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Terrestrial degradation impacts on coral reef health: Evidence from the Caribbean

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Abstract

Coral reefs are in decline worldwide. While coral reef managers are limited in their ability to tackle global challenges, such as ocean warming, managing local threats can increase the resilience of coral reefs to these global threats. One such local threat is high sediment inputs to coastal waters due to terrestrial over-grazing. Increases in terrestrial sediment input into coral reefs are associated with increased coral mortality, reduced growth rates, and changes in species composition, as well as alterations to fish communities. We used general linear models to investigate the link between vegetation ground cover and tree biomass index, within a dry-forest ecosystem, to coral cover, fish communities and visibility in the case study site of Bonaire, Caribbean Netherlands. We found a positive relationship between ground cover and coral cover below 10m depth, and a negative relationship between tree biomass index and coral cover below 10m. Greater ground cover is associated to sediment anchored through root systems, and higher surface complexity, slowing water flow, which would otherwise transport sediment. The negative relationship between tree biomass index and coral cover is unexpected, and may be a result of the deep roots associated with dry-forest trees, due to limited availability of water, which therefore do not anchor surface sediment, or contribute to surface complexity. Our analysis provides evidence that coral reef managers could improve reef health through engaging in terrestrial ecosystem protection, for example by taking steps to reduce grazing pressures, or in restoring degraded forest ecosystems.

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Keywords: sediment; environmental conservation; dry forest; island ecosystems; Bonaire.

1. Introduction

Coral reefs are declining worldwide, due to a range of global, regional and local drivers (Kennedy et al., 2013; Wilkinson, 1999). Globally, climate change-induced ocean warming is recognised as the most significant threat, and coral bleaching arising from ocean acidification threatens corals worldwide (Hughes et al., 2003). Regional threats, such as invasive species (Albins and Hixon, 2008), and local threats such as trawling, over fishing (McClanahan, 1995) or terrestrial sediment run-off (Álvarez-Romero et al., 2011; Fabricius, 2005; Klein et al., 2014; Risk, 2014; Rogers, 1990) also cause significant damage.

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Changes in terrestrial ecosystems can impact coral reefs through sediment and nutrient run-off. Run-off extent is determined by multiple watershed factors, including: soil type (Millward and Mersey, 1999; Renard et al., 2000); slope (Boer and Puigdefábregas, 2005; Millward and Mersey, 1999; Renard et al., 2000); urban development (Hunter and Evans, 1995); river and stream presence and length; land use (Hunter and Evans, 1995); and vegetation (Álvarez-Romero et al., 2011; Mateos-Molina et al., 2015; Risk, 2014; Rodgers et al., 2012). Vegetation impacts on sediment run-off varies by vegetation types, particularly ground cover and tree density. Vegetation ground cover anchors surface sediments, and slows water flow, therefore decreasing the amount of sediment dislodged by surface water (Bartley et al., 2014). Tree roots increase surface complexity through surface roots, which again slow water flow while also creating pools of water. The creation of pools is associated with increased water seeping into the soil, and therefore reduced sediment run-off (Bartley et al., 2014). Land use which changes vegetation cover and tree density or size, or alters soil surface structure such as through ploughing or laying of concrete, can therefore impact sediment run-off (Álvarez-Romero et al., 2011; Mateos-Molina et al., 2015; Risk, 2014; Rodgers et al., 2012). The impacts of sediment run-off on the marine system can also be altered by waves and currents, with sediments remaining in suspension for longer in higher energy environments, while currents may remove sediment from the coastal area (Rodgers et al., 2012).

