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Landscape-Level Consequences of Rising Sea-Level on Coastal Wetlands: Saltwater Intrusion Drives Displacement and Mortality in the Twenty-First Century

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Mei Yu¹ · Elsie Rivera-Ocasio² · Tamara Heartsill-Scalley³ · Daniel Davila-Casanova¹ · Neftalí Rios-López⁴ · Qiong Gao¹

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Abstract

Coastal wetlands are shrinking rapidly due to land-use activities. Accelerated sea-level rise (SLR) associated to the warming climate is also affecting coastal wetlands, particularly in islands with limited coastal plains. We analyzed coastal wetland changes in Puerto Rico by applying the Sea Level Affecting Marshes Model under two scenarios by 2100. We also analyzed mortality and recruitment in a freshwater swamp dominated by the tree *Pterocarpus officinalis* Jacq. in the context of landscape saltwater-intrusion and drought. Our results indicate mangroves and estuarine water would replace the areas currently covered by other saltwater and freshwater wetlands, and saltmarsh would encounter the most relative loss among wetland types. A moderate SLR of 1 m by 2100 allows expansion of mangroves but would decrease saltmarsh and freshwater wetlands. A 2-m SLR would decrease the distributions of all vegetated wetlands, mostly replaced by estuarine water. In the *P. officinalis* forest, saltwater-intrusion and drought increased tree mortality during 2003–2015 compared to 1994–2003. Saltwater intrusion had a more significant negative effect on tree recruitment than on mortality in this *Pterocarpus* forest. Coastal wetlands are facing challenges to their persistence at current locations due to accelerated SLR, limited coastal lands, and a modified hydrological regime.

Keywords Caribbean · Climate change · Coastal · Sea-level rise · Tropical wetlands · Wetland migration

Introduction

Coastal wetlands contribute to regulation of flooding and sequester exceedingly large amounts of C–a significant element whose stocks and cycling are a component of current changes in global climate. Nevertheless, coastal wetland areas are diminishing

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Mei Yu meiyu@ites.upr.edu

- ¹ Department of Environmental Sciences, University of Puerto Rico -Río Piedras, San Juan, PR 00936, USA
- ² Department of Biology, University of Puerto Rico Bayamon, Bayamon, PR 00959, USA
- ³ International Institute of Tropical Forestry, USDA Forest Service, Río Piedras, San Juan, PR 00926, USA
- ⁴ Department of Biology, University of Puerto Rico Humacao, Humacao, PR 00792, USA

rapidly due to a combination of human activities and the changing climate (Kirwan and Megonigal 2013). For example, the rate of coastal wetland loss increased from 24,349 ha yr.⁻¹ between 1998 and 2004 to 32,375 ha yr.⁻¹ between 2004 and 2009 in the US alone (Dahl and Stedman 2013). Additionally, the rising sealevel, in conjunction with changes in land-use, interferes with establishment and survival of vegetation in these wetlands. Further, there are losses of ecosystem functions that coastal wetlands provide to society, such as purification of water, conservation of biodiversity, and recreation (Barbier et al. 2011). Inland protection against hurricane damage, for instance, is another significant service provided by coastal wetlands, a function whose value is estimated to be as high as 23.2 billion yr.⁻¹ in the US (Costanza et al. 2008). Consequently, the rapid disappearance of these wetlands raises concerns about the resulting emission of C from their soils (Nahlik and Fennessy 2016), and the accompanying losses of biodiversity and various ecosystem services they could provide to humanity.

The accelerated rates of sea-level rise (SLR) in combination with the changing climate regimes, as well as associated changes in the frequency of extreme events (e.g., drought and high-intensity hurricanes), further exacerbate the projected scenario in the extent of coastal wetlands loss in the foreseeable future. For example, global mean SLR has been accelerating at a rate between 0.0 and 0.013 mm yr.⁻² since the early twentieth century because of the continuing warming-incurred thermal expansion of oceans and melting of glaciers (Church et al. 2013). The projected rate of SLR under a scenario of continued emission of greenhouse gases (i.e., RCP [Representative Concentration Pathway] 8.5) may reach as high as 8 to 16 mm yr.⁻¹ between 2081 and 2100, in comparison with the global mean rate of SLR of 1.7 ± 0.2 mm yr.⁻¹ between 1901 and 2010. The projected SLR under RCP 8.5 could be 0.52 to 0.98 m by 2100 (Church et al. 2013). On the other hand, changes in regional climate regimes, such as the warmer and drier climate projected for the Caribbean, would reduce the supply of freshwater to coastal wetlands due to a decrease in precipitation and associated water discharge, thus resulting in the lowering of phreatic levels (Gao and Yu 2017). The decreased supply of freshwater to these wetlands is further aggravated by an increased extraction of ground and surficial freshwater for human consumption, which affects present-day coastal wetlands (Heartsill-Scalley 2012; Taylor et al. 2012).

