangrove area was then calculated for each study cay by subtracting the final area from the initial area. Average annual rate of mangrove change for each cay during the study period was calculated using the following equation (Puyravaud 2003):

$$r = \frac{1}{t_2 - t_1} \ln \frac{A_2}{A_1} \quad (1)$$

where r is the average annual rate of change, and A_1 and A_2 are the mangrove areas at times t_1 and t_2 , respectively.

Remote sensing accuracy assessment

A systematic accuracy assessment was conducted on our image classifications by checking each classified thematic

map against reference data at a total of 200 control points (100 for mangrove features and 100 for non-mangrove features). For the six end-date maps, reference data used were a combination of the ground verification points collected during August and October of 2019 and high-resolution Google Earth historical imagery (Morissette et al. 2005; Congalton and Green 2008; Sabins and Ellis 2020). For the six start-date maps, reference data used were the original, unclassified satellite images. Google Earth historical imagery of the cays for the start-date years did not have sufficiently fine spatial resolution to be used as reference data, and other forms of reference data were not available for the cays for those years. Therefore, the original, high-resolution imagery was the best available option for evaluating the accuracy of the start-date maps (Congalton and Green 2008; Sabins and Ellis 2020).

The overall accuracy and Kappa coefficient were calculated for each classified thematic map, as well as the omission and commission error for the mangrove features in each map. Overall accuracy quantifies how accurately the classification process was able to differentiate between mangrove and non-mangrove features. The Kappa coefficient expresses the overall success of the classification relative to a random classification. Mangrove omission error quantifies the amount of classification error attributable to classifying real-world mangrove features as non-mangrove in the map, and mangrove commission error quantifies the amount of error attributable to classifying real-world non-mangrove features as mangrove in the map (Jensen 2015). Our image classification process was highly accurate, with all twelve classified thematic maps having overall accuracies of at least 97% and Kappa coefficients of at least 94% (Supplementary Table A).

Hydro-edaphic characteristics

Hydro-edaphic characteristics were measured on each cay to capture differences among cay type. Three samples for porewater salinity and nutrient analysis were extracted from the ground at 15 cm using a sipper (McKee et al. 1988) from each cay at low tide. Salinity was measured with a handheld refractometer in the field. Porewaters for nutrient analysis were filtered and frozen for transport back to the United States. Nutrient analyses (NO₃–NO₂, PO₄, NO₂, NH₄) were performed on samples using a Skalar San + segmented flow autoanalyzer, following chemistries adapted from standard EPA methods for nutrient analyses, by Technical Support Services at the Dauphin Island Sea Lab, Alabama, USA.

Sediment cores

On each cay, 50 cm deep sediment cores were collected using a 5.2 cm diameter Russian peat corer (Aquatic Research Instruments, Hope, Idaho, USA) to test for

differences in sediment characteristics across cays. Sediment depth was not measured in this study, but has been shown to be 3–10 m on the surrounding cays (Macintyre et al. 2004; McKee et al. 2007; Kauffman et al. 2020). Cores were randomly sampled on the cays: six cores were taken at FC; four cores were taken at PG, SC, and CC; and three cores were taken at MW and TC. The cores were systematically divided into 5 cm increments in the field, bagged, and kept cool and out of direct sunlight prior to being returned to the laboratory. In the lab, sediment samples were stored at 4 °C prior to analysis, then dried at 70 °C until they reached a constant weight. Bulk density (BD, g cm⁻³) of each sample was calculated by dividing the oven-dried mass by the volume of the sample. Samples were then ground with a mortar and pestle to ensure homogeneity prior to analysis for soil organic matter (SOM) by loss-on-ignition, total C (C_{total}), and total N (N_{total}). Sub-samples of the homogenized sediments were combusted at 500 °C for 4 h in an Isotemp muffle furnace (Fisher Scientific) for SOM measurements and the remaining inorganic C in the ashed subsamples was determined with elemental analyzer. A carbonate correction was calculated using the methods outlined by Fourqueen et al. (2014). Remaining subsamples were combusted for C_{total} and N_{total} using an EA 1108 CHNS–O (Carlo Erba Instruments, Milan, Italy) at the University of Alabama, Tuscaloosa, Alabama, USA.

The sediment C per sample depth interval was calculated and C storage (Mg C ha⁻¹) of each interval was then summed to determine total sediment C density for each core. Carbon mass from each sediment section was summed to determine total sediment C stocks at each sampling location. To calculate current sediment C stocks to 50 cm on each cay, the cay area (ha) (calculated with remote sensing) was multiplied by total sediment C stock (Mg C ha⁻¹) to obtain a baseline calculation of sediment C stocks (Mg C) on rookery and control cays (Kauffman and Donato 2012).

Mangrove biomass

To quantify aboveground biomass on each of the cays, five *R. mangle* trees representative of the mature stands were measured for height and diameter at breast height (DBH). Aboveground biomass was calculated using the allometric equation specific to *R. mangle* developed by Fromard and others (1998):

$$B_{TA} = 0.128 \times (D)^{2.60}, \quad (2)$$

where B_{TA} = tree aboveground biomass (kg) and D = tree DBH (cm). Canopy cover was measured on each cay using a forest densitometer (Forestry Suppliers, Inc., Jackson, Mississippi, USA) according to manufacturer specifications.

Nutrient resorption efficiencies

To determine how nutrient inputs from seabirds affected structural and physiological traits of *R. mangle* leaves, green and senescent leaves were collected from five trees on each cay and analyzed for C_{total}, N_{total}, specific leaf area (SLA cm⁻² g) and leaf mass per area (LMA, g cm⁻²). The youngest, fully mature green leaves (n = 5) from penapical stem positions in sunlit portions of each tree's canopy and yellow, senescent leaves (n = 5) from the same tree were collected and transported back to the United States. Leaf area was determined on a LI-3000C portable leaf area meter (LI-COR, Lincoln, Nebraska, USA) at the University of Alabama, USA. Specific leaf area was calculated by dividing leaf area (cm²) by leaf dry mass (g). Leaf mass per area is the inverse of SLA. After leaf area measurements, leaf samples were dried at 60 °C and ground using a Wiley Mill (Thomas Scientific, Swedesboro, New Jersey, USA). Leaves from each cay were homogenized prior to analysis. Total C and N_{total} were determined with an EA 1108 CHNS–O (Carlo Erba Instruments, Milan, Italy). Nutrient resorption efficiencies were quantified as described in Feller et al. (1999).

Statistical analysis

All models were blocked by location as a random effect to account for potential differences along the latitudinal gradient. When block was not significant, the location variable was removed from subsequent models. Differences in percent change between rookery and control cays were analyzed with a *t* test. Porewater salinity and nutrients (NO₃–NO₂, PO₄, NO₂, NH₄) were analyzed using a one-way analysis of variance (ANOVA) with cay type (rookery and control) as a fixed factor. Sediment measurements (SOM, BD, C_{total}, N_{total}, C:N) were analyzed with two-way ANOVAs with cay type and depth as fixed factors. Sediment C stocks of rookery and control cays were analyzed with a *t* test. Porewater salinity and nutrients, biomass measurements (aboveground biomass, canopy height and cover, SLA), nutrient resorption and total lead N were analyzed using a one-way ANOVA with cay type (rookery and control) as a fixed factor. Normality of the data for ANOVAs was assessed using the Shapiro–Wilks test and homogeneity of variance for all variables was assessed using Levene's test. When required, variables were log- or square root transformed to comply with assumptions for linear models. If assumptions failed under transformation, the Kruskal–Wallis non-parametric test was used. When significant differences between cay types were found, pair-wise comparisons were explored with Tukey's honestly significant differences (HSD) test with alpha (α) set at 0.05. Blocked effects are reported

using the Wald test with p values set at 0.05. Analyses were performed using JMP 14.0 (S.A.S Inc., Cary, North Carolina, USA). Data are reported as mean \pm 1 standard error throughout the manuscript.