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Increases in sediment run-off has negative impacts on coral reef ecosystems. Variation between species, and interactions with other reef threats, means that the threshold for damage by sediment is highly context specific (Fabricius, 2005), though some coral species show negative impacts at levels of 3mg/l of suspended particulate matter (Anthony and Fabricius, 2000). High sediment run-off can impact corals through both increasing suspended sediment, and through sedimentation. Suspended sediment increases water turbidity, reducing light availability. In reduced light coral growth rates are slowed (Fabricius, 2005; Pollock et al., 2014; Stender et al., 2014), coral morphology changes, and structural stability is compromised (Erftemeijer et al., 2012; Fabricius, 2005). High turbidity, often associated with increases in nutrient levels, leads to increases in macroalgae growth, which smother hard corals (De'Ath and Fabricius, 2010). Species richness is reduced, because those species most susceptible to low light levels, and competition with macroalgae, undergo disproportionate damage, leaving only tolerant species (De'Ath and Fabricius, 2010; Fabricius, 2005). Smothering of corals through sedimentation directly leads to coral mortality, due to restricting light penetration needed for photosynthesis (Erftemeijer et al., 2012; Weber et al., 2006). Smothering inhibits feeding polyps, reducing energy intake in heterotrophic corals (Erftemeijer et al., 2012), though these may see improvements for moderate increases in suspended sediment (De'Ath and Fabricius, 2010). Coral morphology changes to favour vertical or sloped, rather than horizontal, surfaces (Erftemeijer et al., 2012), morphology changes which also reduce area suited to light absorption, and can therefore increase the detrimental impacts of low light caused by suspended sediment. Coral recruitment decreases, as juvenile corals struggle to become established on high sediment substrates (Edmunds and Gray, 2014; Jones et al., 2015; Rogers, 1990). Mucus production is increased to provide protection from settling sediments, but also increases coral stress (Erftemeijer et al., 2012). Increased mucus production leads to heightened microbial activity on coral tissue surface, which contributes to anoxic conditions, damaging coral tissues (Weber et al., 2012, 2006). Furthermore, reefs under high sediment

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loads have unpredictable recovery (Rogers, 1990), and reduced ability to cope with future ocean warming (Maina et al., 2013; Risk, 2014), or algae invasion (Birrell et al., 2005).

Fish populations are also negatively impacted by both suspended sediments and sedimentation. Suspended sediments are related to more random habitat choices of fish larva, reducing survival and, due to preferences for remaining in clear waters, larva dispersal is restricted (Wenger et al., 2011). Predator-prey interactions are modified, with suspended sediments impacting visual recognition of prey, and interfering with chemical signals (Wenger et al., 2013). Fish increase mucus production in their gills in high sediment waters, reducing efficiency of oxygen uptake (Hess et al., 2015). Reduced oxygen uptake slows development of fish larva (Hess et al., 2015; Wenger et al., 2014), and restricts larval dispersal due to reduced energy availability (Hess et al., 2015). Sedimentation can have direct impacts on fish communities, with herbivorous fish negatively associated to high sedimentation (Goatley and Bellwood, 2012).

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Within the last 15 years an increasing number of studies have emerged highlighting the importance of conserving watersheds for coral reef conservation (Álvarez-Romero et al., 2011; Beger et al., 2010; Carroll et al., 2012; Cox et al., 2006; Klein et al., 2010; Makino et al., 2013; Tallis et al., 2008), and a number of models have been developed to identify erosion threats (Álvarez-Romero et al., 2014), or to integrate threat management between ecosystems (Cox et al., 2006; Klein et al., 2014, 2012, 2010; Tallis et al., 2008). Empirical studies have predominantly focused on the effects of losses in watershed vegetation directly on sediment run-off. For example, reductions in vegetation cover in a watershed increase erosion risk (Bartley et al., 2014, 2010; Maina et al., 2013; Mateos-Molina et al., 2015), and watershed development, such as increases in agriculture (Bartley et al., 2014; Begin et al., 2014; Carroll et al., 2012); land cleared for construction (Nemeth and Nowlis, 2001); and unpaved roads (Begin et al., 2014) correlate with increases in sediment run-off. But the direct link between watershed-wide ecosystem health and coral reef health (combined coral cover and species richness; abundance, diversity and biomass of fish) has been less widely studied. Relationships between watershed vegetation cover and reef health have been found in coral reefs in Hawaii, though this impact was dominated by the influence of reef characteristics (wave action; depth; and degree of shelter; Rodgers et al., 2012). Improvements in terrestrial conservation in Fiji were estimated to result in a 10% improvement in reef health (Klein et al., 2014), and increases in bleaching have been observed following increases in sediment caused by land clearing for construction (Nemeth and Nowlis, 2001). Palaeontological techniques have been used to estimate historical coral reef cover and species in Caribbean Panama (Cramer et al., 2012) and the Great Barrier Reef (Roff et al., 2012). Sediment cores in the Great Barrier Reef showed increases in sedimentation and nutrient levels following European settlement (Roff et al., 2012), and death assemblages of corals in both locations showed a decline in coral cover correlated to recorded land clearances (Cramer et al., 2012; Roff et al., 2012). Though the nature of these studies precludes testing of causation, as these declines were observed prior to ocean warming, acidification, or bleaching and disease events they suggests that land clearance may have led to coral decline as early as the 19th Century (Cramer et al., 2012; Roff et al., 2012).