At a geological time-scale, coastal wetlands have persisted in a given location by changes in the rate of vertical accretion in response to oscillations in the sea level. These wetlands may also survive by landward migration in response to SLR, which may alter the species dominance zonation along the changing seaward-landward gradient (Kirwan and Megonigal 2013; Krauss et al. 2014; Lovelock et al. 2015). Recently, however, humans have affected the potential persistence of these wetlands by developing dense-urban projects in coastal areas and by draining and filling wetlands for agriculture, which then limited, or even halted, the landwardmigration pathways and altered hydrological and biogeochemical dynamics (Verhoeven et al. 2006). Currently, in islands with limited and heavily-populated coastal plains the consequence of altered climatic and land-use conditions could be dramatic for species that depend on coastal wetlands. This may be most evident for species relying on these wetlands for reproduction and survival and now occurring near their physiological limit (e.g., Rivera-Ocasio et al. 2007; Rios-López 2007; Bâ and Rivera-Ocasio 2015; see below), which may further affect species diversity and ecosystem function of these wetlands.

In the insular Caribbean there are various types of coastal wetlands, most of which are limited to coastal plains and occur close to highly populated areas. Rising sea-level for Caribbean islands such as Puerto Rico is one of the factors that contributes to changes in coastal wetland vegetation. In northern Puerto Rico, the SLR rate was recorded as 12.12 mm yr.⁻¹ between 2010 and 2016, which is much higher than the rate of 2.08 mm yr.⁻¹ between 1962 and 2016 (Mercado-Irizarry

2017). Therefore, the present rate of SLR and a more warming/drying climate (Hayhoe 2013; Yu et al. 2017) render Puerto Rico's current coastal wetlands highly vulnerable in the new century.

Landward migration of coastal wetlands in Puerto Rico would be driven and mediated by rising sea-level, associated saltwater intrusion, and reduced freshwater supply resulting from the projected drying/warming climate. However, landward migration is restricted by coastal development and limited to only a few river valleys and non-urbanized riparian zones along the coast. Coastal freshwater wetlands are consequently most vulnerable when there are combined effects of saltwater intrusion and a decreased supply of freshwater, which would result in increased soil salinity. Existing studies on coastal wetlands, however, have mainly focused on historical changes in the extent of mangroves (Martinuzzi et al. 2009), and few studies address and emphasize the consequences of predicted SLR for coastal freshwater wetlands, or their vulnerability in the context of a drying/warming climate (Hayhoe 2013).

In coastal Puerto Rico, freshwater swamps (i.e., palustrine forested) were dominated mostly by the tree Pterocarpus officinalis Jacq. during the last two centuries. The forest stands of this tree can dominate the canopy of these wetlands, with 47% to 100% coverage depending upon the level of salinity (Álvarez-López 1990). This tree is characterized by its sinuous, narrow, and large buttresses (Online Resource 1 Fig. A1) that contribute to the formation of small hummocks in a flooded landscape. The resulting microhabitat matrix provides a fundamental resource for the reproduction and survival of many species of plants and animals, including resident and neotropical migrant birds (Rios-López 2007; Acevedo and Aide 2008). Forest stands of P. officinalis located along the coast and riverbanks reduce erosion of soils and contribute significantly to ecosystem function at local scales (Bâ and Rivera-Ocasio 2015). In addition, forests of P. officinalis are strongly structured by salinity and flooding in coastal areas, by flooding along rivers, and by seasonal variations in mountain water-table levels that supply water to lowland rivers. Although P. officinalis occupies brackish water near mangroves, studies show that it is not a true halophyte: it has a ten-fold reduction in flowering and fruiting and cannot complete its life cycle at concentrations of 200 mM (12%) NaCl (Eusse and Aide 1999; Medina et al. 2007; Rivera-Ocasio et al. 2007). Moreover, under low salinity in coastal soils, P. officinalis shows mechanisms to sequester Na + in leaf rachises as an adaptation to prevent damages of photosynthetic tissue (Medina et al. 2007). Although the specific mechanisms by which *P. officinalis* is affected by high salinity are poorly known, evidence suggests that increased salinity could interfere with the mutualistic symbionts in nodules of P. officinalis (Bâ and Rivera-Ocasio 2015).

Changes in land-use during the last century reduced the area covered by forests of P. officinalis to a total of 240 ha, distributed among 15 scattered patches and located mostly near the coast (Cintrón 1983; Rivera-Ocasio et al. 2007). These remnant forests are subject to altered flooding regimes due to changes in rainfall runoff, reduced overland flow from adjacent rivers, and saltwater intrusion. In coastal areas, trees of P. officinalis are at the extreme of their physiological tolerance due to increased salinity and SLR. Specifically, ongoing saltwater intrusions with the accelerated SLR and reduced supply of freshwater with the warming and drying climate are likely to produce salinity conditions exceeding the tolerance threshold and thus lead to mortality of remaining P. officinalis forests (Rivera-Ocasio et al. 2007). Populations of P. officinalis in coastal localities are also threatened by urban expansion and changes in freshwater flows to these localities, resulted from a combination of human disturbance such as channelization of rivers and construction of roads. These changes at the landscape level further exacerbate the altered hydrological balance of these coastal wetlands.

