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RESEARCH ARTICLE

Evaluating land–sea linkages using land cover change and coral reef monitoring data: A case study from northeastern Puerto Rico

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Abstract

Land cover change that leads to increased nutrient and sediment runoff is an important driver of change in coral reef ecosystems. Linking landscape change to seascape change is necessary for integrated land–sea management of coral reefs. This study explored the use of freely available satellite products to examine long-term patterns of change across the land–sea continuum. We focused on northeastern Puerto Rico, where a widespread decline in live coral cover has occurred despite concomitant watershed reforestation that was expected to reduce land-based threats. The aims of this study were (1) to examine whether these land–sea trends continued in 2000–2015 and (2) to assess the opportunities and limitations associated with using satellite data to inform land–sea management. We applied a Random Forest classifier on Landsat-7 satellite imagery to assess changes in land cover and landscape development intensity, a spatial index to estimate land-based pressure on nearshore marine ecosystems. We used field monitoring data to quantify benthic community change. We found that reforestation continued in 2000–2015 (+11%), suggesting reduced land-based pressure on adjacent reefs in both northern (Luquillo) and eastern (Ceiba-Fajardo) watersheds. Concomitantly, coral cover continued to decline, and a new aggressive expansion of peyssonnelid algal crust was recorded. Clustering analysis indicated that benthic monitoring sites in the same geographic regions (nearshore/offshore, north/east) followed similar community composition trajectories over time. Our results suggest that continued reforestation and the expected reduction in land-based pressure have not been sufficient to halt coral cover decline in northeastern Puerto Rico. To improve the characterization and monitoring of the full causal chain from changes in land cover to water quality to benthic communities, advances in satellite-based water quality mapping in optically shallow waters are needed. A strategic combination of remote sensing and targeted field surveys is required to monitor and mitigate land-based stressors on coral reefs.

Introduction

Coral reefs are highly diverse ecosystems that provide valuable benefits to people (Sing Wong et al., 2022). However, coral reefs are vulnerable to climate change impacts, such as extreme marine heatwaves, increased magnitude and frequency of storms, and ocean acidification (van Hooidonk et al., 2016). In addition to global climate change impacts, coral reefs are threatened by exposure to local land-based sources of stress (Burke

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et al., 2011; Tuttle & Donahue, 2022), such as increased sediment and nutrient runoff to coastal waters from agricultural lands and urban areas (Bainbridge et al., 2018; Bartley et al., 2014; Bégin et al., 2014). Sediment runoff from disturbed watersheds is a major issue affecting 41% of coral reefs globally (Suárez-Castro et al., 2021). High rates of anthropogenic nutrient loading negatively impact coral reefs (Vega Thurber et al., 2014), causing, for example, decreased rates of coral calcification (Fabricius, 2005; Nalley et al., 2023) and reduced resistance to thermal stress (Wooldridge, 2020). While local environmental managers cannot sufficiently alleviate global stressors, local management action can reduce local stressors and support coral reef resilience to climate change impacts (Hughes et al., 2017).

The need to identify and mitigate local stressors and an increased understanding of land–sea interconnections have given rise to calls for integrated land–sea management (Oleson et al., 2017; Palola, Pittman, et al., 2025; Sandin et al., 2022). To support integrated land–sea management and restoration, we must develop efficient ways to collect and synthesize meaningful spatial data on the ecosystem state and anthropogenic stressors across the land and sea interface (Carlson et al., 2021; Wedding et al., 2018). Integrated management of coral reefs incorporates land and sea management into a single framework (Álvarez-Romero et al., 2011; Makino et al., 2013). To inform integrated land–sea management, concomitant monitoring of terrestrial and marine ecosystems is of utmost importance (D'Angelo & Wiedenmann, 2014; Halpern et al., 2009). However, many coastal studies and monitoring programs still focus efforts on either land or sea (Collin et al., 2021; Williams et al., 2022), and implementing integrated land–sea management is in many regions hindered by a lack of data at scales that are most operationally relevant to management (Carlson et al., 2021; Jupiter et al., 2017).

Integrating remote sensing and field surveys can help link patterns and processes across land and sea and avoid scale mismatches between the geographic extents of different stressors, ecological consequences, and their scientific investigation and management (Lutzenkirchen et al., 2024). Yet, only 3% of coral reef ecological studies published between 2012 and 2021 integrated both remote sensing and in situ observations (Lutzenkirchen et al., 2024). Field surveys provide detailed information on ecological community compositions at fine taxonomic scales (genus, species) and allow the classification of terrestrial and marine habitat types at high thematic resolutions (Kerr & Ostrovsky, 2003; Lutzenkirchen et al., 2024). However, field surveys alone typically only cover a limited area and tend to be spatially biased toward a few easily accessible focal sites of special interest (Lutzenkirchen et al., 2024; Rhodes et al., 2015; Shiklomanov et al., 2019). Thus, combining remote sensing with field surveys can enable mapping of environmental change across a range of spatial, temporal, and taxonomic scales (Palola, Pittman, et al., 2025) and inform the design of targeted field surveys to fill critical knowledge gaps that satellite data cannot exclusively address (Lutzenkirchen et al., 2024).

In this study, we explore the extent to which currently available optical satellite products can be used and combined with field monitoring data to examine long-term patterns of change in coastal environments with coral reef ecosystems. To achieve a rapid and cost-effective integrative methodology, our requirements for the choice of satellite products were that (1) satellite datasets are freely available; (2) no field data collection for calibration, training, or validation of satellite algorithms is needed; (3) satellite data preprocessing and analyses use off-the-shelf tools available via free platforms. We focus our study on northeastern Puerto Rico, where coral reefs have been in decline for decades (Burke et al., 2011; Gutierrez et al., 2024), land-based pressure is considered a major driver of coral reef degradation (Otaño-Cruz et al., 2019; Rogers & Ramos-Scharron, 2022), and managers are advancing integrated land–sea management (Carriger et al., 2013; Pittman et al., 2017; Smith et al., 2017). To better manage connected landscapes and seascapes in the region, the integrated management plan for the Northeast Marine Corridor, a large land–sea reserve network, was launched in 2017 (NOAA, 2017).

Long-term monitoring data is important to understand changes in the watersheds and marine water conditions in the region that may impact coral reefs and provides important historical context for future land–sea management strategies (Pittman et al., 2017; Rogers & Ramos-Scharron, 2022). Ramos-Scharrón et al. (2015) documented concomitant changes in watershed land cover and coral reefs in Puerto Rico in 1978-2004. They observed an increase in forested area, suggesting reduced nutrient and sediment runoff to nearshore waters. Yet, over the same time period, they found a significant decline in living coral cover.