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In this paper we investigate the link between watershed vegetation and coral reef health, using the coral reefs on the west coast of Bonaire, Caribbean Netherlands, as a case study. Building on previous studies, links between vegetation biomass and ground cover; and reef health are estimated, in terms of impacts on visibility (turbidity), coral and fish. The paper thus provides insights for watershed restoration programs, and adds to the limited empirical data linking the terrestrial ecosystem to reef health.

2. Methods

2.1 Case study site

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Bonaire, Caribbean Netherlands, is a special municipality of the Kingdom of the Netherlands, situated in the Southern Caribbean (12° 10' N 68° 17' W, Figure 1), with an area of 294km^2.

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Bonaire's terrestrial ecosystem is made up of tropical dry-forest, which receives an average of 500mm of rainfall per year. Rainfall is highest between October and March, and falls predominantly in short, heavy showers. Bonaire has no above ground rivers or streams, and only a single freshwater spring. The island is well known for its healthy coral reef (Steneck et al., 2015), but has a long history of terrestrial degradation, with invasive herbivores introduced in the 16th Century, and widespread tree felling in the early 1900s (Freitas et al., 2005; Westermann and Zonneveld, 1956). Such changes are recognised as threatening Bonaire's marine ecosystems, due to increases in sediment and nutrient run-off associated with reduced root systems in the terrestrial environment (Slijkerman et al., 2011; Wosten, 2013).

Figure 1. Location of Bonaire. Google Earth V 7.1.8.3036 (14/12/2015). Bonaire, Caribbean Netherlands. 12° 10' N 68° 17' W [25/07/2017].

As a fringing coral reef, the majority of Bonaire's corals are found within between 50m-100m offshore, though in some locations the reef is found almost immediately at the water's edge. An often sandy terrace, up to depths of approximately 8m, extends to a sharp drop off to around 12m, followed by a steep slope down to 50m-60m (Bak, 1977). Trade winds are consistent from the south east, and tides are small, at approximately 30cm. The coral reef is largely uniform along the leeward (west) side of the island. The windward (east) experiences large currents and

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wave action, and is therefore more infrequently dived and studied than the west (Bak, 1977). With no permanent above ground rivers or streams, the major input of sediment into Bonaire's coastal waters is expected to be diffuse run-off from land with rainfall, or to a smaller extent by wind.

Bonaire's economy is built on dive tourism, with direct tourist spending making up 16.4% of the island's GDP in 2014 (Statistics Netherlands, 2015). The island is internationally renowned for the quality of its coral reef (Sport Diver, 2016) and there is widespread understanding amongst government, NGOs and local residents of the need to protect Bonaire's reef system.

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2.2 Conceptual framework

Coral reef health is impacted by sediment run-off, which originates from associated watersheds. Rainfall increases sediment run-off rates through increasing surface water run-off which transports sediments from the terrestrial ecosystem. Steeper slopes are associated with increased run off. Coastal sediment levels can also be influenced by disturbance of marine sediments including divers entering the area and changes to currents or wave actions. Inputs from urban systems through sewage and run-off further increases sediment levels. Sediment run-off is decreased through the presence of a salina (salt water lake with direct connection to the sea), which traps sediment; and through the presence of vegetation, whose root systems anchor sediment and slow water flow. Soil type also impacts sediment run-off (Figure 2).

