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Linking terrigenous sediment delivery to declines in coral reef ecosystem services

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Abstract

Worldwide coral reef conditions continue to decline despite the valuable socio-economic benefits of these ecosystems. There is growing recognition that quantifying reefs in terms reflecting what stakeholders value is vital for comparing inherent tradeoffs among coastal management decisions. Terrestrial sediment runoff ranks high as a stressor to coral reefs and is a key concern in Puerto Rico where reefs are among the most threatened in the Caribbean. This research aimed to identify the degree to which sediment runoff impacts production of coral reef ecosystem services and the potential for watershed management actions to improve these services. Ecosystem service production functions were applied to map and translate metrics of ecological reef condition into ecosystem services production under a gradient of increasing sediment delivery. We found that higher sediment delivery decreased provisioning of most ecosystem services, including ecosystem integrity, bioprospecting discovery, and reef-based recreational opportunities and fisheries production. However shoreline protection and services with a strong contribution from non-reef habitats (e.g., mangroves, seagrasses) were higher in locations with high sediment delivery, although there was a strong inshore effect suggesting the influence of distance to shore, depth, and inshore habitats. Differences among services may indicate potential tradeoffs and the need to consider habitat connectivity, nursery habitat, accessibility, and sediment buffering. The relationships we have identified can be used to link stakeholder values to decision alternatives to ensure continued provisioning of these services and the well-being of communities.

Introduction

Although ecosystem condition is usually quantified using ecological attributes such as percent cover or species abundance, there is growing recognition that considering ecosystems in terms of the goods and services they provide to people is key to ensuring their sustainability (MEA, 2005). Conveying the social and economic value of ecosystems to non-scientists, community stakeholders, and decision makers enables a fuller comparison of the suite of costs, benefits, and tradeoffs among decision alternatives (Gregory et al., 2012; Wainger and Boyd, 2009). Worldwide an estimated 60% of ecosystem services are degraded with considerable social and economic costs (MEA, 2005). Understanding the relationships between declines in local stressors and ecosystem services can help inform management

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actions to ensure the continued provisioning of those services (Wainger and Boyd, 2009; Yee et al., 2015).

Coral reefs, in particular, are recognized worldwide as valuable resources that contribute to the economic, social, and environmental well-being of coastal communities (MEA, 2005; Moberg and Folke, 1999; Principe et al., 2012) and even to non-coastal residents who may never in their lives visit a coral reef (Bishop et al., 2011). In the Caribbean, coral reefs provide multibillion dollar (USD) protection of lives and coastal property during storm events, seafood production, employment in fisheries and tourism industries, recreational opportunities, potential pharmaceutical development, and cultural value (Burke and Maidens, 2004). Unfortunately Caribbean coral reefs have declined dramatically in recent decades, and many have shifted to a macroalgal-dominated state (García-Sais et al., 2008; Jackson et al., 2014).

Excessive, chronic, or frequent terrestrial sediment runoff has contributed to the degradation of coral reefs around the world (Burke et al., 2011; Fabricius, 2005; Kroon et al., 2014; Whitall et al., 2013) and can exacerbate the negative effects of climate change and disease (Ban et al., 2014). Sediment runoff is of particular concern throughout Puerto Rico where steep, mountainous watersheds transport runoff containing sediment, contaminants, and nutrients to coastal outlets (Martinuzzi et al., 2007), leading to discharge plumes and subsequent re-suspension of sediment that have contributed to coral reef degradation (Morelock et al., 2001; Warne et al., 2005; Whitall et al., 2013). In the southwestern Puerto Rico, proposed management actions to reduce terrestrial sediment runoff are moving forward (CWP, 2008; Rodriguez, 2013), but it has not been without controversy (Sotomayor-Ramírez and Pérez-Alegría, 2011). Stakeholders in the watershed have expressed uncertainty as to whether proposed management actions to reduce sediment could actually convey social and economic benefits, including tourism, recreation, fishing, and human health, in addition to protecting coral reefs (Bradley et al., 2016; Carriger et al., 2013; Gregory and Gonzales, 2013; Rehr et al., 2014). A lack of quantitative linkages between changes in manageable local threats such as sediment runoff to stakeholder-valued ecosystem services makes it challenging to predict potential socio-economic benefits and integrate those benefits into the decision making process (Yee et al., 2015).

The extent to which coral reef ecosystem service provisioning is affected by excessive sediment runoff, and how potential actions to reduce sediment runoff will affect these services, has largely not been quantified. Research on the impacts of terrigenous sediment typically focus on ecological measures of coral reef condition, such as negative effects on growth, survival, and recruitment of corals through dissemination of contaminants, reduction in light availability, and loss of habitat by sediment covered surfaces, and subsequent population or community-level effects on coral cover, abundance, or diversity (reviewed in Fabricius, 2005). Loss of coral reef habitat have been shown to negatively impact the recruitment and survival of economically important reef fish, including catchable parrotfish and ornamental damselfish (DeMartini et al., 2013; Wenger et al., 2012). Sediment resuspension can also impact visibility, a key factor in determining the quality of dive and snorkeling locations (Wielgus et al., 2003). Wave energy reaching shorelines protected by reefs is also predicted to decline as reefs become increasingly degraded (Sheppard et al.,

2005). Changes in coral reef ecosystem services, such as recreational opportunities, shoreline protection, and fisheries, have been modelled along a human disturbance gradient (Yee et al., 2014) and under coastal development scenarios (Arkema et al., 2015). Consideration of a suite of ecosystem services is important because of the potential for terrestrial sediment runoff to have both negative and positive effects on ecosystem services (Apitz, 2012). To our knowledge, however, a quantitative linkage between terrestrial sediment runoff and a suite of coral reef ecosystem services has yet to be made.

To investigate the relationship between sediment delivery and the potential supply of coral reef ecosystem services, we applied a suite of ecological production functions to coral reef condition data from Puerto Rico. Ecological production functions quantify the relationship between metrics of ecosystem condition and the provisioning of ecosystem services (Wainger and Boyd, 2009). Methods for linking biophysical attributes of reef condition, such as fish biomass, coral cover, or species richness, to provisioning of ecosystem goods and services have previously been identified (Principe et al., 2012; Yee et al., 2014). We applied predictive mapping methods to quantify metrics of coral reef condition directly related to ecosystem services provisioning. Next, using existing ecological production functions for coral reefs (Yee et al. 2014), we translated the maps of coral reef condition into endpoints of ecosystem services reflecting stakeholder-identified concerns, including shoreline protection, fisheries production, tourism and recreation opportunities, bioprospecting discovery, and ecosystem integrity (Bradley et al., 2016; Carriger et al., 2013). Finally, we investigated whether higher levels of sediment delivery, quantified as the potential delivery of sediment from the watershed to the coastal zone, were linked to degradation of coral reef ecosystem services.