Sediment eroded from hillslopes and deposited in valleys may support increased sediment discharge to coastal waters even decades after agricultural lands have been abandoned and reforested (Gellis et al., 2006; Larsen & Santiago Román, 2001). Due to this lag effect, reduced impacts on nearshore reefs may not be immediately observed. In this study, we build on the work of Ramos-Scharrón et al. (2015) and assess whether the trends of watershed reforestation and coral reef decline both continued in 2000–2015. We use a spatial land use-based index to estimate changes in potential

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land-based anthropogenic pressure on adjacent coral reefs (Oliver et al., 2011). We expect that if the estimated land use-based anthropogenic pressure on nearshore reefs continued to decline in 2000–2015, positive impacts of reduced sediment and nutrient loading associated with decades of reforestation should start to become apparent on the nearshore reefs (Ramos-Scharrón et al., 2015). Through our study in northeastern Puerto Rico, we identify opportunities and highlight limitations in applying satellite remote sensing and in situ monitoring data to inform integrated land–sea management of coral reefs.

Materials and Methods

Study site and benthic data

The study area comprises two watersheds in northeastern Puerto Rico: Luquillo and Fajardo-Ceiba (Fig. 1). Large-scale deforestation due to agricultural expansion led to elevated rates of erosion and sediment runoff island-wide in the 19th and 20th centuries, with detrimental consequences to nearshore reefs (Larsen & Santiago Román, 2001; Larsen & Webb, 2009; Ramos-Scharrón et al., 2015). In recent decades, concern over coastal development caused by mass tourism and the associated increase in land-based pressure on nearshore reefs has been rising (Hernández-Delgado et al., 2012).

To assess changes in coral reef communities, we leveraged biological field survey data available from the study region from 2000 to 2015. Coral reef benthic communities were surveyed at eight nearshore monitoring sites (< 400 meters from the mainland) and five offshore monitoring sites (> 1,000 meters from the mainland) (Fig. 1). Benthic surveys were conducted at the same sites using a consistent sampling protocol every 5 years between 2000 and 2015, yielding data from four survey years (2000, 2005, 2010, 2015). Eight random replicate point count transects were conducted at each site using digital video imaging (60 points per transect), with four replicates at a depth of < 5 m and four at a depth of 5–10 m. Each transect was 30 meters long. The substrate was identified to coral species level, or to other categories of benthic substrate (e.g., sponge, cyanobacteria, crustose coralline algae, *Halimeda* – see Appendix S1 for the full list of substrates). The average

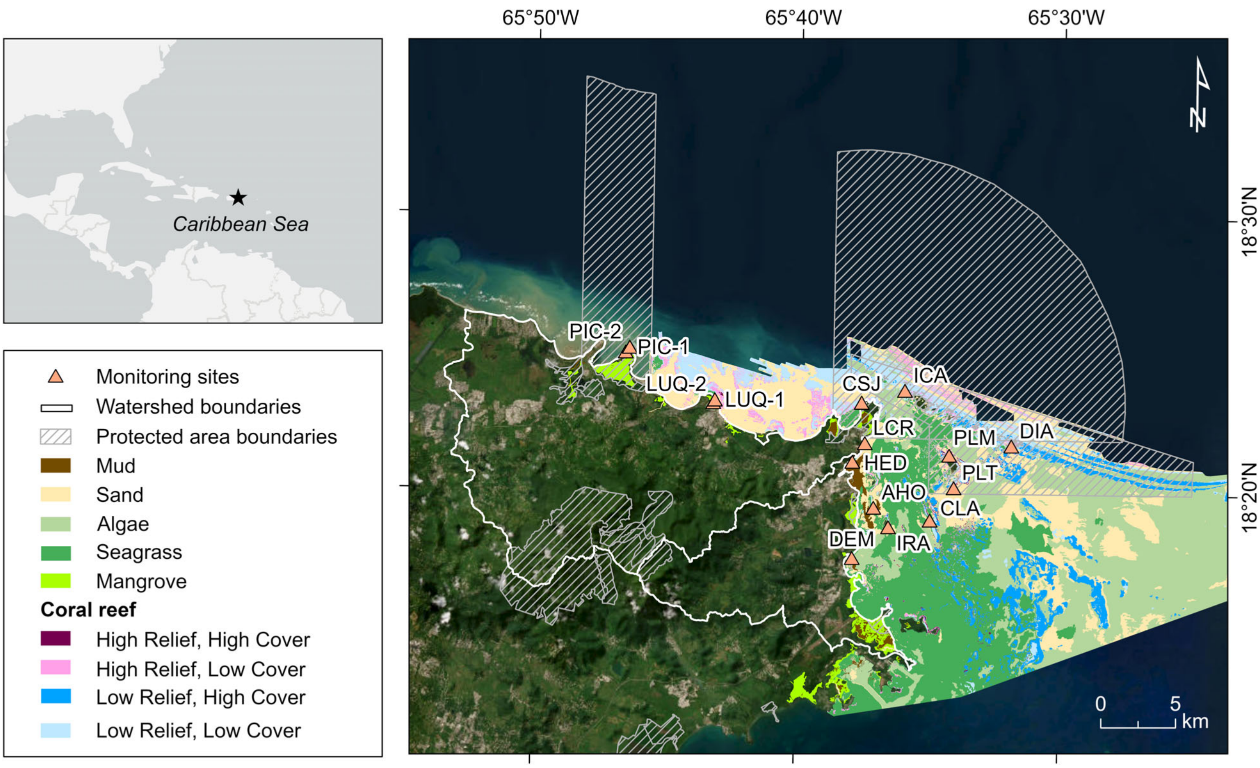

Figure 1. Map of the study region showing the benthic monitoring sites and watershed boundaries of Luquillo (northern coast) and Ceiba-Fajardo (eastern coast). Several important coastal habitat types (NCCOS, 2025) and marine and terrestrial protected areas are located within the study region (UNEP-WCMC and IUCN, 2025). Site abbreviations: AHO = Cayo Ahogado, CLA = Cayo Largo, CSJ = Cabezas de San Juan, DEM = Bahia Demajagua, DIA = Cayo Diablo, HED = Playa Hedionda, ICA = Cayo Icacos, LCR = Las Croabas, LUQ = Luquillo, PIC = Las Picuas, PLT = Cayo Palominitos. Satellite image credit: ESRI, TomTom, FAO, NOAA, USGS, Earthstar Geographics.

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percent cover of the eight replicates for each site was used in the subsequent analyses.