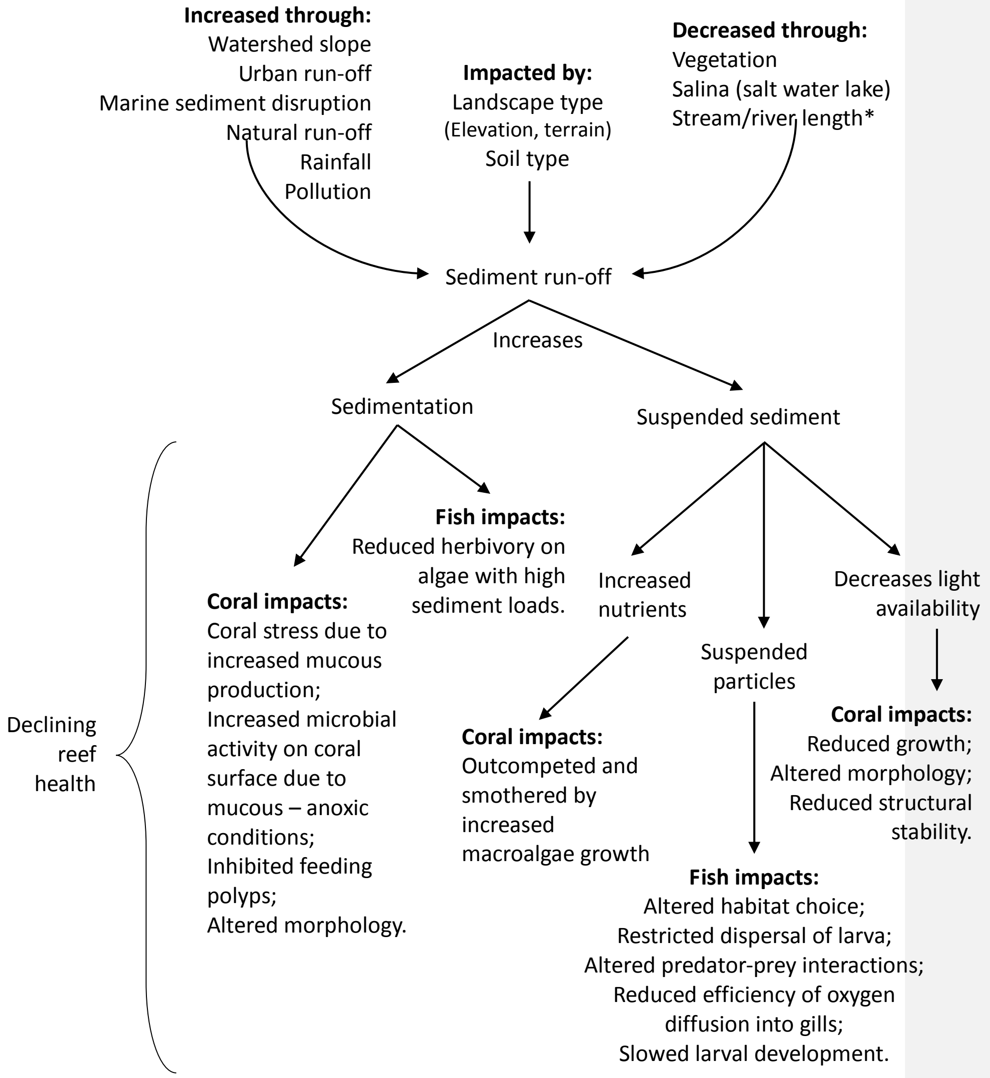

Figure 2. Conceptual model of impacts of watershed characteristics on sediment run-off, and therefore reef health. * not relevant to Bonaire as no streams/rivers present.