Methods

Predictive models of reef condition

From previous work (Principe et al., 2012; Yee et al., 2014), we identified metrics of coral reef condition that are directly relevant to quantifying ecosystem services through the application of ecological production functions (Fig. 1). Ecological production functions used to translate ecological condition to ecosystem services are summarized in Table 1 and include individual metrics, weighted indices based on expert opinion, statistical models from field or survey data, and bio-physical process models (see Yee et al. (2014) for detailed descriptions of individual metrics). We focused on five categories of reef ecosystem services that were directly relevant to stakeholders in Puerto Rico (Bradley et al., 2016; Carriger et al., 2013): reef integrity, shoreline protection, tourism and recreation, fisheries, and the potential for bioprospecting discovery. Reef integrity describes the capacity of the reef to maintain healthy function and retain diversity, and can be quantified by coral and macroalgal cover, fish abundance and richness, coral abundance and richness, and fish biomass (Healthy Reefs Initiative, 2010; van Beukering and Cesar, 2004). Wave energy dissipation by reefs that contributes to shoreline protection is largely related to coral cover, reef height, and friction created by variability in coral colony heights (Sheppard et al., 2005). The quality of sites for recreational diving or snorkeling opportunities is largely influenced by the abundance and richness of fish and coral (Wielgus et al., 2003). Coral cover can influence

the biomass of key commercial fish species (Mumby et al., 2008), and sponge richness may be a good indicator of the potential for bioprospecting discoveries (Hunt and Vincent, 2006).

In total, we identified 19 metrics of coral reef condition (Table 2) as input into ecological production functions (Table 1). Reef condition metrics were calculated using field monitoring data collected by the U.S. Environmental Protection Agency (EPA) and National Oceanic and Atmospheric Association (NOAA) from 2007-2011 (Fig. 2a). EPA data was collected along the southern Puerto Rico coastline during November – December of 2010 and 2011 (field methods described by Oliver et al. 2011); NOAA data was collected semi-annually (January – February and September – October) from 2007 – 2011, encompassing the La Parguera – Guánica region of southwest Puerto Rico, Jobos Bay, and Vieques Island (field methods described by Pittman et al. 2010). EPA surveys, which encompassed a larger area (25 m²) than NOAA surveys (1 m²) and included coral colony counts, were used to calculate coral abundance, richness, and cover. NOAA surveys were primarily used to calculate the additional non-coral metrics, including algal cover, fish richness, and fish biomass (Table 2). Spatial maps of coral reef condition for nearshore waters surrounding Puerto Rico were constructed from available point-survey field monitoring data using regression tree models (Knudby et al., 2010; Pittman et al., 2007; Yee et al., 2014).

Predictor variables in the regression tree models were derived from benthic habitat (NOAA, 2001) and bathymetry maps (NOAA, 2004), both of which are commonly used remote sensing variables and are highly transferable to locations with limited field monitoring data (Knudby et al., 2010; Pittman et al., 2007; Yee et al., 2014). Predictor variables calculated for each point survey location included mean and standard deviation of bathymetry (NOAA, 2004) and percent cover of benthic habitat types, including mangroves, seagrass, patch or linear reefs, sand or mud, uncolonized hardbottom, and macroalgae (Kendall et al., 2001; NOAA, 2001). Without knowing the ecologically-relevant spatial scale for each metric, a multi-scale or moving window approach of increasing spatial extent (1×1 [0.0025 km²]; 3×3 [0.0225 km²]; 5×5 [0.0625 km²]; 9×9 [0.2025 km²]; 17×17 [0.7225 km²]; 33×33 [2.7225 km²]; 65×65 [10.5625 km²]) was applied following the methods of Pittman et al. (2007). Other predictor variables included Euclidean distance to shore (the main island of Puerto Rico or Mona, Vieques, or Culebra islands), distance to the shelf-edge separating the shallow-nearshore from the deeper ocean, and the presence or absence of a marine protected area (<http://marineprotectedareas.noaa.gov>). Lastly, as coral condition may directly influence fish richness and abundance (Gratwicke and Speight, 2005) we also considered predicted values from coral abundance and richness regression trees as potential predictors of fish metrics.

For each metric of reef condition, a sequence of regression trees was generated using the library “tree” in R (<http://www.r-project.org>). To find the optimal tree size and compensate for over-fitting, each final model was selected using multiple iterations of ten-fold cross validation, whereby the most frequently occurring tree with the smallest number of nodes within one standard error of the minimum error rate was selected (De’ath and Fabricius, 2000; Venables and Ripley, 2002). Model accuracy was assessed using the coefficient of determination (R^2) for the relationship between the observed and predicted value for the model data, along with the area under the curve (AUC) of the receiver-operating

characteristic curve. Additionally, when comparable metrics were calculable, models were validated using an independently collected data set (i.e., models fitted to EPA data were validated using NOAA data and vice versa), or when independently collected data were not available, a random 10% subset that was withheld from the model fitting data. Because coral survey data during this time period were unavailable for the west and north sides of the island, we specifically evaluated whether models developed using EPA data from the southern shore could predict observed values that included the eastern shore, specifically near the island of Vieques. Predicted cover of algae and coral from regression tree models were also visually compared to benthic habitat maps (NOAA, 2001) to verify predictions were consistent with what limited information was available for the western and northern shores. EPA and NOAA coral surveys measured different metrics using different spatial scales, some transformations were needed to make comparisons, including individual coral colony size to cover ($\pi * radius^2$) and linearly scaling coral density and cover. Final regression tree models were applied to translate maps of the environmental variables to predicted spatial maps (50×50 m² spatial grid) of coral condition for each metric, which were then used in subsequent ecosystem services calculations. Predicted variables were considered acceptable as input to ecosystem services production functions if at least two of the following criteria held: i) significant model R² between observed and predicted data (p<0.01), ii) AUC at acceptable (>0.7) or outstanding (>0.8) levels (Pittman et al. 2007) for training data set, or iii) AUC at acceptable (>0.7) or outstanding (>0.8) levels for independent validation data set.

Estimation and evaluation of ecosystem services

We applied ecological production functions (Table 1) to translate the 50×50m² gridded maps of coral reef condition into 41 metrics estimating ecosystem integrity, shoreline protection, recreational opportunities, fisheries production, and bioprospecting potential (Moberg and Folke, 1999; Principe et al., 2012; Yee et al., 2014). A subset of the 28 production functions listed in Table 1 were calculated both for all habitat types (e.g., mangroves) and coral reef only habitats, producing a total of 41 ecosystem services metrics (Table 3). Input data to the production function models included the 19 reef condition metrics (Table 2), benthic habitat maps (NOAA, 2001), bathymetry maps (NOAA, 2004), daily estimates of offshore significant wave height and period (NOAA Wavewatch III; <http://polar.ncep.noaa.gov/waves/index2.shtml>), and water visibility (NOAA Ocean Color Web; <http://oceancolor.gsfc.nasa.gov>).