Results

Cay size

Current cay size (ha) was not a function of latitudinal gradient (Wald $p = 0.94$). All six mangrove cays exhibited a loss in total area from the early 2000s through 2019. However, total percentage change in mangrove cay area was significantly different between cay types ($df = 4, t = -2.99, p = 0.047$). Rookery cays lost an average of $51 \pm 16\%$ of their total land area at a mean rate of $3 \pm 0.7\%$ per year. In contrast, control cays lost an average of $4 \pm 1\%$ of their total land area, at a mean annual rate of $0.2 \pm 0.1\%$ per year. Rookeries had an overall mean annual rate of change 13 ± 4 times greater than control islands (Fig. 2, Table 2).

Hydro-edaphic characteristics

Porewater salinity was not significantly different between rookery and control cays. Porewater nutrient analyses revealed that $\text{NO}_3\text{-NO}_2$ was significantly greater on control cays (1.37 ± 0.16) than on rookeries cays (0.70 ± 0.17). No significant differences in PO_4 ($\mu\text{mol/L}$), NO_2 ($\mu\text{mol/L}$), or NH_4 ($\mu\text{mol/L}$) were observed between cay types (Table 3).

Sediment cores

Bulk density was not significantly different between cay types ($F_{1,219} = 0.41, p = 0.52$). However, BD significantly increased down the core profile ($F_{9,218} = 3.15, p = 0.0014$) with greater increases in rookery profiles (island \times depth interaction: $F_{9,218} = 2.67, p = 0.006$; Wald $p = 0.48$) (Fig. 3A). Total sediment C (%) was significantly greater on control cays ($23.6 \pm 0.74\%$) than on rookeries ($17.2 \pm 0.78\%$) ($F_{1,215} = 69.0, p < 0.0001$) and significantly decreased down the core profile ($F_{9,215} = 3.36, p = 0.0007$), regardless of island type (Fig. 3B). Similarly, soil organic matter was significantly greater on control cays ($52.3 \pm 1.37\%$) than rookeries ($36.7 \pm 1.67\%$) ($F_{1,217} = 55.8, p < 0.0001$) and decreased down the depth profile on both rookeries

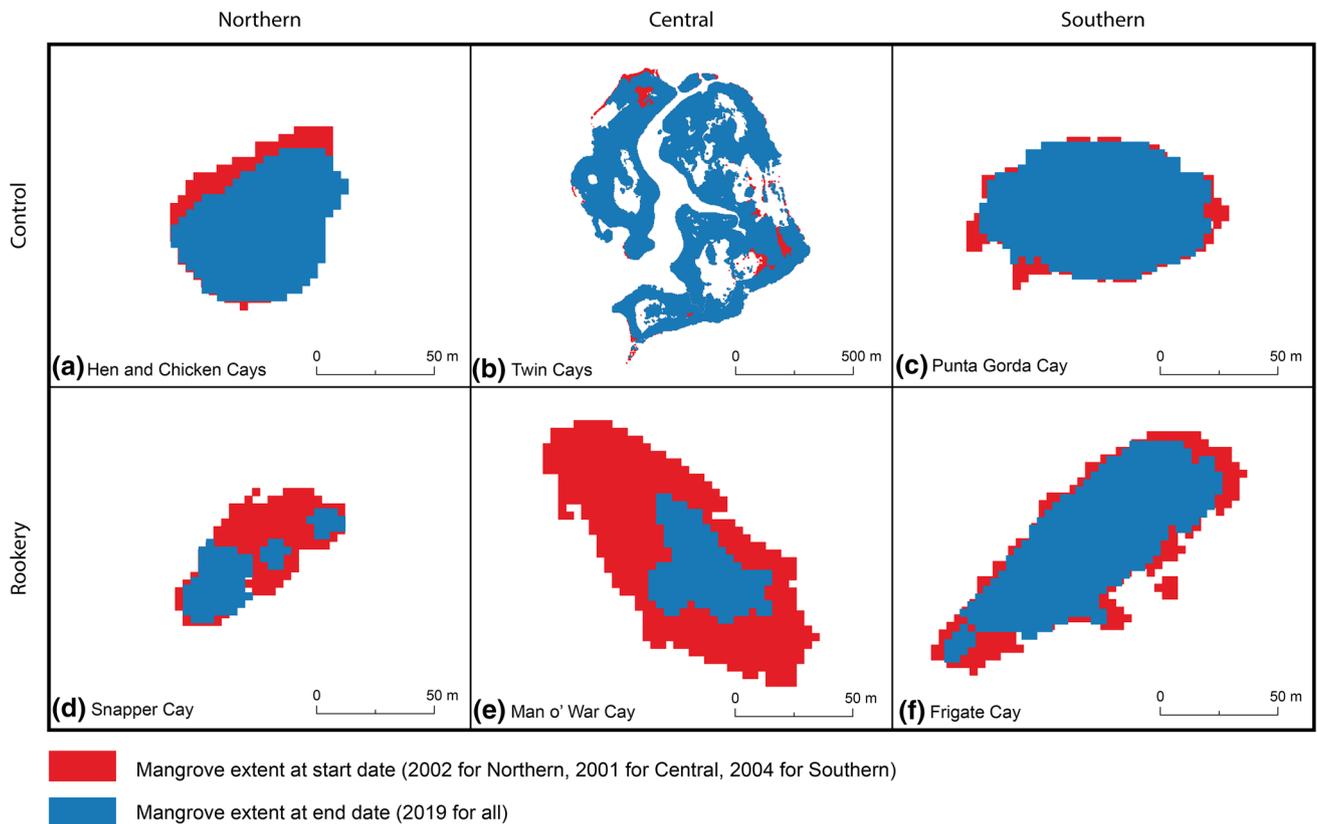


Fig. 2 Composite of maps depicting the changes in area between the start date (mangrove extent shown in red) and end date (mangrove extent show in blue) for each rookery **d–f** and control cay **a–c**

Table 2 Mangrove cay area and sediment carbon change

Cay	Location	Cay type	Area (ha)			Total Mg C			Total % change in area and Mg C	Mean annual % rate of change
			Start date	End date	Loss	Start date	End date	Loss		
SC	Northern	Rookery	0.185	0.085	- 0.100	2.93	1.34	- 1.59	- 54.15	- 3.01
CC	Northern	Control	0.297	0.278	- 0.019	1.96	1.83	- 0.13	- 6.36	- 0.35
MW	Central	Rookery	0.572	0.136	- 0.437	10.79	2.56	- 8.23	- 76.26	- 4.01
TC	Central	Control	57.983	55.937	- 2.046	1156.75	1115.94	- 40.81	- 3.53	- 0.19
FC	Southern	Rookery	0.505	0.392	- 0.113	5.10	3.96	- 1.14	- 22.46	- 1.40
PG	Southern	Control	0.392	0.383	- 0.009	6.47	6.32	- 0.15	- 2.29	- 0.14
	Mean	Rookery	-	-	-	-	-	-	- 50.95 ± 15.61	- 2.81 ± 0.76
		Control	-	-	-	-	-	-	- 4.06 ± 1.20	- 0.23 ± 0.06
Differential rate of change between rookery and control cays									13.31 ± 4.17	13.31 4.17