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2.3 Data Collection

2.3.1 Reef characteristics

Attributes for assessing reef health were identified following a review of the literature (DeMartini et al., 2013; Fabricius, 2005; Pollock et al., 2014; Risk, 2014; Rogers et al., 2014; Rogers, 1990; Schep et al., 2013; Uyarra et al., 2009), and communication with local dive operators. Final attributes to be considered were identified as: coral cover at 5m, and coral cover deeper than 10m; horizontal visibility; fish abundance; species richness; and fish diversity. These attributes were identified as being both impacted by sediment levels and easily recognisable by recreational SCUBA divers. Horizontal visibility was used as a measure of suspended sediment within the water column as this, rather than vertical clarity measured by a Secchi disk, is the attribute valuable to recreational SCUBA divers. Water clarity has been shown to relate to suspended sediment in previous studies (Fabricius et al., 2016). Though measures of sediment directly would have enabled more accurate modelling of watershed impacts on sediment run-off, this was not possible to conduct on Bonaire's coral reefs across at necessary the scale and resolution, due to limits on access and equipment availability. Monitoring reef characteristics anticipated to be impacted by sediment run-off also enables us to directly link the models to expected environmental changes, which are the ultimate goals of coral reef management.

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Coral cover and visibility were recorded by volunteer SCUBA divers. Though the use of volunteer collected data requires careful design of data collection (Conrad and Hilchey, 2011), data validation (Tulloch and Szabo, 2012), and accounting of potential biases (Dickinson et al., 2010; Sullivan et al., 2016; Tulloch and Szabo, 2012), the possibility for collection of large amounts of data at large spatial and temporal scales is important for filling gaps in conservation knowledge (Conrad and Hilchey, 2011; Sullivan et al., 2016), and accurate results have been shown with only a small amount of training (Hassell et al., 2013). To ensure accuracy of reef data SCUBA divers were asked only to record characteristics with which they were already familiar. Recording horizontal visibility is a common practise when recording dives, and estimating such forms part of diver training. To assist with coral cover estimates volunteers were presented with a card showing four levels of coral cover (Figure 4), and asked to match the cover observed on their dive to the cards. Data was also tested for reliability through comparison to data collected by trained scientists.

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A total of 372 reef health surveys were carried out by 61 divers on Bonaire between 13th July 2015 and 12th February 2016, at dive sites on the west coast of the island (Figure 3). No surveys were conducted on the east side of the island due to high waves and currents which prevent diving along the majority of the coast. Surveys were handed out to tourists by 13 dive centres, and at shore dive sites, and were carried out by resident divers following a public presentation of project aims and procedures. During a normal dive, divers were asked to estimate visibility (in either feet or meters), and to select which of four options best represented coral cover at their safety stop (5m) and at their deepest depth (Under 25%; 26-50%; 51-75%; over 75%), using reference images for comparison (Figure 4). Divers recorded weather at each site as: clear; overcast; or raining, because this impacts light levels, and therefore visibility. Diving experience was also recorded.

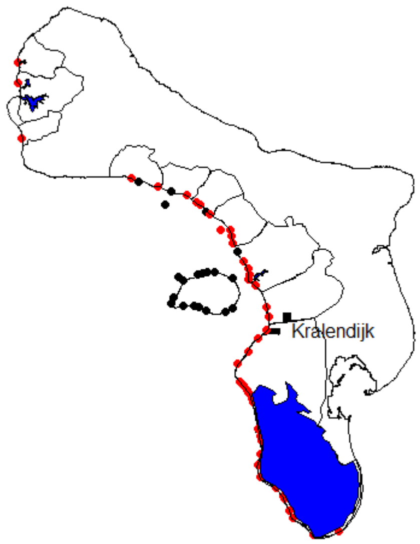

Figure 3. Locations of dive sites surveyed. Red – Shore accessible. Watersheds outlined, and salinas presented in blue. Kralendijk represents the only urban area. The gap in sites surveyed is the oil storage terminal, where access is restricted.