Benthic analysis

All statistical analyses were performed using R v4.3.0 (R Core Team, 2024). To assess differences in community composition between sites and across years, we used the beta diversity metric Bray–Curtis on square-root transformed site-level benthic cover data. We then performed PERMANOVA analysis with 999 permutations on the Bray–Curtis matrix to assess whether the change in community composition across sites over time was statistically significant (R package *vegan* version 2.6) (Oksanen et al., 2024). To identify similarities in temporal patterns of benthic community composition change between sites, we conducted bootstrap hierarchical clustering analysis on the same matrixed data using the "clusterboot" function from the R package *fpc* (version 2.2) (Hennig, 2024). Ordination plots were drawn by nonmetric multidimensional scaling (NMDS) using the "metaMDS" function from the R package *vegan* with distance set to "bray" to visualize each site's clustering and community composition changes across time and space. The "metaMDS" function automatically applies a Wisconsin Double Standardization and square-root transformation to standardize the data and downweigh high abundance values. All the statistical analyses were carried out at the highest available taxonomic resolution (see Section Study site and benthic data and Appendix S1). Additionally, we synthesized broad patterns of change among key taxon groups (hard coral, soft coral and sponge, macroalgae, turf, peyssonnelid algal crust, and others) in a bar plot (see, e.g., Lange et al., 2021).

Land cover change analysis

We used open access, freely available multispectral satellite imagery (30-meter resolution Landsat 7 ETM+) to analyze historical land cover change from 2000 to 2015. All satellite data analyses were conducted in Google Earth Engine, a cloud-based platform for geospatial data analysis (Gorelick et al., 2017). We applied a machine learning decision tree algorithm, the Random Forest (Breiman, 2001), for supervised land cover classification in Google Earth Engine. Random Forests work well in land cover classifications of heterogeneous environments (Jin et al., 2018; Xu et al., 2018). Random Forest classifiers can incorporate different types of ancillary variables in addition to spectral information, allowing for more accurate separation of spectrally similar classes (Jin et al., 2018; Kennaway & Helmer, 2007). We conducted hyperparameter tuning to find the optimal number of trees (25) for the Random Forest (Clinton and Saah, 2018). We included seven land cover types defined by similar physiognomy and moisture: "forest," "woodland and shrubland," "flooded coastal forest," "nonforest vegetation," "plantations," "urban," and "water" (Appendix S1) (Gould, 2008; Gould et al., 2012). As described by Gould (2008); Gould et al. (2012), the three land cover types "forest," "flooded coastal forest," and "plantations" have a similar closed forest physiognomy. Hence, an increase in any of these three land cover types corresponds to reforestation.

The satellite imagery of the USGS GAP 2001 classification dated from 1999 to 2003 (Gould, 2008), and we used Landsat 7 imagery from the same time period to create a cloud-free composite image. We overlaid polygons corresponding to each of the land cover types on the composite image, ensuring sampling over large parts of the study region, as well as a good representation of within-class variation (Appendix S1) (Horning et al., 2016; Wadoux et al., 2021). Then, we extracted random samples from the polygons to create training and validation datasets for the supervised classification. We used separate polygons for the two datasets to ensure training and validation data independence and avoid spatial autocorrelation issues (Ploton et al., 2020; Wadoux et al., 2021). The number of sampled data points for each of the seven land cover types was 980 (70%) and 420 (30%) for training and validation, respectively. In addition to Landsat 7 spectral bands, we derived elevation and slope from the Shuttle Radar Topography Mission digital elevation data (Farr et al., 2007) and added them as ancillary variables (Jin et al., 2018). Thus, the input data for the Random Forest included the Landsat 7 spectral bands, elevation, and slope. We carried out tenfold cross-validation to ensure that the Random Forest classifier did not overfit the training data (Wong, 2015). The classification accuracy was assessed using confusion matrices that compare predicted and actual values of pixels (Foody, 2002).

We used Landsat 7 imagery to create three 5-year composite images so as to align with the benthic monitoring data (see Study site and benthic data Section): 2000–2005, 2005–2010, and 2010–2015. The composites were created in Google Earth Engine using the "ee.Algorithms.Landsat.simpleComposite()" algorithm that computes a Landsat Top-of-Atmosphere (TOA) reflectance composite from a collection of raw Landsat scenes and selects for least cloudy pixels. Specifically, the algorithm applies standard TOA calibration, assigns a cloud score to each pixel, selects the lowest possible range of cloud scores at each point, and finally computes per-band median values from the accepted pixels. The resulting composite was visually inspected to ensure no cloudy pixels remained in the image. Then, we applied the trained and hyperparameter-tuned Random Forest to each composite.

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The resulting three land cover maps were used to detect increases in forest cover (reforestation) or conversion of forested areas to other land use (deforestation).

Landscape development intensity index

Environmental indices provide a means to synthesize complex information about the state of the environment in a way that is easy to measure, communicate, and apply in management (Dale & Beyeler, 2001; Gergel et al., 2002). LDI is a spatial land use-based index to assess potential land-based anthropogenic pressure on coastal marine ecosystems (Brown & Vivas, 2005; Oliver et al., 2011). We calculated the LDI index for both watersheds for each time point as follows: $LDI_{watershed} = (\sum \%LC_i \times LDI_i)/100$, where $\%LC_i$ is the percent cover of land cover type i, and LDI_i is the corresponding LDI coefficient (Appendix S1) (Brown & Vivas, 2005; Oliver et al., 2011). The LDI coefficients range from 1 to 5, with the largest values assigned to land cover types associated with the greatest runoff potential (i.e., impervious surfaces associated with urban land cover) (Oliver et al., 2011).

Results

Watershed change

The Random Forest performed well in the land cover classification (validation accuracy: 0.86; kappa coefficient: 0.83). The 10-fold cross-validation indicated minimal overfitting, with mean accuracy and kappa coefficient across folds of 0.95 and 0.94, respectively. "Urban" and "Water" land cover types were classified most accurately, while the land cover types with similar, closed forest physiognomy ("Plantations" and "Forest") were most difficult to distinguish (Table 1).

From 2000 to 2015, in both Luquillo and Ceiba-Fajardo watersheds, nonforest vegetation decreased (−10 and −11%, respectively) while forested land cover types ("Forest", "Flooded Coastal Forest", and "Plantations") increased by the equivalent amount (see Appendix S2 for additional results). The observed forest regrowth occurred mainly inland and outside protected areas, in a belt between the steep, forested mountainous regions inland and the urbanized areas of the coastal flats (Fig. 2A). Some reforested patches were observed at the land–sea interface, particularly in the nonurban region between the towns of Luquillo and Fajardo (Fig. 2A). These nearshore-reforested patches were classified as coastal flooded forests (mangrove forests and Pterocarpus swamp, Appendix S1). The areas where deforestation occurred were mainly located around urban regions or by the coast (Fig. 2A). Urban cover remained stable over time in both watersheds (Fig. 2B). The relative proportion of different land cover types and LDI levels were similar in both watersheds (Fig. 2B; Table 2). Due to the observed reforestation, LDI decreased in both watersheds between 2000 and 2015 (Table 2).