Historical imagery was analyzed between 2002 and 2019 in the northern cays, 2001 and 2019 in the central cays and 2004 and 2019 in the southern cays

Table 3 Summary of hydro-edaphic variables, mangrove tree and leaf measurements, and data analysis results from rookery and control cays

	<i>N</i>	Rookery	<i>N</i>	Control	ANOVA results	Wald <i>p</i>
Hydro-edaphic variables						
NO ₃ -NO ₂ (μ mol/L)	9	0.70 ± 0.14 ^b	9	1.37 ± 0.16 ^a	$F_{1,14} = 17.9, p = 0.0008$	0.56
NO ₂ (μ mol/L)	9	0.47 ± 0.15 ^a	9	0.45 ± 0.10 ^a	$F_{1,14} = 0.46, p = 0.51$	0.41
NH ₄ (μ mol/L)	9	12.7 ± 3.77 ^a	9	25.3 ± 9.21 ^a	$F_{1,14} = 1.12, p = 0.31$	0.35
PO ₄ (μ mol/L)	9	1.07 ± 0.23 ^a	9	2.23 ± 0.64 ^a	$F_{1,14} = 0.56, p = 0.46$	0.56
Salinity	9	37.5 ± 1.31 ^a	9	36.5 ± 1.09 ^a	$F_{1,14} = 2.11, p = 0.17$	0.34
Mangrove measurements						
Canopy cover	3	77.1 ± 3.87 ^a	3	51.9 ± 26.0 ^a	$F_{1,2} = 0.73, p = 0.48$	0.48
Height (m)	15	6.54 ± 0.74 ^a	15	4.99 ± 0.91 ^a	$F_{1,26} = 2.92, p = 0.09$	0.40
B _{TA} (Kg)	15	2104 ± 529 ^b	15	935 ± 229 ^a	$F_{1,26} = 6.75, p = 0.02$	0.40
Mangrove leaf measurements						
Leaf SLA (cm ² /g)	30	56.1 ± 2.98 ^b	30	40.5 ± 1.27 ^a	$F_{1,26} = 37.7, p = < 0.0001$	0.34
NRE	15	52.5 ± 3.74 ^a	15	55.5 ± 2.62 ^a	$F_{1,1} = 0.43, p = 0.52$	0.01
Total green leaf <i>N</i> (%)	15	1.30 ± 0.07 ^b	15	0.95 ± 0.03 ^a	$F_{1,26} = 33.0, p = < 0.0001$	0.36
Total senescent leaf <i>N</i> (%)	15	0.70 ± 0.35 ^b	15	0.42 ± 0.05 ^a	$F_{1,26} = 13.9, p = 0.0010$	0.95
Total green leaf <i>C</i> (%)	15	46.0 ± 1.57 ^a	15	47.3 ± 2.07 ^a	$F_{1,1} = 3.58, p = 0.07$	0.04
Total senescent leaf <i>C</i> (%)	15	45.6 ± 1.66 ^a	15	46.4 ± 2.06 ^a	$F_{1,26} = 1.29, p = 0.26$	0.38
Green leaf C:N	15	36.4 ± 1.98 ^b	15	65.5 ± 7.89 ^a	$F_{1,26} = 44.1, p = < 0.0001$	0.96

Different letters across rows denote significance. Means ± SE are reported

and control islands ($F_{9,217} = 3.50, p = 0.0005$) (Fig. 3C). Additionally, control cay sediments (0.96 ± 0.03) had significantly greater N_{total} than rookery sediments (0.64 ± 0.02) ($F_{1,216} = 87.3, p = < 0.0001$). Total N decreased down the core profile ($F_{9,216} = 7.08, p = < 0.0001$) of both rookery and control cays (Fig. 3D). However, sediment C:N was not significantly different between cays ($p = 0.65$) or down the core profile ($p = 0.66$; Walds $p = 0.36$). Control cays stored an average of 169 ± 6.46 Mg sediment C ha⁻¹, while rookery cays stored 114 ± 15.38 Mg of sediment C ha⁻¹ ($F_{1,22} = 9.62, p = 0.0052$). Percent change in soil C between cays was significantly greater on rookeries than on control cays (Table 2).

Biomass and leaf nutrient resorption

Tree height and canopy cover were not significantly different between cay types. Rookeries had 125% more above-ground biomass (B_{TA}) (2104 ± 529.6 kg) than control cays (935.7 ± 229.0 kg) and *R. mangle* leaves on rookery cays had a greater SLA (56.1 ± 2.98 cm²/g) than on control cays (40.5 ± 1.27 cm²/g) (Table 3).

Leaf nutrient resorption did not differ between cays. However, total leaf N (%) in green and senescent leaves was significantly greater on rookery cays than on control cays. Total C in green and senescent leaves did not differ between