In this study, we analyzed land-cover data for the decade of 2000–2010 to assess changes in the extent of vegetated wetlands in the coastal zone (i.e., within 1-km buffer from the coastline), and simulated the potential inland-migration of coastal wetlands in Puerto Rico under two SLR scenarios by 2100. To highlight the vulnerability of coastal freshwater wetlands, we analyzed the trends in changes of forest structure, mortality, and recruitment in a forest stand of *P. officinalis* under the effects of drought and SLR in the north coast of Puerto Rico.

Methodology

Study Area

Puerto Rico is a tropical archipelago, composed of Puerto Rico (the largest), Vieques, Culebra, Mona, and other islets and cays. Puerto Rico is located in the northeastern Caribbean, centered at 18°15'N and 66°30'W (Fig. 1). The main island is about 180 km in length and 65 km in width, with a length of coastline about 800 km. The annual temperature ranges from 24° to 27 °C in coastal areas and from 22° to 25 °C in the mountains: August and January are the warmest and coolest months, respectively (Gómez-Gómez et al. 2014). The prevailing northeasterly trade wind brings substantial moisture from the Atlantic Ocean depositing more than 4000 mm of annual rainfall in the windward mountains but less than 1000 mm in the southwestern leeward side of the island (Yu et al. 2017). While moist forests currently dominate the island, the coastal areas were once covered extensively by wetlands including mangroves, saltmarshes (herbaceous saline

wetlands), freshwater swamps, to freshwater marshes (herbaceous non-saline wetlands) (Kennaway and Helmer 2007; Gao and Yu 2014). Puerto Rico is densely populated (i.e., 411 persons km⁻² in 2010, United States Census Bureau 2012), and most populations live in coastal areas (López-Marrero et al. 2012). Historically, the demand for arable lands during Spanish domination between 1493 and 1898 resulted in the drainage of wetlands in the coastal plains of Puerto Rico. The hydrological alterations continued into the early twentieth century under US domination, with the expansion of sugar cane production in the coastal plains and mangroves used for charcoal production (Martinuzzi et al. 2009). Recovery of coastal wetlands started in the 1940s after agricultural lands were abandoned, due to a shift in the island's economy from agriculture to industry (Dietz 1989). This recovery was short-lived because urbanization along coastal areas has followed since the late 1950s, which constrained wetlands restoration efforts (Lugo and Brown 1988; Grau et al. 2003; Martinuzzi et al. 2009). The implementation of various wetland protection policies, and the US Clean Water Act starting in the 1970s, led to the effective protection and the recovery of coastal wetlands. Currently, urbanization and development of infrastructure in coastal areas constrain the remaining wetlands on the island (Martinuzzi et al. 2009).

Quantifying Changes in Coastal-Zone Vegetated Wetlands in 2000–2010

Changes in land cover during the last century, with emphasis on wetlands, have been well documented for Puerto Rico (Kennaway and Helmer 2007; Martinuzzi et al. 2009; Gao and Yu 2014). Considering the accelerated SLR and recent rapid urbanization of the coast, we focused on coastal wetland changes in the twenty-first century concerning the distribution, potential landward migration, and survival. We reconciled various classifications of wetlands according to the Sea Level Affecting Marshes Model (Cowardin et al. 1979; Clough et al. 2016b) and summarized it in the online resource (Online Resource 1 Table A1). The resulting categories of vegetated wetlands include herbaceous and forested wetlands, which are further modified by water chemistry, either saltwater (saline) or freshwater (non-saline), and water regime (e.g., timing and duration of flooding). These wetlands are identified as mangrove forest and shrubland, freshwater Pterocarpus swamp, emergent (and seasonally flooded) herbaceous non-saline wetlands, and emergent (and seasonally flooded) herbaceous saline wetlands in the Puerto Rico Gap Analysis Project (Gould et al. 2008). We adopted the islandwide land-cover maps of 2000 and 2010 as our reference (Gould et al. 2008; Wang et al. 2017) and improved the wetlands classification in the coast via using high-resolution aerial photos. The land-cover map of 2010 for the whole island was created mainly based on the Landsat TM/ETM and the ALOS





(Advanced Land Observing Satellite) SAR (Synthetic Aperture Radar) images using the random-forest classifier (Wang et al. 2017), and to improve the accuracy specifically for the limited coastal wetland we did photo interpretation of the boundary of vegetated wetlands in the coastal zone (i.e., within 1-km buffer from the coastline) according to the 2009-2010 high-resolution orthographic imagery (0.3 m, U.S. Army Corps of Engineers, https://inport.nmfs.noaa.gov/inport/item/ 49483) and the long-term ground experience. This imagery dataset has 4 bands, i.e., blue, green, red, and infra-red bands. We did photo interpretation at the scale of 1:5000 in ArcGIS 10 and the band combination of infra-red, red, and green was used to identify the vegetated wetlands (Guo et al. 2017), which appeared to be dark-red, while the vegetated uplands appeared to be red under this band combination. Any patch of vegetated wetland that straddled the 1-km coastal zone boundary was also delineated in full. For comparison of vegetated wetland changes in the coast between 2000 and 2010, we simplified the coastal-zone vegetated wetland types into forested wetland and herbaceous wetland (Online Resource 1 Table A1). We validated the classification of coastal-zone vegetated wetlands in 2010 using 70 ground truthing points and the Kappa statistics reached 85. 5%. The spatial analyses were conducted with ArcGIS 10 (ESRI, Redlands, CA).