Benthic community change

As a general pattern, at the start of the study period in 2000, sites located far (> 1000 m) from mainland were characterized by higher hard coral cover (+15%) and lower macroalgae and turf cover (−21%) compared to sites located in close proximity (< 400 m) to mainland. Soft coral cover and peyssonnelid algal crust (PAC) were observed at low levels (< 15%) at all sites in 2000. We observed a significant change in community composition across all sites between 2000 and 2015 (PERMANOVA: $F = 9.33$, $P < 0.001$). PAC became more dominant at all sites, increasing by 3–14-fold between 2000 and 2015.

Table 1. Confusion matrix. The rows represent actual values, and the columns represent predicted values. If no pixels were misclassified, all values would fall on the diagonal line (in gray). PA = producer's accuracy. UA = user's accuracy.

	Forest	Woodland and shrubland	Flooded coastal forest	Nonforest vegetation	Plantations	Urban	Water	PA (%)
Forest	268	20	5	9	11	2	0	85
Woodland and Shrubland	21	13	2	11	1	1	0	27
Flooded Coastal Forest	1	0	114	0	0	0	0	99
Nonforest vegetation	20	6	0	163	0	0	0	86
Plantations	28	0	27	0	56	0	0	50
Urban	0	0	0	12	0	174	0	93
Water	0	0	0	0	0	0	281	100
UA	79%	33%	77%	84%	82%	98%	100%	

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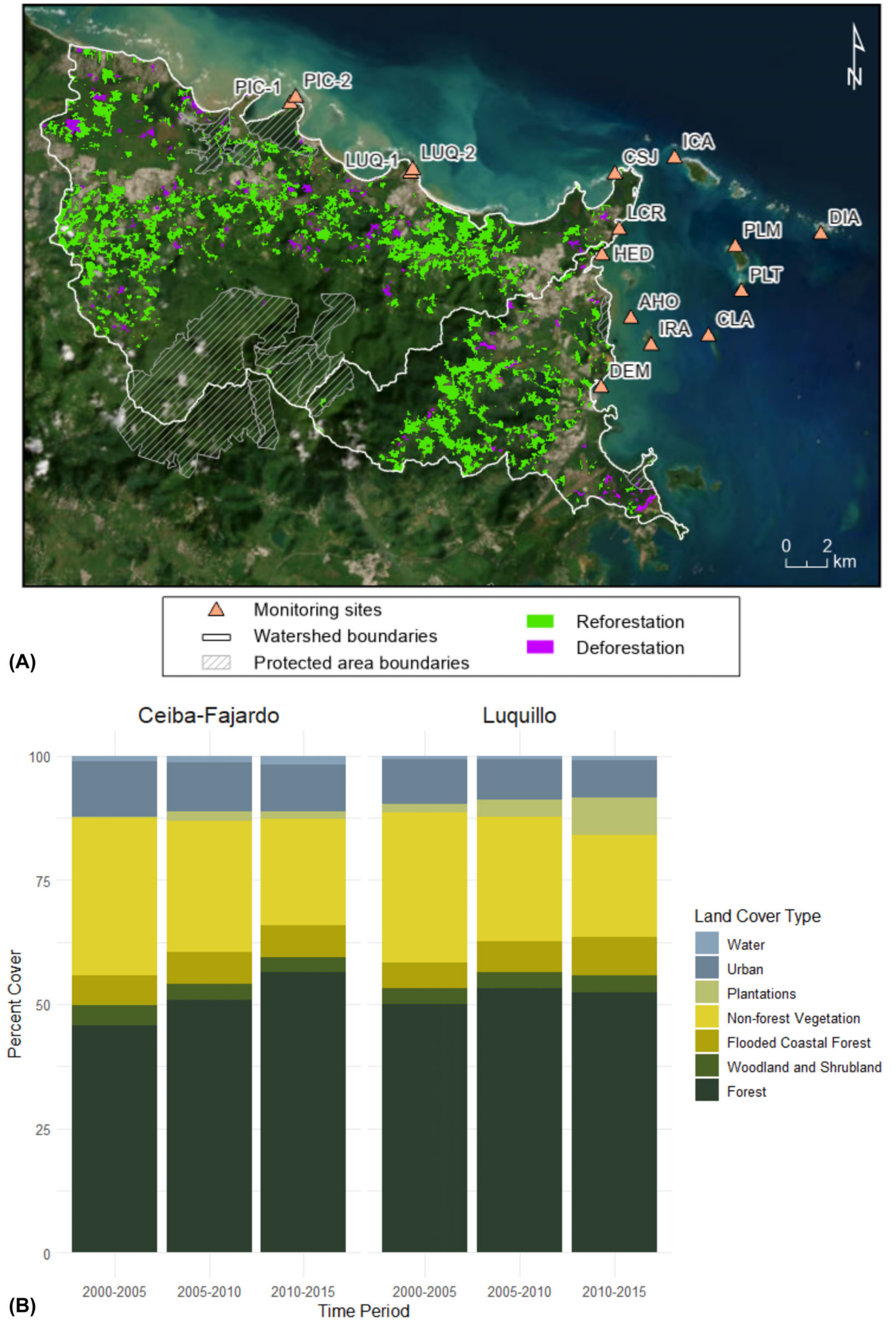

Figure 2. (A) A map of reforestation and deforestation in the Luquillo and Fajardo-Ceiba watersheds between 2000 and 2015. Here, "Forested" is the sum of forested land cover classes ("Forest", "Flooded Coastal Forest", and "Plantations"). Satellite image credit: Earthstar Geographics. (B) Percent land cover change in the Luquillo and Fajardo-Ceiba watersheds between 2000 and 2015. Percent land cover derived from three 5-year composite images (2000–2005, 2005–2010, and 2010–2015).

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Table 2. Change in landscape development intensity index in the Luquillo and Fajardo–Ceiba watersheds between 2000 and 2015.

LDI index	Luquillo	Fajardo-Ceiba
2000–2005	2.05	2.18
2005–2010	1.91	2.00
2010–2015	1.80	1.88

To quantitatively assess dissimilarity in patterns of community composition change between sites, we used bootstrap analysis and identified four clusters (Fig. 3A). Community compositions transition toward a PAC-dominated state (the top left corner of the NMDS plot, Fig. 3B) over time from different starting compositions (the bottom of the plot: more hard coral; the right side of the plot: more macroalgae, Fig. 3B). The clustering broadly corresponds to a geographical division of the sites to northern nearshore (near the Luquillo watershed), eastern nearshore (near the Fajardo-Ceiba watershed), offshore, and Playa Hedionda. Hereafter, we refer to the clusters using these geographical divisions. The main difference between the northern and eastern nearshore clusters was that northern nearshore sites had higher macroalgae cover, while eastern nearshore sites had higher turf cover (Fig. 3). Additionally, northern nearshore sites were the only sites where the decrease in macroalgae had already started in 2000–2005; for other sites, the decreasing trend only started after 2005. However, interestingly, one of the offshore sites (Cayo Ahogado), one of the northern nearshore sites (Luquillo 2), and one of the eastern nearshore sites (Bahia Demajagua) stand out from the overall geographic pattern (Figs 3 and 4).