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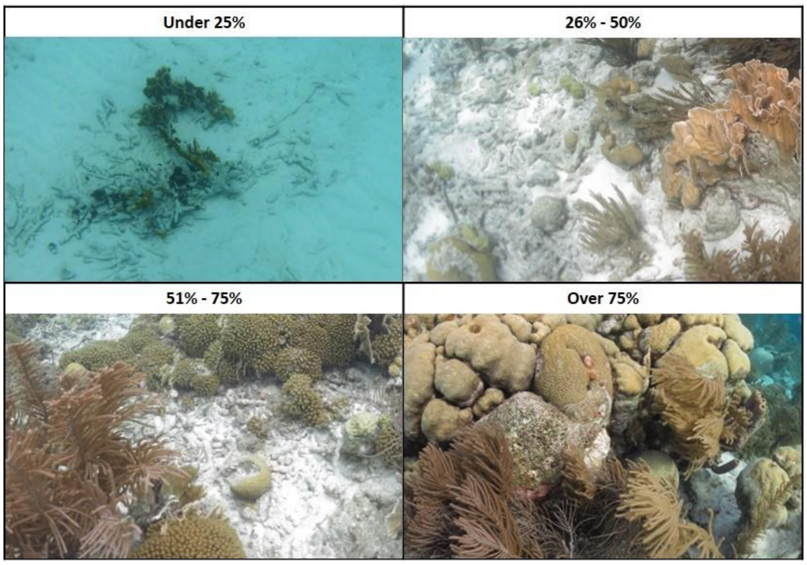

Figure 4. Cards presented to volunteer reef surveyors illustrating four categories of coral cover.

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Weather was not found to impact recorded visibility, though changes were seen for depth, as estimated through use of General Linear Model (Linear Model: Table 1). Visibility estimates were therefore standardised to 18m in all further analysis.

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Table 1. Results from linear model on differences in visibility with varied weather and depth.

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	Est. (m)	SE	P
Intercept (Weather: Clear)	16.14	1.27	<0.01
Weather: Overcast	1.67	1.34	0.22
Weather: Rain	-1.26	3.82	0.74
Depth/m	0.16	0.05	<0.01

Data on fish populations were taken from the REEF database (REEF, 2016), using surveys conducted between 1st January 2015 and 31st December 2015. REEF surveys are conducted by trained volunteers using the Roving Diver Technique to estimate fish density by species at individually identified sites (Pattengill-Semmens and Semmens, 2003). From this data mean fish abundance, species richness and Shannon-Weaver diversity (R package: Vegan) were calculated for each dive site. A composite fish score was also created, to encompass all attributes. This was created through calibrating each of fish abundance, species richness, and diversity to a four point scale, where four represents the highest recorded value, and one represents zero. These calibrated scores were summed to give a composite fish score, ranging from 3-12.

Composite reef score was also calculated to illustrate overall reef health. Visibility was calibrated to a four point scale as with fish attributes above, and the sum of the composite fish score, calibrated visibility score, and both coral cover scores (with each category assigned score of 1 (under 25%) to 4 (over 75%). Composite reef scores therefore ranged from 6-24.

Currents and wave action have not been included, because these are largely similar across the sites studied. Currents are generally low, and move in a north westerly direction along the study site.

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2.3.2 Watershed characteristics

Watersheds for each dive site were estimated using watercourse and contour maps for Bonaire (Dutch Caribbean Nature Alliance, 2016, Figure 2).

Watershed variables were identified to account for variation within the watershed which could lead to increases in sediment run off, these include: slope (Appendix A); tree biomass (Appendix A); ground cover (Appendix A); soil type (Government of the Netherlands Antilles Ministry of Welfare Development plan on land and water, 1967); landscape type (Freitas et al., 2005); and presence of a salina (Figure 3). Shore accessibility (Figure 3) was also included because this may increase re-suspended sediment though divers entering and exiting the site. Distance from urban areas (Figure 3) was included because urban run-off and sewage contributes to sediment levels. Rainfall, leading to surface water which is the main transport of sediment into the marine ecosystem, was not included in models because no spatial variation across the island was found (e.g. no significant difference between monthly rainfall in the north and south of the island, $t = 0.4$, $df = 15.2$ p-value = 0.67; Unpublished data: Cargill & STINAPA). Data was not analysed separately for the wet and dry seasons as the period of data collection was especially dry, and rainfall was not found to vary by season in the period of data collection ($t = -1.91$, $df = 5.5$, p-value =0.1). This low rainfall during the wet season is not an uncommon occurrence for Bonaire. Average watershed slope was calculated using contour maps in R using the package: raster (R Core Team 2016). Bonaire does not have any rivers or streams to transport sediment, so these did not need to be considered.