Simulations of Coastal Wetlands Migration by 2100

We adopted the Sea Level Affecting Marshes Model (SLAMM) in the simulation of coastal wetlands migration under various SLR scenarios (Clough et al. 2016b). SLAMM simulates dominant processes of erosion, inundation, accretion, and salinity, among other processes, when analyzing coastal wetlands conversion under SLR (Clough et al. 2016b). The new SLAMM 6.7 version further improved the mechanism to reflect dynamic accretion in response to accelerated SLR (Clough et al. 2016a; Kirwan et al. 2016). An initial wetland distribution and a high-resolution Digital Elevation Model (DEM) are required input datasets together with the DEM-derived slope. Urban-development land cover was also incorporated, as it interferes with wetland migration potential.

We simplified the NWI (National Wetlands Inventory 1983 for Puerto Rico) data for initial wetlands mapping and converted the wetland types into the SLAMM categories according to the model document (Clough et al. 2016b). We further did photointerpretation of the coastal urban-development areas based on the high-resolution aerial photos of 2009– 2010 abovementioned. We derived the DEM at 5 m from the Lidar ground point data available at the NOAA Digital Coast (https://coast.noaa.gov/dataviewer/#/, 2004 US Army Corps of Engineers Lidar). A spline interpolation tool, provided by the NOAA platform, was applied to derive a smooth surface. We then created the corresponding slope in ArcGIS 10.4 (ESRI, Redlands, CA). The derived DEM covers most of the coastal areas in Puerto Rico except a gap in Vega Baja on the central-northern coast. The distributions of coastal wetlands according to the NWI for Puerto Rico extend from the coastline to as long as 10 km towards the inland. We adopted and adjusted the wetland accretion rates (Online Resource 1 Table A3) according to the SLAMM 6.7 Technical Document and the SLAMM application in Cabo Rojo, Puerto Rico (Clough 2008).

We used measurements from two tide-gauge stations in Puerto Rico to determine the rate of SLR: Old San Juan gauge on the northern coast and Isla Magueyes gauge in the south (https://tidesandcurrents.noaa.gov/sltrends/). The mean SLR rate observed in Old San Juan (2.08 mm yr.⁻¹) was set for the northern and eastern coast facing the Atlantic Ocean, while that observed in Isla Magueyes (1.75 mm yr.⁻¹) was set for the southern and western coast facing the Caribbean Sea. We ran the future SLR scenarios of 1 m and 2 m by 2100, for the coastal areas of the main island of Puerto Rico.

Mortality, Survival, and Recruitment in a Coastal Freshwater-Wetland

As an example of the dynamics of coastal wetland vegetation, a Pterocarpus officinalis forest in Sabana Seca, Toa Baja, Puerto Rico (Online Resource 1 Fig. A1) was assessed for mortality, survival, and recruitment during a twenty-year period (see below). Broadly, this coastal freshwater swamp is within the subtropical moist-forest life zone with soils in the Martin Peña-Saladar-hydraquentes soil association (Boccheciamp 1978). The climate is slightly seasonal with most of the rainfall occurring from May to November, coinciding with the warmer period of the year. Average annual rainfall and temperature are 1693 mm yr.⁻¹ and 27 °C, respectively (Eusse and Aide 1999). To the northeast, the Pterocarpus forest is surrounded by white mangroves, Laguncularia racemosa L. To the southwest, there are cattail marshes, Typha domingensis Pers., which also include arrowheads (Sagittaria latifolia and S. lancifolia) and patches of the mangrove-fern, Acrostichum aureum L.

In this forest, a permanent 1-ha plot was established in 1994 (18°27'23.89"N, 66°12'36.55"W, 200 m east to west by 50 m north to south) at the freshwater-brackish ecotone (Rivera-Ocasio et al. 2007). Soil salinity was measured at the eastern (next to the mangroves) and the western (next to the marshes) edges of the plot (10 m by 50 m each section) between August 1994 and January 1999 by inserting the PVC tubes (1.4 m in length and 12 for each section) into hummocks and pools to a depth of 60 cm. A digital salinity multiparameter YSI-85 (Yellow Spring Instrument Corporation, OH,

USA) was used to monitor the salinity. In addition, surface water salinity was measured eight times during June-July 2003, August-December 2005, and March 2006 at five points (every 50 m from the east to the west of the plot) to verify the salinity gradient (Rivera-Ocasio et al. 2007). The salinity measurements showed that there is a gradient that varies seasonally with rainfall and freshwater inputs from inland areas. Despite the proximity to the sea (c. 1 km) and the low elevation of the area (1 m a.s.l.) the gradient is not affected by storm surges. Surface water salinity indicated an average of 1.6% and a slight increase in salinity near the mangrove end of the plot. At a 1.1 km-long transect covering the plot, surface water salinity increased from the inland pasture/marsh area towards the mangrove area (Rivera-Ocasio et al. 2007; Ríos-López 2008). Between August 1994 and January 1999, the salinity at 60 cm below the soil surface fluctuated from 1.5 to 20%, and the western section close to marshes consistently had lower salinity than the eastern section next to mangroves had, with a mean difference of 1.7% (Rivera-Ocasio et al. 2007).