Discussion

In the face of accelerating climate change and multiple local stressors, it may not be possible to return to the past reef systems characterized by high diversity and abundance of corals (Hughes et al., 2018; Woodhead et al., 2019). Well-designed environmental management and restoration action will be needed to steer the transformation of reef ecosystems in a direction that maintains ecological and social values (Bellwood et al., 2019; Hughes et al., 2017). To support effective coral reef management and restoration, continuous monitoring of anthropogenic pressures and their ecological impacts across land and sea is critically needed. In this study, we used a combination of field monitoring and remote sensing to examine environmental change on land and at sea from 2000 to 2015 in northeastern Puerto Rico, where efforts for integrated coral reef management are underway.

Building on the work of Ramos-Scharrón et al. (2015), who documented trends of reforestation and coral cover decline in Puerto Rico in 1978–2004, we showed that both trends continued in the northeastern region in 2000–2015. Our findings thus indicate that continued watershed reforestation has not been sufficient to halt the loss of corals in northeastern Puerto Rico, and other drivers of change in coral reef ecosystems must be considered. In the next sections, we discuss our results and their implications for integrated land–sea management in the region. We identify future research needs to advance the use of remote sensing to inform land–sea management, and to establish the causal links between changes in land cover and coral reef communities.

Land cover change

Previous studies have documented large-scale deforestation in Puerto Rico in the early 20th century, followed by a shift to reforestation from the 1950s onward (Kennaway & Helmer, 2007; Ramos-Scharrón et al., 2015; Wang et al., 2017). Our results indicate that the reforestation trend continued in northeastern Puerto Rico in the early 21st century.

Historical deforestation and recent reforestation patterns are common in many tropical Caribbean islands and beyond (Farrant et al., 2023; Gobierno de Canarias, 2023; Lugo & Helmer, 2004). Reforestation has typically resulted from the abandonment of agricultural lands (Farrant et al., 2023; Murphy & Stallard, 2012). Agricultural land abandonment could explain the increase in forested areas observed in this study. However, recent food security plans to increase domestic agricultural production in Puerto Rico suggest widespread agricultural land abandonment is no longer occurring (Comas, 2013; Keck, 2015). Additionally, hurricanes play an important role in shaping vegetation patterns in Puerto Rico (Murphy & Stallard, 2012; Van Beusekom et al., 2014). In fact, in their island-wide study, Wang et al. (2017) found that reforestation between 2000 and 2010 was mainly concentrated in eastern Puerto Rico, following widespread damage to vegetation by Hurricane George in September 1998. Thus, the reforestation observed in the Luquillo and Fajardo-Ceiba watersheds could be due to posthurricane forest recovery (Wang et al., 2017).

Compared to the relatively widespread reforestation, we found that deforestation was confined to localized patches around urban regions or by the coast. The deforested patches were characterized by increased nonforest vegetation rather than urban land use, likely as a result of localized land clearance for golf courses and agriculture (Hernández-Delgado et al., 2012). However, further