Because rigorous observational data on ecosystem services is largely unavailable, we evaluated the predictive accuracy of each ecological production function by comparing our ecosystem services estimates to independent spatial maps representing areas where we a priori predicted ecosystem services provisioning would be greater (Fig. 2b). We expected estimates of ecosystem integrity to be greater in marine protected areas (MPA, marineprotectedareas.noaa.gov). Shoreline protection estimates were expected to be highest in areas where the high resolution Caribbean Coastal Ocean Observing System's Simulating Waves Nearshore (SWAN) model (www.caricoos.org) also predicted high wave height attenuation, quantified as the 75% quantile of modeled output. Wave height attenuation was estimated for SWAN model output of bi-daily significant wave heights for October 2012 –

April 2015 by calculating the maximum difference in wave heights between neighbors assuming a wave trajectory perpendicular to shore. SWAN is a phase-averaged spectral wave model capable of capturing wave attenuation over reefs due to bottom friction and changes in depth (Buckley et al., 2014). For recreational opportunities, we expected our estimates to be greater in sites frequented by chartered dive and snorkeling operators, defined as areas with greatest frequency (75th quantile) of chartered diving or snorkeling visits per week (Macko et al., 2008). Estimates of single species fisheries production metrics (density of *Panulirus argus*, density of *Strombus gigas*, and presence of *Eucheuma* spp.) were expected to be highest in areas in the 2007 – 2011 NOAA point-survey data where *P. argus*, *S. gigas*, and macroalgae were present (Fig. 2a). As finfish were observed at most locations, estimates of the relative economic value of finfish for commercial fisheries and key commercial fish biomass were compared to areas with greater than the 75% quantile of abundance in NOAA survey data. The remaining fisheries production metrics (e.g., *E. striatus* density, mangrove connectivity) were not directly comparable to NOAA survey data, and were instead expected to be greater where maximum annual commercial fishing effort was greater than the 75% quantile, obtained from commercial fishing data for Puerto Rico (Shivlani and Koenike, 2011). Production of curios was expected to be more comparable to dive and snorkeling sites than commercial fishing areas. Bioprospecting discovery metrics were expected to be greater in areas of the 2007-2011 NOAA point-survey data with presence of known sources of bioprospecting discovery, identified in the Ocean Biogeographic Information System (www.iobis.org), and including the presence of sponges, tunicates, red algae (*Laurencia* spp.), sharks, or gorgonians (Principe et al., 2012). No acceptable validation data sets were available for sand generation.

We performed one-tailed T-tests using the library “stats” in R to test whether each of the 41 ecosystem services metrics was indeed greater in the spatial region where we a priori predicted it should be higher (Fig. 1). Because using all spatial grid cells in analyses would violate statistical assumptions of independence (i.e., neighboring grid cells are more similar than distant ones), statistical analyses were performed with a randomly selected subset of 5,000 50×50 m² grid cells, approximately 0.5% of the data. Resampling of subsamples, smaller (300) subsamples, and larger (10000) subsamples were also tested to ensure this and subsequent statistical analyses were robust. Metrics that did not significantly match a priori assumptions were eliminated from subsequent analysis.

Linking sediment delivery to ecosystem services provisioning

We assessed whether ecosystem services provisioning was specifically related to levels of sediment delivery into the coastal zone. Because the large number of ecosystem services metrics varied in both their collinearity to one another and in their predictive ability when validated against independent data, we used principal components analysis (PCA) to reduce the validated ecosystem services metrics to a small number of principal components representing groups of ecosystem services exhibiting similar spatial patterns (Fig. 1). Ecosystem services metrics were log-transformed as needed to meet normality assumptions prior to analysis. Principal components explaining the most variance were retained, followed by a varimax rotation to simplify the structure of loadings (Quinn and Keough, 2002), such that in most cases each ecosystem service was positively correlated with only a single

principal component. Loadings >0.4 were used to determine which ecosystem services metrics were associated with each principal component (Stevens, 1992). PCA and varimax rotation were performed in R using the “stats” and “psych” libraries respectively. Principal components scores were used in subsequent analyses to test for effects of sediment delivery on groups of ecosystem services.

Potential sediment delivery into the coastal zone was quantified and mapped spatially over nearshore benthic habitats by NOAA’s Summit to Sea model (Burke and Maidens, 2004; NOAA, 2004). Sediment delivery from each watershed to an outflow point is calculated by a simplified application of the Universal Soil Loss Equation, and then decreases with distance from the point of discharge away from shore, such that each $50 \times 50 \text{ m}^2$ grid cell has an associated value of relative terrestrial sediment delivery. To account for the confounded effects of sediment delivery and distance from shore, we tested the effect of sediment delivery on ecosystem services provisioning using a two-factor (sediment deliver $\times$ distance to shore) multivariate analysis of variance (MANOVA) using library “stats” in R. Univariate analysis of variance (ANOVA) with Tukey’s pairwise post-hoc comparison (significance determined by Wilk’s λ , $\alpha=0.05$) were used to explore significant effects for individual classes of ecosystem services. Quantiles (0 – 24%, 25 – 74%, and 75 – 100% of data) were used to classify sediment delivery in Puerto Rico as low (0), medium (1 – 9,931), and high (9,932 – 327,058; Fig. 3). Similarly, distance to shore was classified by quantiles as inshore (0 – 0.7 km), midshore (0.8 – 5.7 km), and offshore (5.8 – 24.48 km). Analyses were performed on the randomly subsampled 5000 grid cells, as previously described to adhere to assumptions of independence, resulting in 39 to 1616 cells per each of the 9 sediment $\times$ distance factors. Resampling of 5000 cells, and re-analysis of PCA using only reef-based metrics (e.g., wave energy dissipation by reef), was used to ensure statistical analyses were robust.

Results

Predictive models of reef condition

Predictive regression tree models were developed from EPA and NOAA point survey data. Coefficients of determination were all highly significant ($p < 0.001$) but variable, ranging from $R^2=0.05$ for rubble to $R^2=0.53$ for coral abundance (Table 2). In calculating coefficients of determination, continuous values for each observed metric were compared to discrete categorical values predicted by regression tree models, so unexplained variability is expected. The majority of regression tree models had acceptable ($\text{AUC} > 0.7$) or outstanding ($\text{AUC} > 0.8$) ability to predict categorical values for model fitting (Table 2). A few metrics (e.g., coral abundance and fish schools) were borderline in meeting acceptance criteria ($\text{AUC}=0.69$), but were tentatively retained until ecosystem services production functions based on those metrics were validated (see next section). Of particular concern was the ability of models, which were heavily based on data from the southern shore, to predict independent data from the eastern shore. Because predictive ability of models to independent validation data was generally greater than acceptable ($\text{AUC} > 0.7$), models were considered general enough to apply to the continuous shallow-water area (<35 meters deep) surrounding Puerto Rico, including the northern and western shores where data are scarce.

We caution, however, that particularly for some metrics (e.g., coral abundance), predictions along the southern shore may have greater reliability. Coral condition metrics were applied as input into ecosystem services production functions to produce maps of ecosystem services provisioning.

Estimation and evaluation of ecosystem services

Validation of ecosystem services production function models against a priori assumptions resulted in the reduction of the original 41 ecosystem services metrics down to 23, including the two sand generation metrics for which validation data was unavailable. T-tests indicated both predicted measures of ecosystem integrity were consistent with our assumption of being significantly higher in MPAs (Table 3). Three out of four predicted measures of bioprospecting discovery were significantly higher, as expected, in areas with documented presence of known sources. For shoreline protection, bio-physical models of wave attenuation, decrease in erosion, or decrease in wave run-up produced predictions more consistent with SWAN models than production functions based on relative habitat coverages (wave energy dissipation) or indices of reef condition (CRPI).

Predicted estimates of recreational opportunities were more variable across production functions. Estimates of recreational opportunities based on multiple fish and coral attributes (value of a dive and dive site favorability) or reef habitat (ease of access for education on reef and density of *E. striatus* on reef) were significantly greater in areas used in chartered dive and snorkel operations (Table 3). The four metrics based largely on non-reef habitat availability (ease of access for education, sand generation, density of *Epinephelus striatus*, and opportunity for snorkeling) were not significantly comparable to maps of chartered dive operations (Table 3).