Within the 1-ha plot, we measured all individual tree stems with a diameter equal to or greater than 1 cm at 130 cm from the ground (DBH \geq 1 cm) in 1994, 2003, and 2015. The coordinates of each stem within the plot were recorded to show spatial distribution patterns. We classified tree stems that reached a DBH greater than 1 cm between two censuses as new individuals in the subsequent census. We determined mortality based on the disappearance of an individual from previously recorded coordinates or when the identification tag was found in a dead plant or on the ground. Individual stems were classified into juvenile (1 cm \leq DBH < 10 cm) or adult (DBH \geq 10 cm) categories. We analyzed the data from the 2003–2015 census interval and compared it to the 1994– 2003 census interval.

We tested three hypotheses, which are 1) mortality of Pterocarpus will increase, and recruitment will decrease, with increasing salinity; 2) juvenile mortality has a stronger relationship to salinity than adult mortality; and 3) the drought between 2013 and 2015, combined with the SLR-mediated saltwater intrusion from 2003 to 2015, would cause higher mortality in the 2003-2015 census interval than that observed in 1994–2003. To test our hypotheses, we used the distance to the eastern boundary adjacent to the mangroves, the place with the highest measured salinity (Eusse and Aide 1999; Rivera-Ocasio et al. 2007), as an indicator of salinity. We assumed that the closer the point was to the east, the higher the salinity would be within the plot. We first calculated this distance for each stem measured in the plot. Then we grouped these plot-coordinate distances into eight evenly-distributed classes, which are represented by their midpoints. For each distance interval, we counted the individuals that survived from 1994 to 2003 and those that survived from 2004 to 2015 by the categories of adults and juveniles. We calculated

the survival rate for each period as the number of stems that survived through the study period divided by the number of stems first counted.

We applied the logistic regression to regress the survival rate on the distance from the highest point of salinity with the first-order of distance, the second-order of distance, or both, depending on the Akaike Information Criterion (AICs), for each period and per the juvenile and adult stem-categories. Paired-t tests were applied to compare the survival rates between the two periods of time and between the stem categories. We conducted all statistical tests using R 3.3 software interface (R Development Core Team 2014).

Results

Changes of Coastal-Zone Vegetated Wetlands in 2000–2010

In general, the area of vegetated wetlands (forested and herbaceous) in the coastal zone increased from 23,845 ha in 2000 to 26,366 ha in 2010 (Online Resource 1 Table A2). The area of forested wetlands, composed of mangroves and freshwater swamps, increased from 8841 ha to 10,580 ha and contributed to most of this increase. The area of herbaceous wetlands, including saltmarsh and freshwater marsh, increased from 15,004 ha to 15,785 ha during the same period. The changes in the extent of these wetlands were accompanied by changes in urbanized coastal areas which expanded from 11,030 ha to 12,506 ha. An analysis of the land-cover conversion indicated that newly-urbanized areas were mainly developing from upland pastures (953 ha) and bare grounds (440 ha). Only 35 ha of wetlands, 32 ha forested and 3 ha herbaceous, were converted into urban areas. Forested wetlands encroached on herbaceous wetlands (Online Resource 1 Fig. A2), resulting in a net loss of 1144 ha from herbaceous wetlands to forested wetlands. Forested wetlands also expanded into previous upland forests and woodlands. Herbaceous wetlands expanded into previous upland pastures, forests, woodlands, and bare grounds.

Migration of Coastal Wetlands under SLR Scenarios

Under the scenarios of 1-m and 2-m SLR by 2100, saltwater intrudes inland, and coastal wetlands migrate landward (Fig. 2). There is an increase in estuarine open water under the scenarios of 1-m (+8751 ha) and 2-m (+ 26,571 ha) SLR, respectively, while urban (-1807 ha and -5254 ha) and undeveloped uplands (-3008 ha and -7923 ha) decrease (Fig. 3). Coastal vegetated wetlands, including forested and herbaceous wetlands in both freshwater and saltwater, also shrink by 4330 ha and 14,999 ha, respectively under 1-m and 2-m SLR scenarios. The shrinkage of coastal vegetated

wetlands is nonlinear in response to SLR, with more than three times the loss under the 2-m scenario compared to that under 1-m. Mangroves expand 189 ha under the 1-m SLR, but their distribution is diminished by 3697 ha under the 2-m SLR (Figs. 2 and 3). Freshwater swamps, saltmarshes (herbaceous saline wetlands), and freshwater marshes (herbaceous nonsaline wetlands) continue to have decreasing trends under 1m and 2-m SLR scenarios.