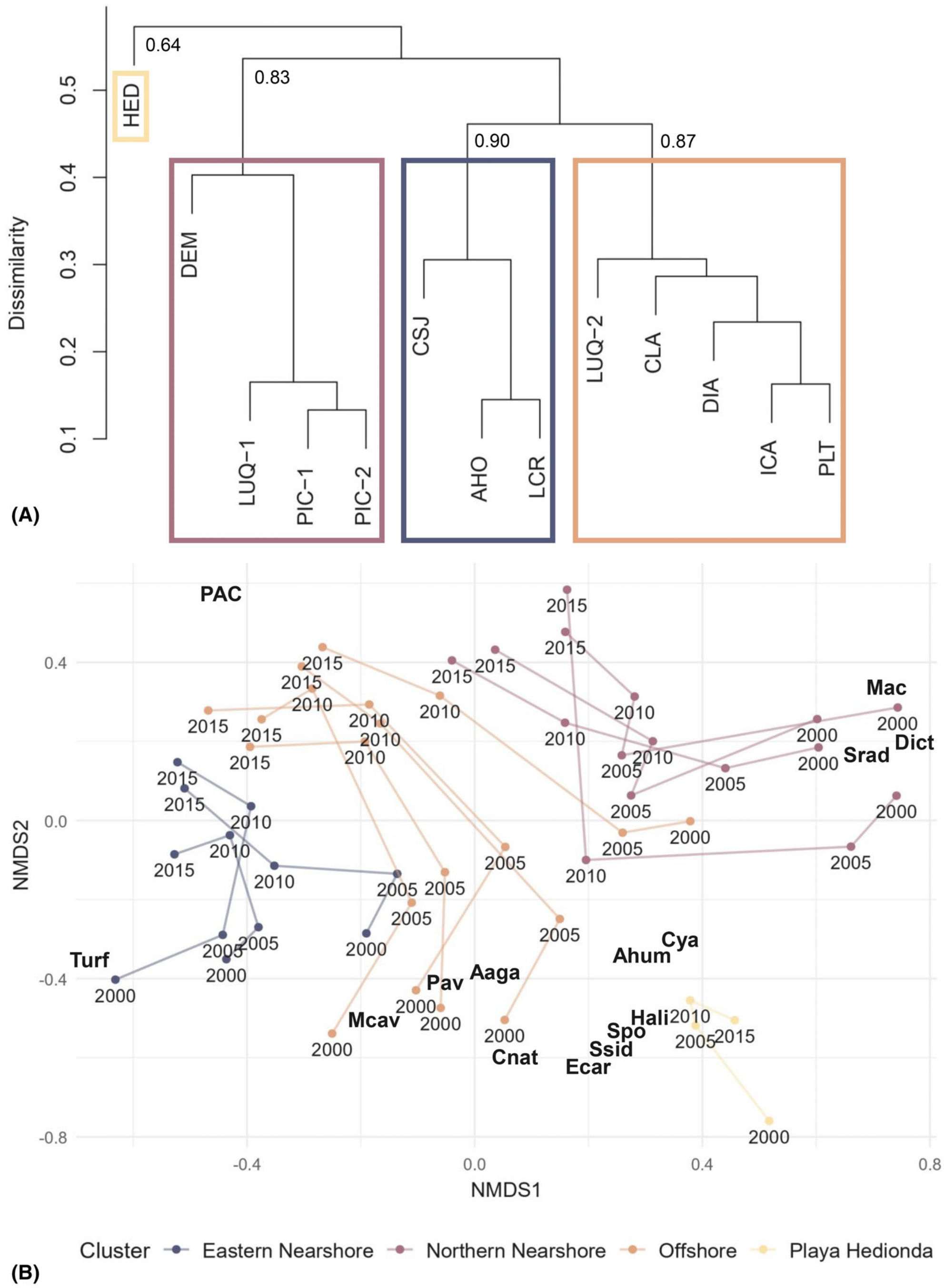

Figure 3. (A) Dendrogram highlighting the clusters identified from bootstrapping ($k = 4$) and (Bray–Curtis) dissimilarity between the sites. Please refer to Figure 1 for the site abbreviations. (B) NMDS plot with sites (points) plotted according to Bray–Curtis dissimilarity of taxa composition and labeled with the year of data collection. The direction of the vectors between the points (years) indicates the compositional shift of each community at each site. The taxa displayed in black text had the most significant influence ($P \leq 0.01$) on the changes in community composition. Sites are colored according to the cluster assigned by bootstrap analysis. Aaga = *Agaricia agaricites*, Ahum = *Undaria humilis*, Cya = Cyanobacteria, Cnat = *Colpophyllia natans*, Dict = *Dictyota* spp., Ecar = *Erythropodium caribaeorum*, Hali = *Halimeda*, Mac = Macroalgae, Mcav = *Montastraea cavernosa*, PAC = Peyssonnellia Algal Crust, Pav = Pavement, Spo = Sponge, Srad = *Siderastrea radians*, Ssid = *Siderastraea siderea*, Turf = Algal turf.

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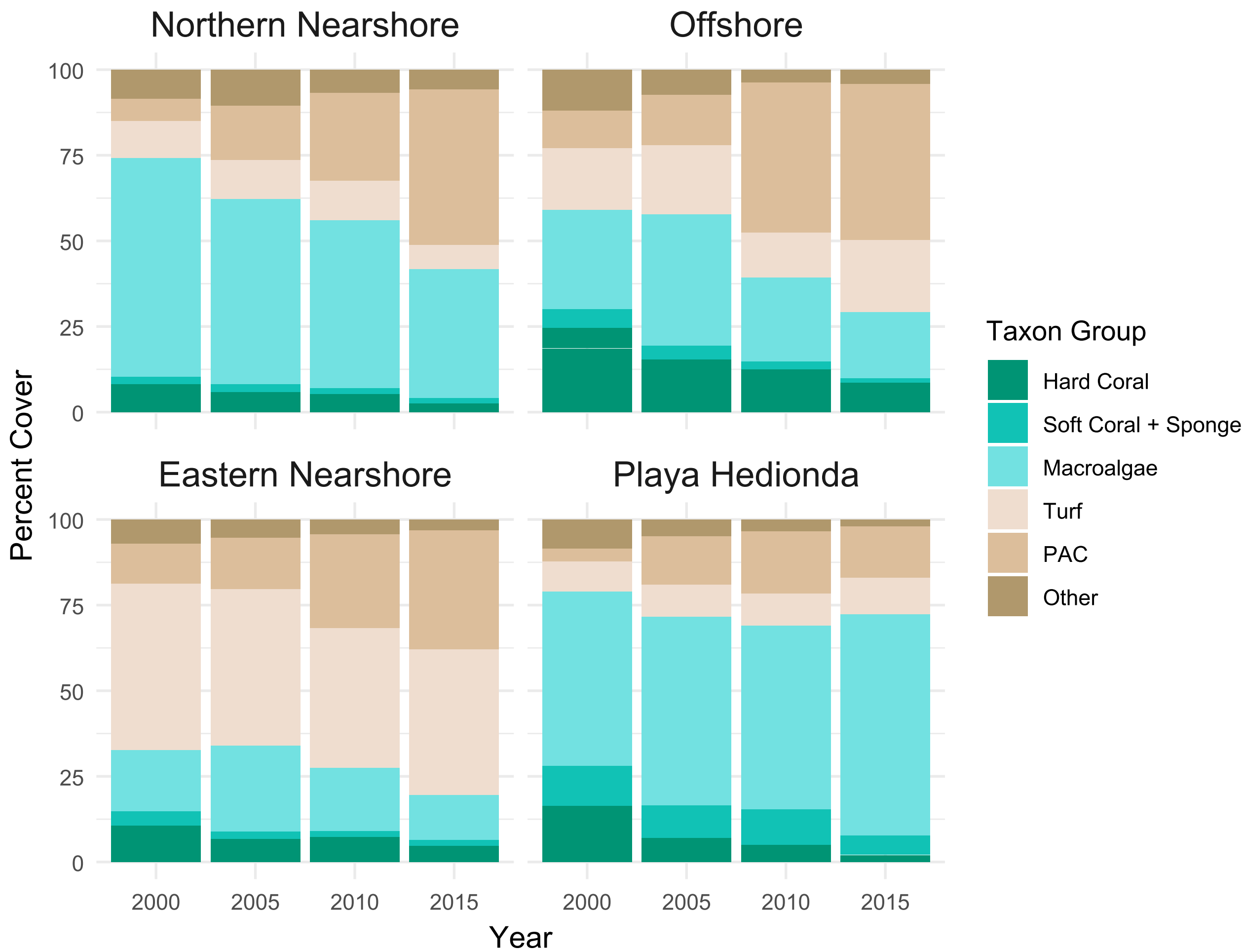

Figure 4. Community composition is indicated by the percent cover of each taxon group in each cluster between 2000 and 2015.

research is needed to confirm the drivers of the observed land cover changes.

Urban expansion in coastal regions has been a key concern for land–sea management in Puerto Rico (Hernández-Delgado et al., 2012). Previous studies have documented significant increases in human population and urban land in the 20th century in coastal regions around Puerto Rico (López et al., 2001; Parés-Ramos et al., 2008; Ramos-Scharrón et al., 2015). In northeastern Puerto Rico, a tenfold increase in urban land was reported between 1936 and 2004 (Ramos-Scharrón et al., 2015). While urban expansion continued between 2000 and 2010 on an island-wide scale (Wang et al., 2017), our results indicate that no significant change in the proportion of urban cover occurred in the Luquillo and Ceiba-Fajardo watersheds over the study period. This finding aligns with reported population declines in the municipalities of Luquillo, Fajardo, and Ceiba (United States Census, 2018).

Estimated land-based pressure on coral reefs

The observed reforestation and lack of urban expansion corresponded to decreased LDI, signaling an estimated reduction in land-based pressure on adjacent coral reefs (Oliver et al., 2011). However, the concomitant reduction in coral cover suggests that the decline in land-based pressure, as quantified by LDI, has not been sufficient to halt the loss of corals in northeastern Puerto Rico.