For fisheries production, predictions of density of *E. striatus* on reef and mangrove connectivity were significantly higher in areas with high commercial fishing activity. Estimates of value of finfish on reef and commercial fish biomass were significantly comparable to NOAA observational data on finfish abundance (Table 3). A number of other fisheries production metrics based on reef habitat (density of *P. argus* on reef, density of *S. gigas* on reef, presence of *Eucheuma* spp. on reef, production of curios and jewelry by reef) were not significantly highest in areas with high commercial fishing activity (Table 3). Production function predictions of density of *S. gigas* were significantly comparable to NOAA observational data on *S. gigas* (Table 3), and production of curios and jewelry was significantly higher in locations favored by dive and snorkeling operations.

Linking sediment delivery to ecosystem services provisioning

The 23 ecosystem services metrics were reduced into four principal components explaining 79% of the cumulative variance (Table 4). Multivariate provisioning of ecosystem services, as measured by the four rotated principal components, varied significantly with levels of sediment delivery, but the magnitude and direction of effect depended on distance from shore (MANOVA; sediment delivery $\times$ distance interaction; Wilk's $\lambda=0.919$, $F_{2,4991}=26.7$, $p<0.001$). Moreover, the interaction of sediment delivery and distance to shore was significant for all four of the principal components, as tested with univariate ANOVAs

following the MANOVA (PC1: $F_{2,4991}=63.3$, $p<0.001$; PC2: $F_{2,4991}=14.4$, $p<0.001$; PC3: $F_{2,4991}=20.2$, $p<0.001$; PC4: $F_{2,4991}=2.6$, $p<0.001$). In general, the four principal components can be summarized by the similarity of their response to sediment delivery as three groups of ecosystem services metrics — i) metrics positively correlated with PC1 or PC3 that had strong negative relationships with sediment, ii) metrics negatively correlated with PC1 or positively correlated with PC4 that were higher with increasing sediment, and iii) metrics positively correlated with PC2 that had relatively weak relationships with sediment (Table 4). Representative ecosystem services metrics for each group are mapped in Fig. 4.

Ecosystem services metrics positively correlated with PC1 or PC3 had strong, negative relationships with sediment delivery, although the strength of the effect varied among inshore, midshore, and offshore locations for each of the principal components (Fig. 5). Together these two groups represented the majority of reef-based ecosystem services where coral cover was a primary input (Table 4). PC1 was positively correlated with reef recreation (value of a dive, dive site favorability, density of *E. striatus* on reefs), as well as bioprospecting potential and the State of the Reef Index (SOR). Ecosystem services positively correlated with PC1 were significantly lower under both medium and high sediment delivery inshore and midshore, and lower only under high sediment delivery at offshore locations (Fig. 5, PC1). PC3 was also positively correlated with reef recreation (sand generation, ease of access on the reef) as well as the value of finfish and pharmaceutical products on reefs. Provisioning of this grouping of ecosystem services declined significantly with increasing sediment delivery at inshore locations, but declined only with high sediment delivery at midshore and offshore locations, with the weakest effect of sediment at midshore locations (Fig. 5, PC3).

Ecosystem services metrics negatively correlated with PC1 and positively correlated with PC4 tended to be higher under increasing levels of sediment delivery. Metrics negatively correlated with PC1 primarily included fisheries production metrics based on a variety of habitats such as mangroves, seagrass, sand, and macroalgae, in addition to coral reefs (density of *S. gigas*, curios production; Table 4). These off-reef based ecosystem services tended to be higher under medium and high sediment delivery than lower sediment delivery at inshore and midshore locations, and highest under high sediment delivery in offshore locations (Fig. 5, PC1; note negative correlation with PC1 means graph depicts inverse of pattern). The relationship in general was stronger for *S. gigas* than curios production, which also weakly positively loaded onto PC3 reflecting weaker relationships with sediment midshore and offshore. Metrics positively correlated with PC4, including key commercial fish biomass and Simplified Reef Health Index (SIRHI), tended to be highest under high sediment delivery for all distances from shore, with the weakest effect midshore (Fig. 5, PC4).

The remaining principal component, PC2, had weak relationships with sediment delivery (Fig. 5). PC2 was positively correlated with shoreline protection metrics based on biophysical wave height models (wave height attenuation, wave energy attenuation, wave energy attenuation by reef height, decrease in erosion, and decrease in wave run-up; Table 4). PC2 was the only principal component for which inshore estimates were consistently and

substantially greater than offshore across all sediment delivery conditions (Fig. 5, PC2). Shoreline protection metrics associated with PC2 were not significantly affected by sediment delivery at either inshore or offshore locations, although there was a slight increase for midshore locations under high sediment delivery.

Discussion

We extended existing predictive mapping methods and ecological production functions to translate coral reef condition into estimates of ecosystem services, and linked the provisioning of these services to sediment delivery in Puerto Rico. While sediment impairs multiple life stages of coral reef organisms (Fabricius, 2005), linking this manageable watershed stressor to the goods and services stakeholders value has previously been only conceptual (Apitz, 2012). We found that high terrigenous sediment delivery was associated with decreased provisioning of most reef-based ecosystem services, although there were some positive relationships with shoreline protection and services based on inshore habitats such as mangroves and seagrass. Differences among ecosystem services may indicate potential tradeoffs between services and the need to consider inshore habitats that provide important connections between habitats, nursery habitat for commercially important fisheries, ease of access for recreation, and possible sediment storage or buffering capacity (McLeod and Salm, 2006; Mumby, 2006).

We applied existing methods to map coral reef condition for the continuous, nearshore area surrounding Puerto Rico. Although field survey data were restricted to the southern coast of Puerto Rico, we were able to validate the predictions using geographically independent data. Resource managers and local decision makers are often challenged to make complex decisions with limited information. Mapping an entire region from spatially limited field survey data along with publicly available remote sensing data and open source mapping and statistical software can work within budget constraints to determine ecological relationships without the additional time and cost of field data collection (Knudby et al., 2013; Pittman and Brown, 2011). Mapping ecosystem services can identify and focus management strategies on areas with high provisioning, diversity of services, or rare services (Knudby et al., 2010). This could be complemented by mapping the demand of ecosystem services to identify decision-making priorities (Crossman et al., 2013).

Ecosystem services production function estimates of ecological integrity, bioprospecting discovery, and shoreline protection based on biophysical models were largely comparable to independent maps of areas where we expected ecosystem services to be high. These results are comparable to St. Croix where the same ecosystem services metrics were compared to similar independent data (Yee et al., 2014). Validation of production function estimates for recreational opportunities and fisheries production was more variable, although metrics based largely on coral attributes tended to be correlated with one another, and produced distinct spatial patterns from metrics based on non-reef habitats. Fisheries production metrics based on reef habitat or mangrove connectivity tended to best match observed areas of high commercial fishing effort. However, observational data on commercial fishing effort may be less relevant for validating metrics of curios and jewelry production, or might even be negatively correlated with key commercial fish biomass. Indeed, key commercial fish

biomass had better predictive accuracy when compared to point survey data on actual fish biomass. Metrics of recreational opportunities based on multiple coral and fish attributes (*i.e.*, dive value and dive favorability) tended to reflect observed areas popular for diving and snorkeling better than metrics based primarily on habitat coverages (e.g., opportunity for snorkeling) or distance to shore (visitation to dive sites). This contrasted results for St. Croix (Yee et al., 2014), and may reflect true differences in recreational preferences or may reflect differences in how observations of popular dive sites were defined in each location.