The transition of land cover showed that mangroves and estuarine water replace the area currently covered by freshwater swamps. Specifically, under the 1-m scenario, these freshwater swamps experience a net loss of 275 ha to mangroves and a net loss of 249 ha to estuarine water. In the 2-m scenario, the net loss of these swamps to mangroves decreases to 122 ha, but that to estuarine water increases to 799 ha, i.e., more than three times the area under the 1-m scenario. Also, freshwater marshes are mostly converted to mangroves and estuarine water. As a result, under the 1-m scenario, these freshwater marshes experience a net loss of 1027 ha to be replaced by mangroves and 1172 ha to estuarine water. In the 2-m scenario, the net loss of these freshwater marshes to mangroves slightly decreases to 968 ha, however, that to estuarine water increases to 4369 ha. Also, under the 2-m scenario, there are net losses of 151 ha of freshwater marshes to saltmarshes and 84 ha to tidal flats.

Saltmarsh would encounter the greatest relative loss among the vegetated wetland types, with 26% and 70% loss of original cover under the 1-m and 2-m SLR scenarios, respectively. Although there is a net gain of saltmarsh from uplands and freshwater wetlands (252 ha and 699 ha under 1-m and 2-m, respectively), the accompanying loss to mangroves and estuarine water mostly counterweights this gain. The losses of saltmarsh to mangroves are 251 ha and 155 ha, and those to estuarine water are 1775 ha and 5288 ha, under 1-m and 2-m scenarios, respectively (with an additional loss of 41 ha to tidal flat under the 2-m scenario).

In the 1-m SLR scenario, mangroves gain 2472 ha from uplands, 1303 from freshwater wetlands, and 251 ha from saltmarshes, which more than compensates for the net loss of 3831 ha of mangroves to estuarine water and results in an expansion of 189 ha. However, when SLR increases to 2-m, the net loss of mangroves to estuarine water increases to 7242 ha, which far outbalances the net gain of 3553 ha (2305 ha from uplands, 1093 ha from freshwater marshes, and 155 ha from saltmarshes).

For the region of Toa Baja on the northern coast, where our *Pterocarpus* forest-plot is located, vegetated wetlands would gain 39 ha under 1-m SLR, but lose 717 ha in the 2-m scenario. Although the area covered by freshwater swamps, saltmarshes, and freshwater marshes continues to shrink in both scenarios, the area of mangroves expands 195 ha and 477 ha under 1-m and 2-m scenarios, respectively (Fig. 4). This expansion occurs at the expense of 32 ha (under 1-m **Fig. 2** Coastal wetlands inland migration under the sea-level rise scenarios of 1 m and 2 m by 2100



scenario) and 232 ha (under 2-m scenario) being lost by freshwater marshes. Moreover, freshwater marshes also lose 44 ha (under 1-m) and 495 ha (under 2-m) to estuarine water. In addition, estuarine water intrudes into saltmarshes, causing a net loss of 59 ha and 386 ha of these marshes under 1-m and 2m, respectively. Although estuarine water will partly replace areas of mangroves (164 ha and 334 ha under 1-m and 2-m scenarios, respectively), mangroves expand their geographic distribution into urban and undeveloped uplands. This expansion of mangroves translates into gains of 314 ha and 538 ha under 1-m and 2-m SLR, respectively. Consequently, the gains of mangroves to estuarine water and result in a net expansion of mangroves under both scenarios.

Mortality and Recruitment in a Pterocarpus Forest

Survival counts for each 25-m interval (Fig. 5) revealed different patterns between adults and juveniles and between the two census periods. The survival rates (Fig. 6) indicated a decrease in the survival of individuals with the increased proximity to high salinity, a higher survival of adults compared to juveniles, and a higher mortality of both, adults and juveniles, during the 2003–2015 census compared to 1994–2003. The corresponding spatial distribution of the mortality of trees (Fig. 7a, b) confirmed that a higher mortality occurred on the eastern section of the plot, characterized by higher salinity. In this section of the plot, a higher mortality also occurred during 2003–2015 compared to 1994–2003, which also



Fig. 3 Changes in total area distribution of coastal urban, undeveloped upland, and open ocean (a), and those of coastal wetlands (b), under the sea-level rise scenarios of 1 m and 2 m by 2100

resulted in reduced recruitment. Recruitment during 2003–2015 appeared only in the western section of the plot, characterized by lower salinity (Fig. 7c).

The logistic regressions of survival rate (Online Resource 1 Fig. A3) resulted in the following four equations (Eqs. 1–4). All the coefficients are significant at p < 0.05 except the coefficient of -0.00013 for the second-order term in Eq. 3 (Surviv.Adult and Surviv.Juvenile refer to survival rate of adults and juveniles, respectively, and z indicates the distance to the east, i.e., 200 - X coordinate).