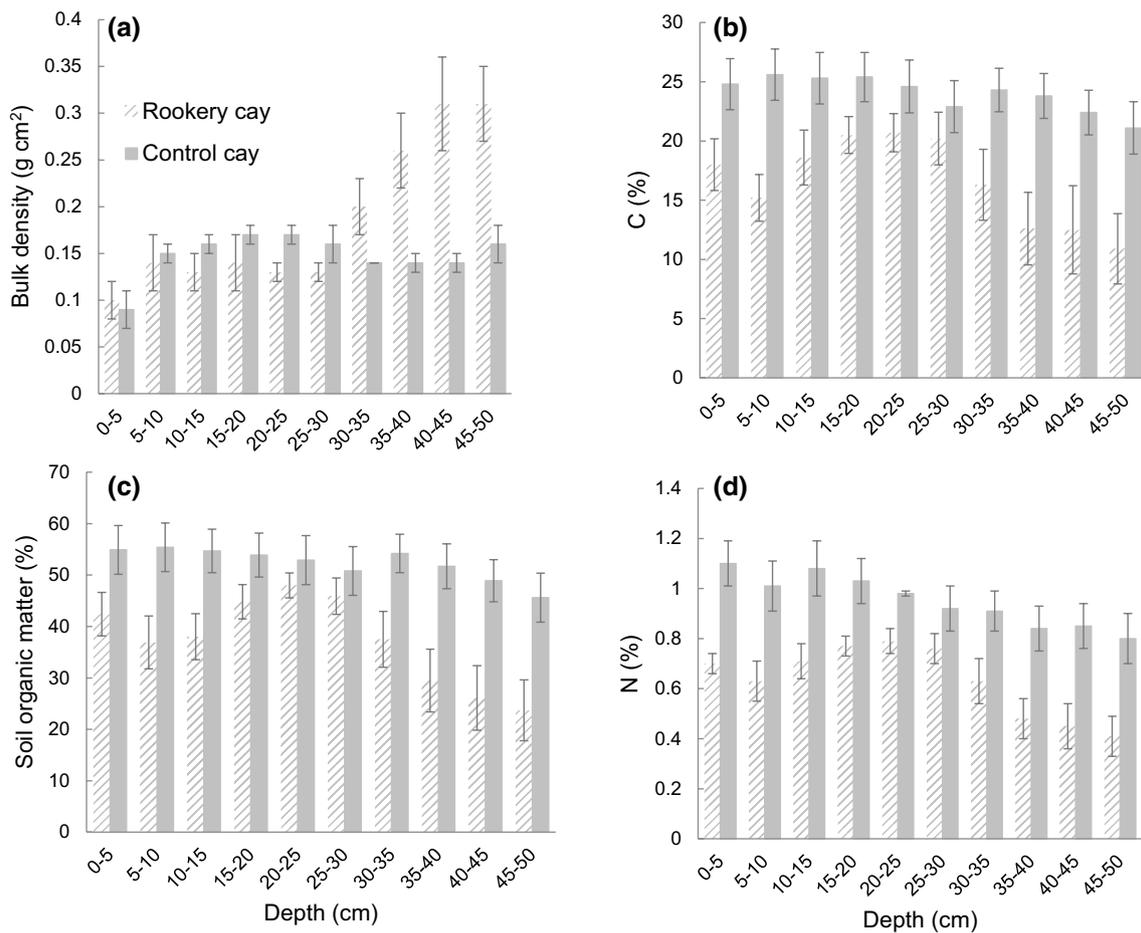


Fig. 3 Sediment data across cay types and down the core profile for **a** bulk density (g cm⁻²), **b** total C (%), **c** soil organic matter (%), and **d** total N (%). Data presented are means ± SE for control () and rookery () cays

cay types. C:N was significantly lower in green leaves on rookery cays than on control cays (Table 3).

Discussion

Although all mangrove cays lost area over the 19-year study period, those with rookeries disappeared approximately 13 times faster than those without seasonal or resident seabird populations. Rookery mangrove cays were associated with significantly greater aboveground biomass and a higher percentage of N concentration in both green and senescent leaves, suggesting that bird guano contributes to eutrophication of these cays. Patterns of sediment chemistry supported these results, with greater percentages of SOM, total N and total C on control cays than on rookeries. Such differences suggest that eutrophication of mangrove cays from bird guano accelerates decomposition of organic matter in the sediments, resulting in decreases in total C stocks. This work forecasts the potential for accelerated mangrove cay land

loss due to eutrophication, regardless of origin, especially under global climate change scenarios.

Nesting birds can supply nutrients at rates that compare to intensive agriculture practices (Young et al. 2010; McFadden et al. 2016). For bird guano (urea) to be denitrified (N₂ gas), microbial communities within the wetland soil matrix must first transform it to NH₄⁺ and CO₂ (Reddy and Delaune 2008). However, nitrification (NH₄⁺ to NO₃⁻) is not favored in oxygen-poor soils, thereby limiting the loss of urea by denitrification. Rather, this organic N is transferred to a soil pool to be taken up by the plant, which translates to increases in plant productivity. While we were unable to confirm the magnitude of N-loading by birds on these cays, rookeries had 2.25 times greater aboveground biomass and 37% more foliar N in green leaves as compared to control cays, suggesting bird guano stimulates aboveground plant biomass production. The remote location of these cays, in characteristically oligotrophic waters, coupled with the lack of soil porewater nutrient differences (NO₂, NH₄, and PO₄), suggests that nutrients are quickly utilized as electron

acceptors by microorganisms, further signifying that avian-delivered nutrients alleviated nutrient limitations for plant growth on rookeries. Additionally, LMA was significantly lower on rookery cays, which is associated with eutrophication (Wright et al. 2002). Thus, the roosting of waterbirds on mangrove cays suggests alterations to mangrove growth through N-loading and highlights the implications of anthropogenic nutrient loading to these ecosystems.

Eutrophication has been linked to an increase in species sensitivity to stochastic disturbances due to increased allocation to shoots rather than roots (Grime 1979). Shifts in a species biomass ratio can indirectly increase mortality rates in response to extreme events (Lovelock et al. 2009; Feller et al. 2015), as well as decrease the rate of sediment C accumulation (McKee et al. 2007), potentially decreasing the ability of these ecosystems to keep pace with sea-level rise (Deegan et al. 2012). Mangroves in the Caribbean region have been shown to adjust to changing sea level through belowground root accumulation since the Holocene (McKee et al. 2007). Soil organic matter was lower on rookery cays, suggesting less root input and/or more decomposition than on control cays. Additionally, soil C, N and SOM decreased, while BD increased, down the soil profile in rookery cays. Fewer roots with shorter lifetimes would result in decreased C content and SOM in deeper horizons, and the percolation of nutrients to deeper sediments could destabilize older sediment layers (Nowinski et al. 2008). Furthermore, decreased root biomass at depth likely reduced plant competition for N, leading to increased potential for nitrification and leaching losses of N to the aquatic ecosystem (Giblin et al. 1991). Decreases in root input or increases in sediment subsidence results in limited or no vertical accretion of sediments, and undermines sediment stability (e.g., Deegan et al. 2012), which can reduce resilience to environmental stressors (Spivak et al. 2019) and result in peat collapse (Chambers et al. 2019) in coastal wetlands. McKee and others (2007) observed that control *R. mangle* fringe plots in Belize had an average elevation gain of 4.1 mm year⁻¹, whereas fringe plots enriched with P only gained 1.6 mm year⁻¹, and plots enriched with N gained only 0.1 mm year⁻¹. Without root and other organic inputs, or with an increase in decomposition, submergence of these tidal forests is inevitable due to peat collapse, physical compaction and eustatic sea-level rise.

Rising sea level will have the greatest impact on mangroves experiencing decreases in sediment elevation, especially where there is limited area for landward migration (Gilman et al. 2008; Krauss et al. 2014). Current mean sea-level rise from nearby NOAA long-term water level stations is estimated to be between 3.69 and 4.21 mm per year (NOAA), and our findings suggest mangroves cays are not keeping pace with these sea-level rise rates. Mangrove cay rookeries lost between 23 and 77% of their total area, at a

mean rate of 3% per year, compared to control cays which lost between 2 and 6% of their total area, at a mean rate of 0.2% per year. Differences in the loss of mangrove areal extent of rookery cays may be due to fluctuations in nutrient inputs, due to the presence of permanent versus seasonal rookeries, coupled with hydrological conditions and stochastic disturbances. However, these rates of loss bring to light the drastic influence of nutrient enrichment to these systems and may serve as a portent of future losses due to anthropogenic nutrient loading. More work needs to be done to tie nutrient loading to cay submergence, as changes in nutrient regimes of peat-forming mangroves may alter the balance among biotic processes controlling the accumulation of organic matter and soil elevations relative to sea level. Thus, increases in tree growth, coupled with decreased cay area, suggest that the positive feedbacks of nutrient over-enrichment are superseded by decreases in mangrove resilience.