Ecosystem services provisioning was significantly related to sediment delivery, even after accounting for distance to shore. Ecosystem services based on coral reef habitat or multiple coral reef attributes, including reef-based recreational opportunities, reef-based fishing, reef-based pharmaceutical products, and the State of the Reef Index, were significantly lower in locations with medium to high levels of sediment delivery. In general, inshore locations tended to be more severely impacted by increasing sediment delivery than midshore or offshore locations, with midshore locations typically showing the weakest response to sediment delivery. Inshore locations also typically had the highest provisioning of reef-based ecosystem services, at least under low sediment delivery, followed by offshore locations under either low or medium sediment delivery. This variability could be attributed to differences in habitat and species composition with increasing depth at increasing distances from shore. For instance, in southwest Puerto Rico *Acropora* spp. were most abundant in shallow habitats while *Orbicella* spp. (formerly *Montastraea* spp.) were more dominant at intermediate depths (Ballantine et al., 2008). Higher diversity at highly connected nearshore habitats and offshore shelf-edge locations may contribute to overall higher ecosystem services provisioning, but also increase vulnerability to sediment delivery. Coral reef ecosystem services in the Caribbean may be especially vulnerable to a loss of species diversity, as few species have similar ecological functions (Micheli et al., 2014).

Shoreline protection estimates based on biophysical models were consistently highest, and unaffected by sediment delivery, at inshore locations. Estimates of shoreline protection were slightly higher under high sediment delivery at midshore locations, although still well below the levels of shoreline protection at inshore locations. Biophysical models of shoreline protection are largely driven by subtle changes in reef depth relative to the height of surface waves, and may reflect more accurate representations of wave attenuation than models based predominantly on attributes of coral cover (CRPI, wave energy dissipation by reef), which did decline significantly with increasing sediment delivery. However, wave energy dissipation by off-reef habitats, including mangroves and seagrasses, was estimated to be higher under higher levels of sediment delivery. In addition to wave energy dissipation by off-reef habitats, provisioning of recreational, fisheries production, and pharmaceutical services based on off-reef habitats such as mangroves and seagrasses tended to be higher under increasing levels of sediment delivery, particularly at inshore or offshore locations. Commercial fish biomass was also associated with mangrove and seagrass habitats, and consequently tended to be higher in areas of high sediment. Similarly, the Simplified Integrated Reef Health Index (SIRHI) included commercial fish biomass as a component of reef integrity and tended to be higher in areas of high sediment.

The higher estimates of shoreline protection, recreational opportunities, and fisheries production on off-reef habitats in locations of highest sediment delivery was predominantly driven by the spatial distribution of mangrove and seagrass habitats, which had a tendency to co-occur with areas of high sediment. Mangrove habitats, in particular, may benefit from sediment as long as it is not excessive or highly contaminated (Gilman et al., 2008), and have been demonstrated to trap and retain sediment (Ballantine et al., 2008), and are more tolerant of either seagrasses or coral reefs to changes in water quality (Orth et al., 2006). In areas where coral reefs are impacted by excessive sediment delivery, mangroves and seagrasses may help to buffer potential negative socio-economic effects by contributing to alternative recreational opportunities, additional shoreline protection, and juvenile nursery habitat for valuable commercial fisheries (Aguilar-Perera and Appeldoorn, 2008; Mumby, 2006). Our spatial analysis, however, does not account for potential changes over time due to excessive sediment that might reduce overall ecosystem services production. Furthermore, our results illustrate that alternative metrics can lead to different predictions of impacts of sediment delivery on ecosystem services. For Puerto Rico, observed chartered dive visits and areas of commercial fishing activity were predominantly correlated with metrics based on reef habitats, not seagrass or mangroves. Depending on the location, decision context, and specific needs of stakeholders, the ability of these non-reef ecosystems to provide alternative recreational or fishing opportunities may or may not be relevant.

Worldwide, sediment runoff is a significant local threat to coral reefs (Burke et al., 2011; Fabricius, 2005). Puerto Rico's mountainous watersheds, high intensity storms, and history of land clearing for agriculture and urban development contribute to high sediment loads, along with contaminants and nutrient pollution (Whitall et al., 2013), associated with extensive reef degradation (Warne et al., 2005). Besides excessive sediment, reef-based ecosystem services are likely to be affected by multiple, interacting stressors such as increased storm frequency, warming water temperatures, and increases in pathogens (Ban et al., 2014; MEA, 2005). However under effective and adaptive management, key ecosystem services may be able to be maintained even under uncertain or changing ecological condition (Kroon et al., 2014; Rogers et al., 2014). Across the Caribbean, reefs in areas with well-managed fisheries and coastal development (including Bermuda, Grand Cayman, Curaçao, and Flower Garden Banks) were more resilient in recovering from extreme heating events and hurricanes (Jackson et al., 2014). However, coral mortality in the U.S. Virgin Islands and Puerto Rico were among the most affected by extreme heating events despite greater temperature stress in the southern Caribbean, possibly due to greater macroalgal abundance and subsequent coral disease (Jackson et al., 2014). As thermal stress, coral bleaching, storms, and ocean acidification become more severe, managing local threats to coral reefs may be key to maintaining the supply of vital ecosystem services (Kroon et al., 2014).

Conclusions

Integration of available scientific information, stakeholder values, and the consequences of potential management actions is key to formal decision making frameworks (Yee et al., 2015). Coral reef monitoring is rarely spatially complete, representative of available habitats, and temporally consistent, which inhibits effective management (Burke et al., 2011). The

methods applied in this research are widely transferable to coastal communities with limited field monitoring data and the need to translate ecological endpoints to better reflect stakeholder values. Puerto Rico, like many coastal communities, has high sediment loads due to development, agriculture, and industry. With an important but not exclusive reef tourism industry, decision makers are required to balance diverse and sometimes competing objectives. Decision making can be more effective by incorporating stakeholder values into formal and transparent frameworks that link scientific information to identify tradeoffs and evaluate potential consequences among alternatives (Gregory et al., 2012; Yee et al., 2015).

Our results indicate that excessive terrestrial sediment decreases the provisioning of most reef-based services regardless of distance to shore. However, sediment delivery was positively related to ecosystem services for which mangroves and seagrasses provided a significant contribution. This suggests tradeoffs among services and the importance of coastal habitats such as mangroves and seagrass for habitat connectivity, nursery habitats, ease of access, and sediment buffering should not be overlooked in the valuation of coral reef ecosystem services. Tradeoffs among ecosystem services are inherent and management decisions directed at one ecosystem service can have positive and negative effects on multiple services simultaneously (Butler et al., 2013). Incorporating ecosystem services into coastal management decisions can identify potential conflicts or prioritize decisions that can have benefits for multiple services (Needles et al., 2015). However, our results show that alternative metrics can lead to very different predictions, demonstrating why it is an important part of any decision-making process to clarify stakeholder objectives and define appropriate indicators (Gregory et al., 2012).

Ecosystems services in combination with ecological and economic assessments can improve decision making outcomes for ecosystem conservation and restoration (Yoskowitz and Russell, 2015). Management actions that use the best available scientific information to promote goods and services valued by stakeholders and communities are necessary to maintain the supply of coral reef ecosystem services. Integrated into coastal decision making, the relationships we have identified between sediment delivery and ecosystem services can support decisions to ensure continued provisioning of coral reef ecosystem services and the well-being of coastal communities.

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Fig. 1.