The LDI assessment did not indicate any important differences between the Luquillo and Ceiba-Fajardo watersheds in the potential exposure risk of monitored coral reefs to land-based sources of pollution. However, LDI does not account for point sources of pollution, such as wastewater outlets, that can significantly impact local nearshore water quality (Santavy et al., 2023). Additionally, the watershed-scale LDI assessment does not capture finer-scale patterns, such as potential spatial clustering of

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land-based pollution close to river mouths (Brown et al., 2017, 2019; Palola, Pittman, et al., 2025) or the dispersion patterns of land-derived materials driven by currents and waves (Garnier et al., 2025; Gundlach et al., 2024). For example, two nearshore benthic monitoring sites in our study, Playa Hedionda and Bahia Demajagua, are located close to the mouths of major rivers along the eastern coast (Río Fajardo and Río Demajagua, respectively) and likely experience elevated sediment and nutrient loading compared to the other nearshore sites (Ramos-Scharrón et al., 2015). The coral reef community compositions at these two monitoring sites stood out from the overall geographic pattern—i.e., they were not clustered along with the other nearshore eastern sites. Our findings raise the need for further research to determine the causal drivers of the observed patterns in community composition and the extent to which the benthic communities are shaped by differences in exposure to land-based pressure.

In addition to area-based metrics, such as LDI, it is important to note that other spatial pattern metrics could be leveraged for more detailed modeling of land-based pressure on nearshore marine ecosystems (Palola, Pittman, et al., 2025). For example, the ecological impacts of nutrient loading depend not only on the magnitude of the loading but also on its stoichiometric composition (i.e., the relative proportions of different nutrients, such as nitrogen, phosphorus, and iron) (Shantz & Burkepile, 2014; Palola, Pittman, et al., 2025). The stoichiometry of a nutrient flow is transformed as it moves through space and interacts with the surrounding biotic and abiotic features (Schade et al., 2001; Sitters et al., 2015). Consequently, spatial pattern metrics such as habitat composition and configuration could be used to model and predict the stoichiometric transformation of land-to-sea nutrient flows (Sitters et al., 2015; Smithwick, 2021; Palola, Pittman, et al., 2025). However, developing a model for northeastern Puerto Rico that links land cover composition and configuration metrics to nutrient and sediment loading into coastal waters would require validation using in situ data of nutrient and sediment concentrations along the land–sea continuum (Jones et al., 2001).

Finally, it is important to note that similarly to the work of Ramos-Scharrón et al. (2015) that our study builds on, we do not assert causality between the changes in land cover and coral reef communities. Determining changes in water quality is the missing link in the causal chain from land cover change to coral reefs (Brown et al., 2017). However, no water quality data, neither field-measured nor remotely sensed, were available for our study region and time period. Additionally, we emphasize that coral reefs in Puerto Rico are subject to multiple stressors (Hughes, 1994; Lessios et al., 1984). Thus, as discussed below, the impacts of land-based pressure on coral reef communities should be understood in the context of simultaneous impacts from, *inter alia*, climate change, hurricanes, and coral diseases (Ellis et al., 2019; Ramos-Scharrón et al., 2015).

Coral reef change

Over the past decades, multiple disturbances and anthropogenic stressors have impacted Caribbean coral reefs (Hughes, 1994; Lessios et al., 1984). Subjected to stress, Caribbean reefs can exhibit hysteresis: the inability of coral-dominated communities to recover from disturbances due to altered system dynamics (Hughes, 1994; Scheffer et al., 2001). This study assessed coral reef community dynamics between devastating hurricanes that hit Puerto Rico in 1998 and 2017. The resilience of many reef ecosystems might have already been undermined before Hurricane George in 1998 due to the loss of herbivores, the spread of coral diseases, and high levels of land-based pollution, sedimentation, and anthropogenic nutrient loading (Lessios et al., 1984; Ramos-Scharrón et al., 2015). This loss of resilience likely precluded the reef ecosystems from fully recovering from the 1998 hurricane and possibly made them more vulnerable to PAC expansion (Wilson et al., 2020). Indeed, at all benthic sites in this study, hard coral cover was low at the beginning of the study period, suggesting that the reefs had already undergone a regime shift to coral-poor states dominated by macroalgae and turf.

Patterns of change in hard coral

At the start of the study period, we observed higher hard coral abundance at offshore sites compared to nearshore sites, which could be linked to greater historical exposure to land-based sources of stress (García-Sais et al., 2008). By 2015, differences in hard coral abundance between sites were less pronounced, as hard coral cover had plummeted at all sites. Reefs in Puerto Rico experienced a major bleaching event in 2005, with extensive bleaching reported in eastern Puerto Rico (García-Sais et al., 2008; Wilkinson & Souter, 2008). Our data showed a continued decline in hard coral cover throughout the study period, with no indication of recovery from the 2005 bleaching event.

Widespread proliferation of PAC

Concomitantly with the continued decline of hard coral cover, we observed a ubiquitous shift in benthic community composition to PAC domination across both

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nearshore and offshore sites. PAC are crustose red algae native to the Caribbean (Pueschel & Saunders, 2009; Taylor & Arndt, 1929) that have expanded considerably across Caribbean reefs since the early 2000s (Eckrich & Engel, 2013; Edmunds et al., 2019). The mechanisms behind recent PAC proliferation are poorly understood, with suggestions that macroalgae-dominated coral communities – such as our study sites in 2000—may be more vulnerable to PAC proliferation (Wilson et al., 2020). In northeast Puerto Rico, PAC proliferation occurred while both macroalgae and corals declined in relative abundance between 2000 and 2015. Thus, our findings raise the need for rethinking the possible range of alternative states on Caribbean coral reefs beyond the conventional coral-macroalgae phase shifts, and consider an alternative system state dominated by PAC. PAC is less negatively affected by ocean acidification and exposure to high irradiance compared to other coralline algae, contributing to a competitive advantage in a changing climate (Cornwall et al., 2019; Dutra et al., 2016; Edmunds et al., 2023). Furthermore, PAC actively deter the settlement of coral larvae, likely leading to hysteresis as corals are unable to re-establish (Wilson et al., 2020). More information about PAC ecology and physiology is needed to understand the mechanisms that underlie the recent aggressive expansion of these encrusting algae (Hollister et al., 2021; Stockton & Edmunds, 2021), and to identify management interventions that could be used to limit further PAC expansion (Edmunds et al., 2023). Finally, we note that in addition to PAC expansion documented here, a highly virulent stony coral tissue loss disease has emerged as an important new threat for corals in the Caribbean after the time period covered by our study (2000–2015) (Walton et al., 2018; Brandt et al., 2021).