Nutrient enrichment can invoke a series of positive feedbacks by altering ecosystem processes that affect belowground dynamics and shoreline stability. Mounting evidence suggests that extreme weather events will increase in their frequency, intensity, and/or duration in coming decades (Schär et al. 2004; Ummenhofer and Meehl 2017), which will have deleterious consequences for the resilience of stressed populations (Neilson et al. 2020). Cays experiencing nutrient over-enrichment will be more susceptible to the erosive forces of storms (e.g., windthrow and waves) and to the stresses caused by rising sea level (Naidoo 1983; Ellison 1993, 2000). Over the time period studied for historical imagery, there were eight hurricanes and four tropical storms that made landfall in Belize. Of those, three hurricanes (Categories 1, 2, and 5) and one tropical storm passed directly over the study sites (NOAA). While these stochastic events cannot be definitively linked as tipping points for the over-enriched rookery systems, these events have been shown to affect mangrove resilience (Feller et al. 2015) and shape other systems globally (e.g., Gardner et al. 2005; Leonardi et al. 2016; Simard et al. 2019). Hence, simultaneous increases in nutrient loading and sea-level rise, coupled with stochastic disturbances and extreme events, may result in the synergistic loss of mangrove cays in Belize, and globally.

The loss of mangrove cays reported here, regardless of cause, has serious ecological implications for mangroves and adjoining communities. Mangroves provide coastal protection, cay erosion control, water purification, maintenance of fisheries, C sequestration, as well as tourism, recreation, education and research opportunities (Barbier et al. 2011 and references therein), with an estimated annual value of US \$174–249 million per year to Belize (Cooper et al. 2009). Mangrove islands and cays constitute approximately 27% of the Belizean coastline (Murray et al. 2003) and a large proportion of the country's mangroves are intimately inter-connected with the Belize Barrier Reef

Complex (Macintyre et al. 1995), the largest coral reef system in the Americas (UNESCO 1996). Loss of mangrove cays associated with the MAR, which have been shown to be a major hotspot of biodiversity (Ruetzler and Feller 1996; Macintyre et al. 2000; Ruetzler 2004), will result in a loss of habitat for diverse marine species (e.g., Mumby 2006; Macintyre et al. 2009; Nagelkerken et al. 2010; Yates et al. 2014; Rogers and Mumby 2019; Mishra and Apte 2020). The decline and subsequent loss of interconnected habitats may increase vulnerability of coastal communities to natural impacts (Guannel et al. 2016), which will have serious implications to their resilience. Hence, the loss of these cays from nutrient over-enrichment would be detrimental on many levels, and not only has implications for habitat interconnectivity and human livelihoods, but also for the mitigation of global climate change through C storage.

The loss of mangrove areal extent has implications not just for C sequestration, but also C storage. The six cays included within this study currently contain an estimated 1256 Mg of C stored in the top 50 cm of their sediments, and lost an estimated 52 Mg C during the study timeframe. However, studies from the region suggest that mangrove peat can extend 3–10 m deep (Macintyre et al. 1995, 2004; McKee et al. 2007; Kauffman et al. 2020), and can be stored for millennia if undisturbed. Therefore, the total C stored in these mangrove cays could be as much as 25,000 Mg C, and the loss of mangrove C calculated in this study could actually be much greater. The greatest loss in sediment C was associated with rookery cays, which lost an estimated 50% of sediment C (in the top 50 cm) between 2001 and 2019. At the rate of loss calculated in this study, rookery cays may completely disappear in ≤ 15 years, underscoring the deleterious effects that nutrient over-enrichment has on mangrove cay maintenance and longevity. Cay loss has significant implications for regional and global C pools, as mangrove habitats have been shown to sequester significantly greater concentrations of C relative to their spatial extent (Duarte et al. 2005; McLeod et al. 2011). For example, mangroves sediments can store up to three times more C per hectare than typical upland tropical forests (Donato et al. 2011; Kauffman et al. 2011), and when buried in accreting sediments, this C can remain stored for centuries to millennia (Mateo et al. 1997). These globally significant C pools contribute substantially to long-term C storage that would otherwise remain as atmospheric CO₂ and exacerbate climate change (e.g., Chmura et al. 2003; Duarte et al. 2005). Loss of mangrove area is of concern as countries, such as Belize, are looking to include mangrove C within their Nationally Determined Contributions to mitigate C emissions. However, the loss of mangrove area increases C emissions and contributes to climate change (Donato et al. 2011).

Conclusions

The Caribbean islands and parts of Central America are forecasted to lose more mangrove-associated species than other parts of the world due to global climate change (Record et al. 2013), which will be further exacerbated by nutrient over-enrichment from coastal communities. Given the strength of the effect of N-enrichment on mangrove mortality (Lovelock et al. 2009; Feller et al. 2015), die-back of mangrove forests would be expected to occur in coastal areas that receive large nutrient influxes from anthropogenic sources and are subject to acute or chronic environmental stressors. In this study, all mangrove cays exhibited a decrease in area, while those experiencing localized eutrophication from colonial waterbirds exhibited a significantly greater rate of loss. Our findings highlight some of the synergies between natural processes (roosting waterbirds) and climate change (e.g., sea-level rise), which are causing significant feedbacks that may not only accelerate global climate change, but reduce the resiliency of marine ecosystems and coastal communities to disturbances. Thus, the benefits of increased mangrove growth in response to eutrophication (e.g., Adame et al. 2015) will be offset by the costs of lower resilience of mangrove forests to environmental stressors, bringing to light the delicate balance of mangrove ecosystem stability. By studying rookery cays, we can forecast the effects of increased anthropogenic nutrient loading to mangrove cay ecosystem structure, function and climate change resilience. Given these insights, the challenge now is to incorporate this information into coastal management plans to minimize nutrient enrichment to local watersheds, and the loss of mangroves and their ecosystem services. Localized management activities can build resilience to stressors; however, climate change, particularly sea-level rise, is a global phenomenon and requires global action.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00442-021-05056-w>.

Acknowledgements The authors would like to thank Toledo Institute for Development and Environment (TIDE) and Belize River Lodge for regional information. We would also like to thank the Belize Fisheries Department, Belize Forestry Department and the Mining Unit of the Ministry of Natural Resources for permits and unabridged access to mangrove cays. A special thanks to Z.R. Foltz and M.S. Jones for CCRE coordination. Thank you to N. Singh and M. Bell for laboratory assistance. Thank you to K.V. Curtis for sediment nutrient analysis and L. Linn for porewater analysis. This is Contribution No. 1053 of the Caribbean Coral Reef Ecosystems program, and contribution no. 1159 of the Smithsonian Marine Station.

Author contribution statement LTS, SWJC, JAC, MKS and ICF designed the study; LTS, SWJC, JRC and ICF performed the research; LTS and JRC analyzed the data; all authors contributed to the writing of the paper. JAC and ICF are co-senior authors.

Funding This research was funded by The Summit Foundation.

Availability of data and materials The data were deposited in Mendeley Data under the <https://doi.org/10.17632/ymzp3grrrp.1>

Code availability All software used and reference to specific code is provided in this manuscript.

Declarations

Conflict of interest None.