Summary of methods used to translate point survey data of coral condition to gridded spatial maps of predicted coral condition, map predicted ecosystem services provisioning and validate it against observational data, and analyze relationships between sediment delivery and ecosystem services.

Fig. 2.

Maps of a) locations of 2007 – 2011 NOAA and 2010 – 2011 EPA point surveys used for predictive models of reef condition and evaluation of bioprospecting discovery and habitat-based fisheries ecosystem services and b) independent maps used to validate predicted ecosystem services metrics include presence of a marine protected area, areas with highest wave energy attenuation predicted by SWAN model, areas with highest average chartered divers or snorkelers per week, and areas with highest commercial fishing visits per year.

Fig. 3. Map of Summit-to-Sea modeled sediment delivery for Puerto Rico NOAA (NOAA, 2004) where unitless values of sediment delivery are categorized as low (0 – 25% quantile; sediment delivery=0), medium (25 – 75% quantile; sediment delivery=1 – 9,932), and high (75 – 100% quantile; sediment delivery=9,933 – 327,058). To maximize figure size, Mona Island is shifted east of true location.

Fig. 4.

Maps of a representative subset of predicted ecosystem services, as determined by PC loadings (Table 4): (a) positive correlations with PC1 represented by value of a dive, (b) negative correlations with PC1 represented by density of *S. gigas*, (c) PC2 represented by wave energy attenuation (%), (d) PC3 represented by value of finfish on reef, (e) positive correlations with PC4 represented by the Simplified Reef Health Index. To maximize figure size, Mona Island is shifted east of true location.

Fig. 5.
Mean ecosystem services provisioning by sediment delivery and distance to shore for principal components with a varimax rotation (see Table 4 for principal component loadings)

Table 1

Methods applied to translate reef condition to estimates of relative ecosystem services provisioning. Equations are described in detail by Yee et al. (2014).

Ecosystem service	Equation
Simplified Reef Health Index (SIRHI)	$\sum_i G_i$ where G are the grades (1 – 5) for each habitat type i based on: coral cover (<5, 5 – 10, 10 – 20, 20 – 40, 40%), macroalgae cover (>25, 12 – 25, 5 – 12, 1 – 5, <1 %), herbivorous fish biomass (<960, 960 – 1920, 1920 – 2880, 2880 – 3480, 3480 g/100 m ²), and commercial fish biomass (<420, 420 – 840, 840 – 1260, 1260 – 1680, 1680 g/100 m ²); (Turner et al., 2000)
State of the Reef Index (SOR)	$0.30C_{coral} + 0.15C_{macroalgae} + 0.15R_{fish} + 0.20R_{coral} + 0.20A_{fish}$ where C is cover (%), R is species richness, A is abundance/100 m ² , and numeric weights are from expert judgment originally developed for Hawaii (van Beukering and Cesar, 2004)
Relative wave energy dissipation	$\sum_i c_i M_i$ where c_i is the fraction of area for each habitat type i and M_i is the relative magnitude of wave energy dissipation for each habitat type i on a scale of 0 – 3: mangroves=3, dense seagrass=0, medium density seagrass=0, sparse seagrass=0, sand=0, macroalgae=0, patch reef=0, $A. palmata$ =3, gorgonians=2, $Montastraea$ =2. Wave energy dissipation by reef is calculated with only reef habitats (patch reef, $A. palmata$, gorgonians, $Montastraea$); (Mumby et al., 2008)
Coral Reef Protection Index (CRPI)	$\sum G_i * 0.4$ where G are grades (1 – 4) for each habitat type i based on: reef type (other, fringe, patch, barrier), reef distribution (discontinuous or continuous), and reef distance (>1 km, 0.5 – 1 km, 250 – 500 km, <250 km); (Burke et al., 2008)
Wave height attenuation (%)	$-\frac{f_w}{3\pi} \frac{H_{rs}^2}{(\bar{\eta}_r + h_r + \eta_w)^2}$ where f_w is wave bottom frictional factor, H_{rs} is significant wave height (m), $\bar{\eta}_r$ is wave set-up on reef flat (m), h_r is water depth on reef flat (m), and η_w is meteorological surge (m); (Sheppard et al., 2005)
Wave energy attenuation (%)	$\frac{1}{8} \rho g H^2$ where ρ is density of seawater (1025 kg/m ³), g is gravitational acceleration (9.81 m/s ²), and H is wave height attenuation (%); (Sheppard et al., 2005)
Wave energy attenuation (%) by reef type	$\frac{1}{8} \rho g H^2$ where ρ is density of seawater (1025 kg/m ³), g is gravitational acceleration (9.81 m/s ²), and H is Sheppard et al. (2005) wave height attenuation (%) where f_w is estimated according to coral reef type, based on depth (8 m or >8 m), distance (1/50 m or >1/50 m), and coral density (low or high); (van Beukering et al., 2011)
Wave energy attenuation (%) by reef height	$\frac{1}{8} \rho g H^2$ where ρ is density of seawater (1025 kg/m ³), g is gravitational acceleration (9.81 m/s ²), and H is Sheppard et al. (2005) wave height attenuation (%) where f_w is estimated by coral rugosity (standard deviation in colony heights (σ_r); (Lowe, 2005)
Decrease in erosion (%)	$\frac{H_0^{2.5}}{1 - (\frac{H}{H_0})}$ where H_0 is wave height attenuation (%) due to the presence of the reef and H is wave height in the absence of the reef (CETS, 1987; Dean and Galvin, 1976)
Decrease in wave run-up (%)	$H \frac{\tan^{\alpha}}{\sqrt{H/H_0}}$ where α is beach slope angle, H is nearshore wave height and H_0 is offshore wave height (FEMA, 2007; Hughes, 2004)
Relative ease of access for education	$\sum_i c_i M_i$ where c_i is the fraction of area for each habitat type i and M_i is the relative magnitude of ease of access for each habitat type i on a scale of 0 – 3: mangroves=3, dense seagrass=3, medium density seagrass=3, sparse seagrass=1, sand=1, macroalgae=1, patch reef=3, $A. palmata$ =2, gorgonians=1, $Montastraea$ =1. Ease of access for education on reef is calculated with only reef habitats (patch reef, $A. palmata$, gorgonians, $Montastraea$); (Mumby et al., 2008)
Relative sand generation	$\sum_i c_i M_i$ where c_i is the fraction of area for each habitat type i and M_i is the relative magnitude of sand generation for each habitat type i on a scale of 0 – 3: mangroves=0, dense seagrass=0, medium density seagrass=0, sparse seagrass=0, sand=0, macroalgae=2, patch reef=1, $A. palmata$ =3, gorgonians=1, $Montastraea$ =3. Sand generation by reef is calculated with only reef habitats (patch reef, $A. palmata$, gorgonians, $Montastraea$); (Mumby et al., 2008)