Remote Sensing to Inform Integrated Land–Sea Management

Thanks to technological and analytical advancements, a range of Earth observation satellite products are now freely available to the scientific community and environmental practitioners. In this study, we explored the extent to which these satellite products can be used to map long-term changes in a tropical coastal environment with coral reefs. We monitored terrestrial environmental change using freely available satellite imagery and a Random Forest classifier. This allowed us to examine watershed-scale patterns of land cover change and estimate how potential land-based pressure on nearshore reefs changed over time. However, the watershed-scale analysis did not capture finer-scale spatial variability in land–sea runoff and missed potentially important point-based sources of pollution, such as wastewater outlets, that cannot be detected from satellite imagery (Santavy et al., 2023). Quantitative modeling of land–sea runoff rates would require complementing the land cover data with a digital elevation model, precipitation data, and information on soil hydraulic properties (Álvarez-Romero et al., 2016; Delevaux et al., 2018). While satellite-derived digital elevation models are freely available and have near-global coverage (Farr et al., 2007), precipitation data and soil hydraulic properties must be measured in situ and are rarely available at relevant resolution and extent for watersheds.

Applying marine remote sensing to monitor change in northeastern Puerto Rico proved more challenging compared to terrestrial remote sensing. Different benthic cover types have distinct spectral signatures and could be mapped using remotely sensed optical data (Hochberg, 2003). However, distinguishing between benthic cover types, such as coral and algae, remains challenging due to the optical complexity of the underwater light field in shallow reef environments (Bell et al., 2020; Kutser et al., 2020; Palola, Theenathayalan, et al., 2025) and therefore satellite-derived benthic maps have limited thematic resolution and significant uncertainties (Lutzenkirchen et al., 2024; Serge et al., 2024). Additionally, most satellite-derived benthic maps are currently only available at a single time point and cannot be used to detect environmental change (Allen Coral Atlas, 2022). In areas characterized by turbid conditions, the optical signal from the benthos may not be detectable. Due to the limited thematic resolution, lack of temporal data, and data uncertainties, we relied on traditional field surveys to assess change in the benthic environment.

In addition to mapping the benthos, satellite remote sensing could be used to map key water quality parameters, such as suspended sediment concentration or turbidity (Mobley, 1994; Palola et al., 2025). However, most satellite algorithms for water quality mapping have been developed in deep waters where the signal is not confounded by bottom reflectance (Werdell et al., 2018). To our knowledge, Allen Coral Atlas turbidity data is the only available off-the-shelf satellite product suitable for nearshore, shallow coral reef waters (Li et al., 2022). However, this turbidity dataset does not cover our study period (2000–2015). Furthermore, the Allen Coral Atlas turbidity data is characterized by high uncertainty as it assumes spatial homogeneity in water column optical properties. Encouragingly, recent analytical advancements leveraging probabilistic, physics-informed machine learning are enabling water quality mapping in optically shallow coral reef environments without assuming spatial homogeneity (Palola et al., 2025).

In summary, despite the great potential of remote sensing to inform integrated land–sea management, we found

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that its application in practice is hindered by the lack of freely available, off-the-shelf algorithms and data products, especially in the marine environment. We highlight here the need for further research developments and technological innovations, including user-friendly tools for mapping key water quality parameters from satellite imagery in optically shallow coastal waters. Accurately estimating water constituents would also improve the accuracy of satellite-derived benthic maps (Theenathayalan & Shanmugam, 2021). Critically, not all variables important for land–sea management can be quantified from optical data, and there is a need to strategically combine remote sensing with in situ field surveys. On land, to quantitatively model sediment and nutrient runoff, satellite-derived land cover and topography data must be complemented with precipitation and soil hydraulic data measured in the field. At sea, ecological field surveys are still needed to identify the presence or absence of specific species in Puerto Rico, for example, to detect and track PAC proliferation. Additionally, even with analytical advances in shallow water remote sensing, field surveys will remain necessary in highly turbid conditions, where the optical signal of the benthos is not detectable from the water surface. Finally, laboratory experiments may help establish the specific mechanisms underlying the combined impacts of multiple stressors on coral reefs and quantify potential time lags for biological responses to environmental change.

Conclusions

A range of terrestrial and marine stressors threaten coral reefs around the world. In northeastern Puerto Rico, we observed drastic declines in coral cover despite a concomitant reduction in landscape development intensity in the adjacent watersheds. Our findings signal that continued reforestation and associated decline in estimated land-based pressure has not been sufficient to halt the loss of corals in northeastern Puerto Rico. In addition to land-based pressure, coral reefs in Puerto Rico have been affected by the loss of herbivores, the spread of coral diseases, hurricanes, and heatwaves. Additionally, nearshore reefs may be impacted by point sources of land-to-sea pollution that are not captured in the watershed-scale land cover assessment. It is therefore essential to consider the potential impacts of land cover change in the context of multiple interacting stressors. Our results underline the need to better understand the spatial and temporal patterns of multiple land-based and sea-based stressors and their combined impact on reef ecosystems in Puerto Rico and beyond.

Compared to expensive field studies of limited extent, remote sensing enables low-cost mapping of environmental change and anthropogenic stressors over time and across a broad spatial extent. A range of satellite data products, especially in the terrestrial realm, are already freely available and provide an important source of environmental information for local management. However, in marine remote sensing, shallow coral reef waters still pose a formidable challenge due to the optical complexity of the underwater light field. While both sensor technologies and analytical approaches are rapidly advancing, remote sensing approaches cannot provide the same level of detailed ecological information that can be acquired via traditional field surveys. The high spatial and temporal variability in water column and benthic optical properties in reef environments makes it extremely challenging to develop global and regional remote sensing products that have sufficient local accuracy. Nevertheless, recently developed algorithms, such as the SIMA algorithm for water quality mapping in shallow reef environments (Palola et al., 2025), suggest that what was not possible over our study period (2000-2015) may be possible in the future. We call for a strategic and coordinated combination of field surveys and remote sensing to support integrated land–sea management.

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Author Contributions

Pirta Palola: Conceptualization; funding acquisition; writing – original draft; formal analysis; methodology; visualization. **Sasha Hills:** Writing – review and editing; formal analysis; visualization. **Simon J. Pittman:** Writing – review and editing; supervision; data curation. **Edwin A. Hernández-Delgado:** Writing – review and editing; data curation; resources; investigation. **Antoine Collin:** Writing – review and editing; supervision. **Lisa M. Wedding:** Writing – review and editing; supervision.

Data Availability Statement

The data that support the findings of this study are openly available in Ridge_to_reef_Puerto_Rico at https://osf.io/c7ujr/?view_only=4d311d2638704da5a35e8d25a68115e4. The Google Earth Engine script for the satellite data analyses and the R scripts for the benthic analyses are also freely available in the Open Science Framework repository. The benthic dataset is available upon request from Edwin Hernández-Delgado (email address: edwin.hernandezdelgado(at)gmail.com).

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Full details on the benthic surveys, land cover classification, and landscape development intensity index calculation.

Appendix S2. Additional results.

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