For 1994–2003,

$$Surviv.Adult.94_03 = \frac{\exp(1.76 - 0.0102z)}{1 + (1.76 - 0.0102z)}$$
(1)

$$Surviv.Juvenile.94_03 = \frac{\exp(-0.91 + 0.043z - 0.0018z^2)}{1 + \exp(-0.91 + 0.043z - 0.0018z^2)}$$
(2)

and for 2003-2015,

$$Surviv.Adult.03_{15} = \frac{\exp(-1.85 + 0.038z - 0.00013z^2)}{1 + \exp(-1.85 + 0.038z - 0.00013z^2)}$$
(3)

Surviv.Juvenile.03_15 =
$$\frac{\exp(-8.06 + 0.17z - 0.00077z^2)}{1 + \exp(-8.06 + 0.17z - 0.00077z^2)}$$
(4)

The regressions predicted a general trend of decreased survival rate with the increased proximity to high salinity (except slightly lowered survival rates occurred at the western end of the plot and for the category of juvenile-stems during 2003–2015; Online Resource 1 Fig. A3). The regressions also revealed a higher survival rate of adults than that of juveniles in both census periods and higher mortality of both adults and juveniles in 2003–2015 compared to 1994–2003. Paired-t tests confirmed the significance of these comparisons above (p < 0.01).

Discussion

Coastal wetlands are among the ecosystems most vulnerable to the effects of climate changes, including SLR, and to the land-use changes. In Puerto Rico, coastal wetlands face the additional challenge of having limited areas into which they can migrate because of the coasts altered by urban development and the constraints imposed by the topography of the island. Our analysis and simulation of the island's coastal wetlands revealed that a moderate SLR of 1 m by 2100 allows expansion of mangroves, but would decrease the areas of freshwater swamp, saltmarsh, and freshwater marsh. A 2-m SLR scenario would eventually shrink all vegetated wetland types because of intrusion of estuarine water (Figs. 2 and 3). The observed changes of wetlands along the coast also exhibited the phenomenon that mangroves replaced the areas previously covered by marshes during the first decade of the twenty-first century (Online Resource 1 Fig. A2).

Among the types of vegetated wetland herein considered, saltmarshes (herbaceous saline wetlands) are most sensitive to SLR and will lose 10.3% and 66.5% of their total extent under the 1-m and 2-m SLR scenarios, respectively (Fig. 3). Also, the composition of the vegetation in saltmarshes will change into the one that characterizes a regularly-flooded saltmarsh (from 85% under initial condition to 91% under 2-m SLR scenario). The regularly-flooded saltmarsh (i.e., low marsh) is expected to have higher productivity than the irregularly-flooded saltmarsh (i.e., high marsh) (Kirwan et al. 2016). A similar pattern of changes in vegetation composition in these marshes was documented for coastal areas of New York, where studies predicted an 80.7% loss in irregularly-flooded saltmarsh under 1-m SLR scenario (Clough et al. 2016a).

Saltwater intrusion gradually salinizes freshwater swamps and will threaten the survival of their species in their current location even before the full manifestation of the projected SLR. In our *Pterocarpus* forest-plot, the mortality of both adults and juveniles of *P. officinalis* was higher towards the *Pterocarpus* / mangrove extreme of the plot which we related to increased salinity, yet modulated by the densities of stems **Fig. 4** Coastal wetlands migration in Toa Baja under the sea-level rise scenarios of 1 m and 2 m by 2100



(Figs. 5 and 6). A high rate of the survival of trees appeared only in the mid-salinity sections in the census-plot of this forest (Fig. 6a). This phenomena could be partly attributed to a low density of trees in the middle of the plot (Fig. 5), which, in turn, might result in reduced density-dependent mortality (Rivera-Ocasio et al. 2007).

Juveniles of *P. officinalis* are more sensitive to salinity than adults (Fig. 6), and the saltwater intrusion will affect recruitment of *P. officinalis* more significantly compared to its effect on mortality (Fig. 7). Moreover, the higher mortality of adults in the high-salinity area result in canopy gaps, which facilitate the growth of a common species of woody-liana native to this forest, *Heteropterys laurifolia* (L.) A. Juss. (Malpighiaceae), a hydrophyte that occurs in wetlands and non-wetlands. As more trees die because of increased salinity, more gaps are generated, resulting in vast extents of the forest covered by this liana. The combination of the forest gaps and liana abundance alters the previous dominance hierarchy of the vegetation within the forest. The expansion of this liana may further inhibit the growth of seedlings and decrease survival of juveniles of *P. officinalis* by decreasing their access to light.

The simulation of the changes in the landscape under SLR scenarios reveals that saltwater intrudes into the plot from its eastern side (Fig. 4). Moreover, the canals (Online Resource 1 Fig. A1) created for drainage of these wetlands during historical agricultural activities further facilitate the intrusion of saltwater inland, which exacerbates the salinization of the landscape (unpublished data). Urbanization and associated road construction to the east and the south fragment the wetland-landscape and disconnect this *Pterocarpus* forest



Fig. 5 Counts of surviving (solid bars) individual stems of adult and juvenile *Pterocarpus officinalis* during 1994–2003 (**a** and **b**) and during 2003–2015 (**c** and **d**) within each 25 m-interval, as well as the counts of living individual stems at the beginning of each census period (open bars)

from its main freshwater sources, which include the Cocal River to the east and the freshwater springs and marshes to the south (Online Resource 1 Fig. A1). The changes in the water table documented from around the plot and in other sites, along with the associated fluctuations in salinity, generate drier soils that result in a further stress of individuals of *P. officinalis* (Medina et al. 2007; Colón-Rivera et al. 2014). This modification in hydrology has profound consequences on the conditions of the wetland-soils and facilitates the changes in the composition of species at these sites.