Ethical approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

References

- Adame MF, Fry B, Gamboa JN, Herrera-Silveira JA (2015) Nutrient subsidies delivered by seabirds to mangrove islands. *Mar Ecol Prog Ser* 525:15–24. <https://doi.org/10.3354/meps11197>
- Alongi DM, Clough BF, Roberston AI (2005) Nutrient-use efficiency in arid-zone forests of the mangroves *Rhizophora stylosa* and *Avicennia marina*. *Aquat Bot* 82:121–131
- Anderson WB, Polis GA (1999) Nutrient fluxes from water to land: seabirds affect plant nutrient status on Gulf of California islands. *Oecologia* 118:324–332. <https://doi.org/10.1007/s004420050733>
- Barbier EB, Hacker SD, Kennedy C et al (2011) The value of estuarine and coastal ecosystem services. *Ecol Monogr* 81:169–193. <https://doi.org/10.1890/10-1510.1>
- Bland LM, Regan TJ, Dinh MN et al (2017) Using multiple lines of evidence to assess the risk of ecosystem collapse. *Proc R Soc B Biol Sci* 284:660. <https://doi.org/10.1098/rspb.2017.0660>
- Buck DG, Esselman PC, Jiang S et al (2019) Seasonal fluxes of dissolved nutrients in streams of catchments dominated by Swidden agriculture in the Maya forest of Belize Central America. *Water* 11:664
- Buelow C, Sheaves M (2015) A birds-eye view of biological connectivity in mangrove systems. *Estuar Coast Shelf Sci* 152:33–43
- Burke L, Sugg Z (2006) Hydrologic modeling of watersheds discharging adjacent to the meso-American reef analysis summary. World Resources Institute, Washington, DC
- Burkholder JM, Tomasko DA, Touchette BW (2007) Seagrasses and eutrophication. *J Exp Mar Bio Ecol* 350:46–72
- Cabaco S, Apostolaki ET, García-Marín P et al (2013) Effects of nutrient enrichment on seagrass population dynamics: evidence and synthesis from the biomass-density relationships. *J Ecol* 101:1552–1562. <https://doi.org/10.1111/1365-2745.12134>
- Canfield DE, Glazer AN, Falkowski PG (2010) The evolution and future of earth's nitrogen cycle. *Science*. 330:192–196. <https://doi.org/10.1126/science.1186120>
- Canty SWJ, Preziosi RF, Rowntree JK (2018) Dichotomy of mangrove management: a review of research and policy in the Mesoamerican reef region. *Ocean Coast Manag* 157:40–49. <https://doi.org/10.1016/j.ocecoaman.2018.02.011>
- Chambers LG, Steinmuller HE, Breithaupt JL (2019) Toward a mechanistic understanding of “peat collapse” and its potential contribution to coastal wetland loss. *Ecology* 100:1–15. <https://doi.org/10.1002/ecy.2720>
- Chmura GL, Ainsfeld SC, Cahoon DR, Lynch JC (2003) Global carbon sequestration in tidal, saline wetland soils. *Global Biogeochem Cycles* 17:1111–1123
- Congalton RG, Green K (2008) Assessing the accuracy of remotely sensed data: principles and practices, 2nd edition. CRC Press, Boca Raton
- Congedo L (2021) Semi-automatic classification plugin: a python tool for the download and processing of remote sensing images in QGIS. *J Open Source Soft* 6(64):3172. <https://doi.org/10.21105/joss.03172>
- Cooper E, Burke L, Bood N (2009) Coastal Capital: Belize The economic contribution of Belize's coral reefs and mangroves. World Resources Institute, Washington
- Dakos V, Matthews B, Hendry A et al (2018) Ecosystem tipping points in an evolving world. *bioRxiv* 197:463. <https://doi.org/10.1101/447227>
- Deegan LA, Johnson DS, Warren RS et al (2012) Coastal eutrophication as a driver of salt marsh loss. *Nature* 490:388–392. <https://doi.org/10.1038/nature11533>
- Donato DC, Kauffman JB, Murdiyarso D et al (2011) Mangroves among the most carbon-rich forests in the tropics. *Nat Geosci* 4:293–297. <https://doi.org/10.1038/ngeo1123>
- Duarte CM, Middelburg JJ, Caraco N (2005) Major role of marine vegetation on the oceanic carbon cycle. *Biogeosciences* 2:1–8
- Ellis JC (2005) Marine birds on land: a review of plant biomass, species richness, and community composition in seabird colonies. *Plant Ecol* 181:227–241. <https://doi.org/10.1007/s11258-005-7147-y>
- Ellison JC (1993) Mangrove retreat with rising sea-level, Bermuda. *Estuar Coast Shelf Sci* 37:75–87
- Ellison JC (2000) How South Pacific mangroves may respond to predicted climate change and sea-level rise. *Climate change in the South Pacific: impacts and responses in Australia, New Zealand, and small island states*. Springer, Dordrecht, pp 289–300
- Feller IC (1995) Effects of nutrient enrichment on growth and Herbivory of Dwarf Red Mangrove (*Rhizophora mangle*). *Ecol Monogr* 65:477–505
- Feller IC, Dangremond EM, Devlin DJ et al (2015) Nutrient enrichment intensifies hurricane impact in scrub mangrove ecosystems in the Indian River Lagoon, Florida, USA. *Ecology* 96:2960–2972. <https://doi.org/10.1890/14-1853.1>
- Feller IC, Lovelock CE, Berger U et al (2010) Biocomplexity in mangrove ecosystems. *Ann Rev Mar Sci* 2:395–417
- Feller IC, Whigham DF, McKee KL, Lovelock CE (2003) Nitrogen limitation of growth and nutrient dynamics in a disturbed Mangrove Forest, Indian River Lagoon, Florida. *Oecologia* 134:405–414. [https://doi.org/10.1007/s00442-002-9658\(1999\)080\[2193:EONEOW\]2.0.CO;2](https://doi.org/10.1007/s00442-002-9658(1999)080[2193:EONEOW]2.0.CO;2)
- Feller IC, Whigham DF, O'Neill JP, McKee KL (1999) Effects of nutrient enrichment on within-stand cycling in a Mangrove forest. *Ecology* 80:2193–2205. [https://doi.org/10.1890/0012-9658\(1999\)080\[2193:EONEOW\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080[2193:EONEOW]2.0.CO;2)
- Fourqueen J, Johnson B, Kauffman JB, et al (2014) Field sampling of soil carbon pools in coastal ecosystems. *Coast Blue Carbon Methods Assess carbon Stock Emiss factors mangroves tidal marshes seagrass meadows* 39–66
- Fromard F, Puig H, Mougín E et al (1998) Structure, above-ground biomass and dynamics of mangrove ecosystems: new data from French Guiana. *Oecologia*. 115: 39–53
- Galloway JN, Townsend AR, Erismán JW et al (2008) Transformation of the nitrogen cycle. *Science*. 320:889–892
- Gardner TA, Côté IM, Gill JA et al (2005) Hurricanes and Caribbean coral reefs: impacts, recovery patterns, and role in long-term decline. *Ecology* 86:174–184. <https://doi.org/10.1890/04-0141>