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Terrestrial vegetation data was collected at 101 locations, randomly located across Bonaire, stratified by landscape type (Table 2), including: tree abundance; tree species; tree diameter at breast height; percentage grass cover; and percentage herb cover, estimated within 10x10m quadrats. From this data average tree abundance; tree species richness; tree size; grass cover; and herb cover was calculated for each landscape type (Table 2). Average watershed values were derived from the mean weighted by percentage cover of landscape type of these landscape level values.

Table 2. Descriptions of landscape types. Taken from Landscape ecological vegetation map of Bonaire (Freitas et al., 2005)

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Landscape type	Percentage land cover	Elevation	Terrain
Higher terrace	7.2 %	50-85 m	Fragmented, slants to join middle terrace.
Middle terrace	24.6 %	15-50 m	Continuous, small hills or cliffs bordering coast.
Lower terrace	15 %	4-15 m	Flat continuous, slight dip landwards.
Undulating landscape	30.9 %	0-241 m	Peaks and valleys, slopes can be steep, but rarely form cliffs.

Variables were consolidated into:

$$Mean\ tree\ biomass\ index = mean\ tree\ abundance\ \times mean\ tree\ size$$

$$Mean\ ground\ cover = mean\ grass\ cover + mean\ herb\ cover$$

Soil type was identified using the Bonaire Soil Map (Government of the Netherlands Antilles Ministry of Welfare Development plan on land and water, 1967) and landscape type from the

Landscape Vegetation Map of Bonaire (Freitas et al., 2005). Google Earth (Bonaire, 2016) was used to identify salina presence on the watershed, and distance of dive site from urban areas. Sites was identified as being accessible from shore using the Bonaire dive map (STINAPA Bonaire, 2016). Land use was identified from the Bonaire Zoning Plan (Openbaar Lichaam Bonaire, 2011), as urban or nature area. Nature areas have limited permanent structures, and are not farmed, though are grazed by free ranging and feral livestock. Sediment from sources other than Bonaire, such as continental sediments, were not included in the model, as they would not be expected to vary across the spatial scales considered.

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2.4 Data analysis

Statistical analysis was carried out using R Statistical Software (R Core Team 2016).

2.4.1 Data reliability

The use of volunteer data can be limited by the ability of untrained individuals to successfully identify and record data, and through potential biases in data collection. Data collected by volunteers should therefore be tested to account for potential inaccuracies. We tested data reliability using a paired t-test against data collected by van Beek (2011), which measured coral cover at 5m depth during 2011 using visual estimation during snorkel surveys (van Beek, 2011). Data showed a significant difference between cover estimated by all recreational divers (residents and tourists combined) and data collected in van Beek's (2011) study ($t = -2.4$, $df = 61$, $p=0.02$). No significant difference was seen between data collected by resident divers only and van Beek's (2011) data (Paired t-test: $t = 0.9$, $df = 41$, $p = 0.4$). Data collected by Bonaire residents only was therefore used in further analysis. Mean scores were calculated from this data for each dive site.

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2.4.2 Coral cover categories

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Coral cover was organised into categories for analysis. 'Deepest depth' coral scores were categorised as: low-level (under 10m); mid-level (10m-18m); deep (19m-30m); and very deep (deeper than 30m). The 'low-level' and 'very deep' categories included only one and eight values, and so were pooled with the mid-level and deep categories respectively. An ANOVA was carried out to determine differences in coral cover between 'safety stop' (5m depth, hereafter 'shallow'), mid and deep level coral scores. Shallow coral cover was significantly lower than deep and mid coral cover (Table 3). No significant difference was observed between deep and mid-level coral cover (Table 3), and these scores were therefore combined for further analysis. Due to the similarities in coral cover with depth, and previous work indicating that Bonaire's reef habitats are largely similar across space (Bak, 1977; van Beek, 2011), we did not therefore further separate data by habitat.