Ecosystem service	Equation
Relative density of <i>E. striatus</i>	$\sum_i c_i M_i$
Relative opportunity for snorkeling	$\sum_i c_i M_i$
Relative value of a dive	$0.1227(S_{coral} + S_{fish} + A_{coral} + A_{fish}) + 0.0565V$
Relative dive site favorability	$\sum_i p_i R_i$
Visitation to dive sites (boats/site)	$2.897 + (0.0701 * coral\ cover) - (0.133 * dive\ time_{hrs})$
Visitation to dive sites (boats/site) with topography	$2.897 + (0.0701 * coral\ cover) - (0.133 * dive\ time_{hrs}) + (0.0417 * topography)$
Relative density of <i>P. argus</i>	$\sum_i c_i M_i$
Relative density of <i>S. gigas</i>	$\sum_i c_i M_i$
Relative presence of <i>Eucheuma</i> spp.	$\sum_i c_i M_i$
Relative value of finfish	$\sum_i c_i M_i$
Relative production of curios and jewelry	$\sum_i c_i M_i$
Mangrove connectivity	$D - \sqrt{\left(m_{ix} - r_{ix} \right)^2 + \left(m_{iy} - r_{iy} \right)^2}$
Key commercial fish biomass	$\sum_i B_i$

where c_i is the fraction of area for each habitat type i and M_i is the relative magnitude of *E. striatus* for each habitat type i on a scale of 0 – 3: mangroves=3, dense seagrass=1, medium density seagrass=1, sparse seagrass=0, sand=0, macroalgae=3, patch reef=0, *A. palmata*=0, gorgonians=3, *Montastraea*=3. Density of *E. striatus* on reef is calculated with only reef habitats (patch reef, *A. palmata*, gorgonians, *Montastraea*); (Mumby et al., 2008)

where c_i is the fraction of area for each habitat type i and M_i is the relative magnitude of snorkeling for each habitat type i on a scale of 0 – 3: mangroves=0, dense seagrass=0, medium density seagrass=0, sparse seagrass=1, sand=3, macroalgae=1, patch reef=3, *A. palmata*=2, gorgonians=1, *Montastraea*=3. Opportunity for snorkeling on reef is calculated with only reef habitats (patch reef, *A. palmata*, gorgonians, *Montastraea*); (Mumby et al., 2008)

where S is richness, A is abundance/m², and V is water visibility (m); (Wielgus et al., 2003)

where p_i is the proportion of respondents indicating each attribute i that positively affected dive enjoyment and R_i is the mean relative magnitude for fish attributes (fish schools and fish richness) and coral attributes (coral cover, rubble cover, coral richness, and standard deviation of coral heights); (Uyarra et al., 2009)

where *dive time* is estimated as distance to shore * 5 knot boat speed (Pendleton, 1994)

where *topography* is the standard deviation in depth among grid cells within 150 m that are greater than 75th percentile of all grid cells (Pendleton, 1994)

where c_i is the fraction of area for each habitat type i and M_i is the relative magnitude of *P. argus* for each habitat type i on a scale of 0 – 3: mangroves=3, dense seagrass=3, medium density seagrass=2, sparse seagrass=0, sand=0, macroalgae=3, patch reef=3, *A. palmata*=1, gorgonians=1, *Montastraea*=3. Density of *P. argus* on reef is calculated with only reef habitats (patch reef, *A. palmata*, gorgonians, *Montastraea*); (Mumby et al., 2008)

where c_i is the fraction of area for each habitat type i and M_i is the relative magnitude of *S. gigas* for each habitat type i on a scale of 0 – 3: mangroves=0, dense seagrass=3, medium density seagrass=3, sparse seagrass=3, sand=3, macroalgae=1, patch reef=1, *A. palmata*=1, gorgonians=1, *Montastraea*=0. Density of *S. gigas* on reef is calculated with only reef habitats (patch reef, *A. palmata*, gorgonians, *Montastraea*); (Mumby et al., 2008)

where c_i is the fraction of area for each habitat type i and M_i is the relative magnitude of *Eucheuma* spp. for each habitat type i on a scale of 0 – 3: mangroves=0, dense seagrass=2, medium density seagrass=3, sparse seagrass=3, sand=1, macroalgae=0, patch reef=1, *A. palmata*=0, gorgonians=0, *Montastraea*=0. Presence of *Eucheuma* spp. on reef is calculated with only reef habitats (patch reef, *A. palmata*, gorgonians, *Montastraea*); (Mumby et al., 2008)

where c_i is the fraction of area for each habitat type i and M_i is the relative magnitude of finfish for each habitat type i on a scale of 0 – 3: mangroves=1, dense seagrass=1, medium density seagrass=1, sparse seagrass=2, sand=1, macroalgae=2, patch reef=1, *A. palmata*=3, gorgonians=1, *Montastraea*=3. Value of finfish on reef is calculated with only reef habitats (patch reef, *A. palmata*, gorgonians, *Montastraea*); (Mumby et al., 2008)

where c_i is the fraction of area for each habitat type i and M_i is the relative magnitude of curio production for each habitat type i on a scale of 0 – 3: mangroves=0, dense seagrass=2, medium density seagrass=3, sparse seagrass=2, sand=0, macroalgae=1, patch reef=3, *A. palmata*=1, gorgonians=1, *Montastraea*=3. Production of curios and jewelry by reef is calculated with only reef habitats (patch reef, *A. palmata*, gorgonians, *Montastraea*); (Mumby et al., 2008)

where D is maximum migratory distance (10 km) between mangrove (m) and reef (r) grid cells, $|m_x - r_x|$ is longitude between cells, and $|m_y - r_y|$ is latitude between cells (Mumby, 2006)

where B is biomass (g/100 m²) of commercial fish groups i : snappers and groupers (HRI, 2010)

Ecosystem service	Equation
Bioprospecting potential	Directly proportional to State of the Reef Index (Principe et al., 2012)
Sponge richness	Morphological richness estimated using regression tree (Table 2); (Hunt and Vincent, 2006)
Relative potential for pharmaceutical products	$\sum_i c_i M_i$ where c_i is the fraction of area for each habitat type i and M_i is the relative magnitude of pharmaceutical products for each habitat type i on a scale of 0 – 3: mangroves=3, dense seagrass=1, medium density seagrass=1, sparse seagrass=0, sand=0, macroalgae=1, patch reef=1, <i>A. palmata</i> =1, gorgonians=1, <i>Montastraea</i> =3. Pharmaceutical products by reef is calculated with only reef habitats (patch reef, <i>A. palmata</i> , gorgonians, <i>Montastraea</i>); (Mumby et al., 2008)

Table 2

Summary of predictive models of reef condition from regression trees fitted to EPA or NOAA survey data, including the number of nodes in the most parsimonious tree, goodness of model fit (R^2), and classification accuracy (AUC) for both model data and independent, model validation data

Variable	Data source	Nodes	Fitted model		Validation
			R^2	AUC	AUC
Sand + fine sediments (% cover)	NOAA	4	0.33 ***	0.77	0.82
Rubble (% cover)	NOAA	3	0.05 ***	0.91	0.91
Hardbottom (% cover)	NOAA	4	0.38 ***	0.75	0.66
Seagrass (% cover)	NOAA	3	0.38 ***	0.89	0.88
Macroalgae (% cover)	NOAA	3	0.11 ***	0.74	0.76
Gorgonians (% cover)	NOAA	3	0.23 ***	0.73	0.70
Live hardcoral (% cover)	EPA	3	0.38 ***	0.75	0.87
Live hardcoral cover / total hardcoral cover	EPA	2	0.11 ***	0.79	0.79
<i>Montastraea</i> cover / total hardcoral cover	EPA	3	0.38 ***	0.86	0.81
<i>Acropora palmata</i> cover / total hardcoral cover	EPA	3	0.29 ***	0.80	0.94
Sponge richness/m ²	NOAA	3	0.34 ***	0.52	0.81
Coral abundance/100 m ²	EPA	6	0.53 ***	0.69	0.62
Coral richness/transect area	EPA	3	0.34 ***	0.74	0.79
Standard deviation in coral heights	EPA	3	0.24 ***	0.80	0.79
Fish richness/100 m ²	NOAA	5	0.48 ***	0.59	0.75
Fish abundance/100 m ²	NOAA	3	0.31 ***	0.91	0.90
Fish schools	NOAA	2	0.13 ***	0.65	0.69
Key herbivorous fish biomass (g/100 m ²)	NOAA	3	0.22 ***	0.79	0.69
Key commercial fish biomass (g/100 m ²)	NOAA	7	0.20 ***	0.80	0.74

p < 0.001

*
p < 0.05

NS
not significant

Table 3

Summary of predicted ecosystem services for Puerto Rico across the entire spatial study area, and results of one-tailed T-tests evaluating whether each metric was significantly greater in areas where we a priori predicted ecosystem services would be higher.