- Giblin AE, Nadelhoffer KJ, Shaver GR et al (1991) Biogeochemical diversity along a riverside toposequence in arctic Alaska. *Ecol Monogr* 61:415–435
- Gilman E, Ellison J, Coleman R (2007) Assessment of mangrove response to projected relative sea-level rise and recent historical reconstruction of shoreline position. *Environ Monit Assess* 124:105–130. <https://doi.org/10.1007/s10661-006-9212-y>
- Gilman EL, Ellison J, Duke NC, Field C (2008) Threats to mangroves from climate change and adaptation options: a review. *Aquat Bot* 89:237–250. <https://doi.org/10.1016/j.aquabot.2007.12.009>
- Gischler E (2018) Marine research in the Belize atolls, gloves reef, lighthouse reef, and Turneffe islands since the pioneering work of David Stoddart: a review. In: *Reefs in Space and time: recognizing David Stoddart's contribution to Coral Reef Science*, p 19
- Goldberg L, Lagomasino D, Thomas N, Fatoyinbo L (2020) Global declines in human-driven mangrove loss. *Glob Chang Biol* 26:5844–5822
- Green EP, Clark CD, Mumby PJ et al (1998) Remote sensing techniques for mangrove mapping. *Int J Remote Sens* 19:935–956
- Grime JP (1979) *Plant strategies and vegetation processes*, 2nd edn. Wiley, England
- Guannel G, Arkema K, Ruggiero P, Verutes G (2016) The power of three: coral reefs, seagrasses and mangroves protect coastal regions and increase their resilience. *PLoS One* 11:1–22. <https://doi.org/10.1371/journal.pone.0158094>
- Heumann BW (2011) Satellite remote sensing of mangrove forests: recent advances and future opportunities. *Prog Phys Geogr* 35:87–108
- Holguin G, Gonzalez-Zamorano P, de-Bashan LE et al (2006) Mangrove health in an arid environment encroached by urban development—a case study. *Sci Total Environ* 363:260–274. <https://doi.org/10.1016/j.scitotenv.2005.05.026>
- Hughes T, Baird AH, Bellwood DR et al (2003) Climate change, human impacts and the resilience of coral reefs. *Science* 301:929–933
- Hutchings P, Saenger P (1987) *Ecology of mangroves*. *Ecol mangroves* 388pp
- Ibharim NA, Mustapha MA, Lihan T, Mazlan AG (2015) Mapping mangrove changes in the Matang Mangrove Forest using multi temporal satellite images. *Ocean Coast Manag* 114:64–76
- Jensen JR (2015) *Introductory digital image processing: a remote sensing perspective*, 4th edn. Prentice Hall, New Jersey
- Kauffman JB, Adame MF, Arifanti VB et al (2020) Total ecosystem carbon stocks of mangroves across broad global environmental and physical gradients. *Ecol Monogr* 90:1–18. <https://doi.org/10.1002/ecm.1405>
- Kauffman JB, Donato DC (2012) Protocols for the measurement, monitoring and reporting of structure, biomass and carbon stocks in mangrove forests. *Cent Int For Res*. 86:40. <https://doi.org/10.17528/cifor/003749>
- Kauffman JB, Heider C, Cole TG et al (2011) Ecosystem carbon stocks of Micronesian mangrove forests. *Wetlands* 31:343–352. <https://doi.org/10.1007/s13157-011-0148-9>
- Kjerfve B, Rutzler K, Kierspe GH (1982) Tides at Carrie Bow Cay, Belize. The Atlantic barrier reef ecosystem at Carrie Bow Cay, Belize, 1: structure and communities. *Smithson Contrib Mar Sci* 12:47–51
- Koltes KH, Opishinski TB (2009) Patterns of water quality and movement in the vicinity of Carrie Bow Cay, Belize. *Smithson Contrib Mar Sci* 38:379–390
- Koop K, Booth D, Broadbent A et al (2001) ENCORE: the effect of nutrient enrichment on coral reefs. Synthesis of results and conclusions. *Mar Pollut Bull* 42:91–120. [https://doi.org/10.1016/S0025-326X\(00\)00181-8](https://doi.org/10.1016/S0025-326X(00)00181-8)
- Kramer PA, Kramer PR (2002) In: McField M (ed) *Ecoregional conservation planning for the Mesoamerican Caribbean Reef*. World Wildlife Fed., Gland, Switzerland, p 140
- Krauss KW, McKee KL, Lovelock CE et al (2014) How mangrove forests adjust to rising sea level. *New Phytol* 202:19–34
- Kuenzer C, Bluemel A, Gebhardt S et al (2011) Remote sensing of mangrove ecosystems: a review. *Remote Sens* 3:878–928
- Ledwin S (2010) *Assessment of the ecological impacts of two shrimp farms in Southern Belize* (Doctoral dissertation)
- Lefebvre G, Poulin B (1996) Seasonal abundance of migrant birds and food resources in Panamanian Mangrove Forests. In: Gaëtan Lefebvre and Brigitte Poulin (Eds), *The Wilson Bulletin*, Wilson Ornithological So, Wilson Bull, 108: 748–759
- Leonardi N, Ganju NK, Fagherazzi S (2016) A linear relationship between wave power and erosion determines salt-marsh resilience to violent storms and hurricanes. *Proc Natl Acad Sci U S A* 113:64–68. <https://doi.org/10.1073/pnas.1510095112>
- Lovelock CE, Ball MC, Martin KC, Feller IC (2009) Nutrient enrichment increases mortality of mangroves. *PLoS One* 4:4–7. <https://doi.org/10.1371/journal.pone.0005600>
- Lovelock CE, Feller IC, McKee KL et al (2004) The effect of nutrient enrichment on growth, photosynthesis and hydraulic conductance of dwarf mangroves in Panama. *Funct Ecol* 18:25–33
- Lugo AE (1989) *Fringe wetlands. Forested Wetlands: ecosystems of the World*, Elsevier, pp 143–169
- Macintyre IG, Goodbody I, Rützler K et al (2000) A general biological and geological survey of the rims of ponds in the major mangrove islands of the Pelican Cays, Belize. *Atoll Res Bull* 467:13–44
- Macintyre IG, Littler MM, Littler DS (1995) Holocene history of Tobacco Range, Belize, Central America. *Atoll Res Bull* 430:1–18
- Macintyre IG, Toscano M, Lighty RG, Bond GB (2004) Holocene history of the mangrove islands of Twin Cays, Belize, Central America. *Atoll Res Bull* 510:1–15
- Macintyre IG, Toscano MA, Feller IC, Faust MA (2009) Decimating Mangrove forests for commercial development in the pelican cays, Belize: long-term ecological loss for short-term gain? *Smithson Contrib Mar Sci*. 281–290
- Mateo MA, Romero J, Perez M et al (1997) Dynamics of millenary organic deposits resulting from the growth of the Mediterranean seagrass *Posidonia oceanica*. *Estuar Coast Shelf Sci*. 44:103–110
- McFadden TN, Kauffman JB, Bhomia RK (2016) Effects of nesting waterbirds on nutrient levels in mangroves, Gulf of Fonseca, Honduras. *Wetl Ecol Manag* 24:217–229. <https://doi.org/10.1007/s11273-016-9480-4>
- McKee KL, Cahoon DR, Feller IC (2007) Caribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation. *Glob Ecol Biogeogr* 16:545–556. <https://doi.org/10.1111/j.1466-8238.2007.00317.x>
- McKee KL, Mendelssohn IA, Hester MW (1988) Reexamination of pore water sulfide concentrations and redox potentials near the aerial roots of *Rhizophora mangle* and *Avicennia germinans*. *Am J Bot* 75:1352–1359
- McLeod E, Chmura GL, Bouillon S et al (2011) A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO₂. *Front Ecol Environ* 9:552–560. <https://doi.org/10.1890/110004>
- Mishra AK, Apte D (2020) Ecological connectivity with mangroves influences tropical seagrass population longevity and meadow traits within an island ecosystem. *Mar Ecol Prog Ser*. 644:47–63
- Moore JC (2018) Predicting tipping points in complex environmental systems. *Proc Natl Acad Sci* 115:635–636
- Morisette JT, Privette JL, Strahler A et al (2005) Validation of global land-cover products by the Committee on Earth Observing Satellites. In: Luneta RL, Lyons JG (eds) *Remote sensing and GIS accuracy assessment*. CRC Press, Boca Raton, pp 36–46
- Mumby PJ (2006) Connectivity of reef fish between mangroves and coral reefs: algorithms for the design of marine reserves at seascape scales. *Biol Conserv* 128:215–222