In addition to SLR and the accompanying saltwater-intrusion, weather events in the Caribbean, such as the severe



Fig. 6 Survival rates of adult or juvenile Pterocarpus officinalis in 1994–2003 and in 2003–2015 (a) and the predicted versus observed survival rates (b)

Fig. 7 Spatial distributions of *Pterocarpus officinalis* mortality from 1994 to 2003 (**a**) and 2003–2015 (**b**), and survivor / recruitment during 2003–2015 (**c**)



drought that occurred in Puerto Rico between 2013 and 2015 (Herrera and Ault 2017; Mote et al. 2017), would affect the supply of freshwater significantly and may exacerbate the threats faced by freshwater coastal-wetlands. Our analysis of the freshwater swamp in Toa Baja revealed mortality increased drastically between 2003 and 2015 compared to the period of 1994–2003 (Figs. 6, 7a, and b). As a consequence, the recruitment of young trees of *P. officinalis* for the period of 2003–2015 was reduced to zero in areas of high salinity (Fig. 7c).

The limit in the extent of coastal plains also constrains the migration of coastal wetlands. For example, the Toa Baja region on the northern coastal plain has 92% area with lower than 5° slopes. The 1-m SLR predicts a 2.1% increase in mangroves island-wide, but the 2-m SLR shows a 40.4% decrease (Fig. 3). However, mangroves in the Toa Baja region (Fig. 4) will benefit from the flat landscape closest to sea and expand in both scenarios with increases of 40.2% and 98.3%, respectively. Our simulation revealed that under the 2-m SLR scenario, there would be 51% loss in the distribution of mangroves in the south/southwest, compared to only 33% loss in the north/northeast with relatively greater areas of coastal flat plains (Fig. 2). Therefore, the loss of area and the pattern of replacement of coastal wetlands are spatially heterogenous under the projected SLR scenarios, which has profound consequences for conservation.

There might be an overestimation of marsh vulnerability to scenarios of SLR if the vertical accretion could keep pace with changes in sea level due to the accumulation of sediments and organic matter (Kirwan et al. 2016). However, recent studies

also highlighted that low supply of sediments and low tidalrange would still render both marshes and mangroves vulnerable to predicted SLR (Lovelock et al. 2015; Kirwan et al. 2016). Caribbean wetlands have a relatively low supply of sediment, and the adjustment of mangroves to rising sea level is mainly dependent on the accumulation of subsurface organic matter, which decomposes slowly in an anaerobic environment (McKee et al. 2007; Lovelock et al. 2015). In Puerto Rico, many dams and reservoirs (established to meet water demands from more than 3 million people) could have largely reduced the supply of water and sediment from the highlands to the coastal wetlands. Coastal wetlands in Puerto Rico also exist within an environment with low tidal-range (e.g., the mean tidal range in the capital of San Juan, northern Puerto Rico, is 0.34 m; https://tidesandcurrents.noaa.gov). According to the relationship between predicted threshold-rate of SLR and tidal range and rate of supply in sediment (Kirwan et al. 2010), we estimated that the coastal wetlands in Puerto Rico might only withstand a rate of SLR lower than $5-10 \text{ mm yr.}^{-1}$. Episodic events, such as heavy rainfall and floods, might deposit large amounts of sediments to the coastal wetlands and lead to elevated accretion. Therefore, the biophysical factors interact with the socio-economic variables and the climate extremes to influence the ecosystems in complex ways, which makes a broader understanding of how coastal wetlands may respond to predicted SLR more challenging for management and conservation purposes.

In conclusion, coastal wetlands in Puerto Rico are facing several threats that challenge their ability to persist in their current geographic location. Among these threats are 1) accelerated SLR; 2) altered precipitation regime and frequent droughts and hurricanes; 3) limited space for retreat due to coastal-land availability constraints; and 4) coastal urban expansion and the changes interacting with the preexisting hydrological regime. From a conservation perspective, urbanized coastal lands add to the challenges of restoring coastal wetlands in the midst of accelerated SLR and a changing climate. We are already experiencing these changes in coastal wetlands and their consequences on areas such as the Pterocarpus forest in Puerto Rico (e.g., mass mortality bringing this species to the edge of disappearance at local scale). Consequently, we need further studies that couple landscape-to-regional ecohydrological models to incorporate the biological, hydrological, and anthropogenic components of vertical accretion in response to scenarios of drought, frequent extreme rainfall events, warming, and CO₂ enrichment. We understand that such approaches will elucidate mechanisms and the potential fate of coastal wetlands under projected SLR and climatic disturbances. Hopefully, these approaches may also offer valuable recommendations for the conservation and management efforts aimed at the restoration of wetlands in Puerto Rico, the Caribbean, and elsewhere.

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