Ecosystem service	Min.	Mean	Max.	T-statistic	Validation data
<i>Ecosystem integrity</i>					
Simplified Reef Health Index (SIRHI) [†]	1.25	1.84	4.00	5.75 ^{***}	Marine Protected Area
State of the Reef Index (SOR) [†]	0.01	0.33	0.80	7.00 ^{***}	Marine Protected Area
<i>Shoreline protection</i>					
Wave energy dissipation [†]	0.02	0.09	2.06	1.15 ^{NS}	SWAN model
Wave energy dissipation by reef [†]	0.01	0.07	0.75	-9.11 ^{NS}	SWAN model
Coral Reef Protection Index (CRPI) [†]	0.00	0.58	3.20	-0.78 ^{NS}	SWAN model
Wave height attenuation (%)	0.00	0.55	77.84	3.48 ^{***}	SWAN model
Wave energy attenuation (%)	0.00	0.86	93.54	3.70 ^{***}	SWAN model
Wave energy attenuation (%) by reef type	0.00	2.95	95.50	1.74 [*]	SWAN model
Wave energy attenuation (%) by reef height	0.00	1.34	94.67	5.77 ^{***}	SWAN model
Decrease in erosion (%)	0.00	1.17	97.69	3.97 ^{***}	SWAN model
Decrease in wave run-up (%)	0.00	0.29	52.92	3.29 ^{***}	SWAN model
<i>Recreational opportunities</i>					
Ease of access for education [†]	0.35	1.08	2.36	-4.75 ^{NS}	Chartered dives
Ease of access for education on reef [†]	0.08	0.38	1.61	2.31 [*]	Chartered dives
Sand generation [†]	0.16	0.56	1.30		None available
Sand generation by reef [†]	0.04	0.17	0.96		None available
Density of <i>E. striatus</i> [†]	0.24	0.72	2.26	-4.99 ^{NS}	Chartered dives
Density of <i>E. striatus</i> on reef [†]	0.02	0.09	0.73	2.05 [*]	Chartered dives
Opportunity for snorkeling [†]	0.55	1.84	2.53	-3.98 ^{NS}	Chartered dives
Opportunity for snorkeling on reef [†]	0.10	0.40	1.68	1.63 ^{NS}	Chartered dives
Value of a dive [†]	2.28	3.76	7.04	6.55 ^{***}	Chartered dives
Dive site favorability [†]	0.03	0.33	0.95	7.66 ^{***}	Chartered dives
Visitation to dive sites (boats/site)	3.24	3.61	6.84	-4.22 ^{NS}	Chartered dives
Visitation to dive sites with topography (boats/site)	3.24	3.51	6.89	-1.35 ^{NS}	Chartered dives
<i>Fisheries production</i>					
Density of <i>P. argus</i> [†]	0.37	1.05	2.41	1.12 ^{NS}	NOAA 2007 – 2011
Density of <i>P. argus</i> on reef [†]	0.10	0.40	1.68	0.10 ^{NS}	NOAA 2007 – 2011

Ecosystem service	Min.	Mean	Max.	T-statistic	Validation data
Density of <i>S. gigas</i> [†]	0.46	1.67	2.46	2.73 [*]	NOAA 2007 – 2011
Density of <i>S. gigas</i> on reef [†]	0.03	0.13	0.53	-3.00 ^{NS}	NOAA 2007 – 2011
Density of <i>E. striatus</i> [†]	0.24	0.72	2.26	-10.24 ^{NS}	Commercial fishing
Density of <i>E. striatus</i> on reef [†]	0.02	0.09	0.73	7.81 ^{***}	Commercial fishing
Presence of <i>Eucheuma</i> spp. [†]	0.15	0.64	1.28	-2.13 ^{NS}	NOAA 2007 – 2011
Presence of <i>Eucheuma</i> spp. on reef [†]	0.02	0.11	0.52	1.30 ^{NS}	NOAA 2007 – 2011
Value of finfish [†]	0.37	1.04	1.51	-5.55 ^{NS}	NOAA 2007 – 2011
Value of finfish on reef [†]	0.04	0.17	0.96	3.38 ^{***}	NOAA 2007 – 2011
Production of curios and jewelry [†]	0.17	0.69	1.93	7.75 ^{***}	Chartered dives
Production of curios and jewelry by reef [†]	0.10	0.40	1.68	1.42 ^{NS}	Chartered dives
Mangrove connectivity [†]	0.00	585.03	7222.25	9.81 ^{***}	Commercial fishing
Key commercial fish biomass (g/100m ²)	188.48	402.68	2940.49	8.60 ^{***}	NOAA 2007 – 2011
<i>Bioprospecting discovery</i>					
Bioprospecting potential [†]	0.01	0.33	0.80	7.48 ^{***}	NOAA 2007–2011
Sponge richness (#/m ²)	0.74	1.16	1.81	9.91 ^{***}	NOAA 2007–2011
Pharmaceutical products [†]	0.14	0.41	2.11	-5.22 ^{NS}	NOAA 2007–2011
Pharmaceutical products by reef [†]	0.04	0.17	0.66	5.11 ^{***}	NOAA 2007–2011

p < 0.001

*
p < 0.05

NS
not significant

[†]
relative score (unitless index)

Table 4

Loadings of principal components with varimax rotation. Loadings less than |0.4| are omitted.

Ecosystem service	PC1	PC2	PC3	PC4
Simplified Reef Health Index (SIRHI)				0.9
State of the Reef Index (SOR)	0.7		0.45	
Wave height attenuation (%)		0.98		
Wave energy attenuation (%)		0.98		
Wave energy attenuation (%) by reef type	0.57			
Wave energy attenuation (%) by reef height		0.82		
Decrease in erosion (%)		0.99		
Decrease in wave run-up (%)		0.97		
Ease of access for education on reef			0.88	
Sand generation			0.64	
Sand generation by reef	0.41		0.87	
Density of <i>E. striatus</i> on reef	0.71			
Value of a dive	0.82			
Dive site favorability	0.88			
Density of <i>S. gigas</i>	−0.91			
Density of <i>E. striatus</i> on reef	0.41		0.87	
Value of finfish on reef	−0.61		0.57	
Production of curios and jewelry				
Mangrove connectivity				0.91
Key commercial fish biomass	0.81			
Bioprospecting potential	0.4		0.88	
Sponge richness				0.9
Pharmaceutical products by reef	0.7		0.45	
Eigenvalue	5.46	4.73	4.60	1.81
Total variance (%)	26	23	22	9
Cumulative Variance (%)	26	49	70	79