- Murray MR, Zisman SA, Furley PA et al (2003) The mangroves of Belize Part 1. distribution, composition and classification. For *Ecol Manage* 174:265–279. [https://doi.org/10.1016/S0378-1127\(02\)00036-1](https://doi.org/10.1016/S0378-1127(02)00036-1)
- Nagelkerken I, Blaber SJM, Bouillon S et al (2008) The habitat function of mangroves for terrestrial and marine fauna: a review. *Aquat Bot* 89:155–185. <https://doi.org/10.1016/j.aquabot.2007.12.007>
- Nagelkerken I, De Schryver AM, Verweij MC et al (2010) Differences in root architecture influence attraction of fishes to mangroves: a field experiment mimicking roots of different length, orientation, and complexity. *J Exp Mar Bio Ecol* 396:27–34
- Naidoo G (1983) Effects of flooding on leaf water potential and stomatal resistance in *Bruguiera gymnorrhiza* (L.) Lam. *New Phytol* 93:369–376
- Neilson EW, Lamb CT, Konkolics SM et al (2020) There's a storm a-coming: ecological resilience and resistance to extreme weather events. *Ecol Evol* 10:12147–12156. <https://doi.org/10.1002/ece3.6842>
- Nguyen HH, Nghia NH, Nguyen HTT et al (2020) Classification methods for mapping mangrove extents and drivers of change in Thanh Hoa Province, Vietnam, during 2005–2018. For *Soc* 4:225–242
- Norris MD, Avis PG, Reich PB, Hobbie SE (2013) Positive feedbacks between decomposition and soil nitrogen availability along fertility gradients. *Plant Soil*. 367:347–361
- Nowinski NS, Trumbore SE, Schuur EA et al (2008) Nutrient addition prompts rapid destabilization of organic matter in an arctic tundra ecosystem. *Ecosystems* 11:16–25
- Onuf CP, Teal JM, Valiela I (1977) Interactions of nutrients plant growth and Herbivory in a Mangrove. *Ecosystem* 58:514–526
- Pham TD, Yokoya N, Bui DT et al (2019) Remote sensing approaches for monitoring mangrove species, structure, and biomass: opportunities and challenges. *Remote Sens* 11:230
- Planet Team (2017) Planet application program interface: In space for life on earth. San Francisco, CA. <https://www.api.planet.com>
- Puyravaud JP (2003) Standardizing the calculation of the annual rate of deforestation. For *Ecol Manage* 177:593–596
- Record S, Charney ND, Zakaria RM, Ellison AM (2013) Projecting global mangrove species and community distributions under climate change. *Ecosphere* 4:1–23. <https://doi.org/10.1890/ES12-00296.1>
- Reddy KR, Delaune RD (2008) Biogeochemistry of Wetlands. CRC Press, Boca Raton
- Reef R, Feller IC, Lovelock CE (2010) Nutrition of mangroves. *Tree Physiol* 30:1148–1160
- Rivas A, Gonzalez C, Canty SWJ et al (2020) Regional strategy for Mangrove Management, conservation, restoration and monitoring in the Mesoamerican Reef 2020–2025
- Rivera-Monroy VH, Twilley RR (1996) The relative role of denitrification and immobilization in the fate of inorganic nitrogen in mangrove sediments (Terminos Lagoon, Mexico). *Limnol Oceanogr* 41:284–296
- Rogers A, Mumby PJ (2019) Mangroves reduce the vulnerability of coral reef fisheries to habitat degradation. *PLoS ONE* 17:1–12
- Ruetzler K (2004) Sponges on coral reefs: a community shaped by competitive cooperation. *Boll Dei Musei Instituti Dell' università Di Genova* 68:85–148
- Ruetzler K, Feller IC (1996) Caribbean mangrove swamps. *Sci Am*. 247:94–99
- Sabins FF, Ellis JM (2020) Remote sensing: Principles, interpretation, and applications, 4th edn. Waveland Press, Illinois
- Schär C, Vidale PL, Lüthi D et al (2004) The role of increasing temperature variability in European summer heatwaves. *Nature* 427:332–336
- Serra P, Pons X, Saurí D (2003) Post-classification change detection with data from different sensors: Some accuracy considerations. *Int J Remote Sens* 24:3311–3340
- Simard M, Fatoyinbo L, Smetanka C et al (2019) Mangrove canopy height globally related to precipitation, temperature and cyclone frequency. *Nat Geosci* 12:40–45
- Spivak AC, Sanderman J, Bowen JL et al (2019) Global-change controls on soil-carbon accumulation and loss in coastal vegetated ecosystems. *Nat Geosci* 12:685–692
- Tilman D (1990) Constraints and Tradeoffs: toward a predictive theory of competition and succession. *Oikos* 58:3–15
- UNESCO (1996) Convention concerning the protection of the world cultural and natural heritage. Merida, Yucatan
- Ummerhofer CC, Meehl GA (2017) Extreme weather and climate events with ecological relevance: a review. *Philos Trans R Soc B Biol Sci* 372:1–15
- Veerendra TM, Latha BM (2014) Estimation of growth rate of Davanagere district using multispectral image using ENVI 4.7. *Int J Sci Res* 3:704–708
- Verhoeven JTA, Arheimer B, Yin C, Hefting MM (2006) Regional and global concerns over wetlands and water quality. *Trends Ecol Evol* 21:96–103. <https://doi.org/10.1016/j.tree.2005.11.015>
- Viennois G, Proisy C, Feret J-B et al (2016) Multitemporal analysis of high-spatial-resolution optical satellite imagery for mangrove species mapping in Bali, Indonesia. *IEEE J Sel Top Appl Earth Obs Remote Sens* 9:3680–3686
- Wells CE, Webb AW, Prouty CM et al (2019) Wastewater technopolitics on the southern coast of Belize. *Econ Anthropol* 6:277–290
- Whelan CJ, Wenny DG, Marquis RJ (2008) Ecosystem services provided by birds. *Ann N Y Acad Sci* 1134:25–60. <https://doi.org/10.1196/annals.1439.003>
- Wright IJ, Westoby M, Reich PB (2002) Convergence towards higher leaf mass per area in dry and nutrient-poor habitats has different consequences for leaf life span. *J Ecol* 90:534–543
- Yates KK, Rogers CS, Herlan JJ et al (2014) Diverse coral communities in mangrove habitats suggest a novel refuge from climate change. *Biogeosciences* 11:4321–4337. <https://doi.org/10.5194/bg-11-4321-2014>
- Young NE, Anderson RS, Chignell SM et al (2017) A survival guide to Landsat processing. *Ecology* 98:920–932
- Young HS, McCauley DJ, Dunbar RB, Dirzo R (2010) Plants cause ecosystem nutrient depletion via the interruption of bird-derived spatial subsidies. *Proc Natl Acad Sci U S A* 107:2072–2077. <https://doi.org/10.1073/pnas.0914169107>