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Table 3. Results from ANOVA on differences in mean percentage coral cover by depth class. Residual degrees of freedom 107. Est – Estimated model coefficients. SE – Standard Error. P – Calculated probability.

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	Est. (%)	SE	P
Intercept (shallow)	60.50	3.00	<0.01
Mid depth	20.25	5.25	<0.01
Deep	26.25	4.50	<0.01

2.4.3 Vegetation-Reef health relationship

General linear models were used to investigate the relationship between terrestrial vegetation and reef health. In addition to directly measured reef attributes composite scores for reef health and fish communities were also created. Individual models were created for the following reef health indicators: composite reef score; shallow coral cover; deep coral cover; composite fish score; and visibility (full data and excluding one outlier). Data for composite reef score, shallow coral cover, deep coral cover, and visibility (full data) showed a normal distribution, and were therefore not transformed. Data were normalised through log transformation for composite fish score. Plotting model estimates indicated a single high visibility estimate as over 35m, which was deemed larger than possible visibility. Models were therefore repeated excluding this estimate, normalising data through log transformation, with both models reported. General

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linear models were used for these data to avoid potentially over fitting the models to complex ecosystem data. Model fit in each case was assessed through plotting of residuals, and consideration of model outputs, which suggest good model fit.

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The full model in each case included the variables: tree biomass index; mean percentage ground cover; shore accessibility; distance along coast from town centre; predominant soil type; presence of a salina; average watershed slope; and tree biomass index-percentage ground cover interaction. Interactions were limited to vegetation characteristics because these are characteristics that the study is concerned with likely to impact reef health. Model simplification was carried out using the information theoretic approach (Burnham and Anderson, 1998), in which the Akaike weights of variables occurring in models within 2AIC of the top model were calculated, and a representative model created using variables with an Akaike weight of greater than 0.5. The full model is reported alongside the representative model in each case, except where no variable had an Akaike weight of over 0.5, or models had poor AIC values and deviance when compared to the full model, when only the full model is reported.

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3. Results

3.1 Vegetation-Reef health relationship

3.1.1 Reef composite score

A single top model was identified to describe reef composite score, containing variables salina presence and soil type. Reef score decreased where a salina was present, and was lowest with rocky soil types (Table 4. For figures see Appendix B).

Table 4. Results from General Linear Models investigating effects of watershed vegetation on composite reef health. n=47. Variable deletions did not improve the model. Full model deviance = 72.356, df=28. Representative model deviance = 81.15, df=35. Intercept for full model set to soil type: loam; shore access: no; salina: no, land use: nature. Intercept for representative model set to soil type: loam; salina: no. Significant terms in bold.

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	Full Model AIC: 163.22				Representative Model AIC: 153.81			
	Est.	SE	t	P	Est.	SE	t	P
Intercept	**19.68**	**3.39**	**5.80**	**<0.01**	**15.18**	**0.92**	**16.42**	**<0.01**
Tree biomass index	-1.66	1.04	-1.60	0.12				
Percentage ground cover	-0.04	0.05	-0.75	0.46				
Shore accessible	-0.16	0.89	-0.17	0.86				
Distance from town	<0.01	0.00	0.47	0.64				
Rocky soil	-3.56	2.14	-1.66	0.11	-1.17	1.12	-1.05	0.30
Terrace soil	-3.76	3.02	-1.24	0.22	0.87	0.97	0.90	0.38
Terrace/rocky soils	-1.54	3.34	-0.46	0.65	2.70	1.07	2.52	0.02
Salina present	0.50	2.29	0.22	0.83	**-2.53**	**0.85**	**-2.96**	**0.01**
Slope	-18.86	21.16	-0.89	0.38				
Urban use	-0.89	4.12	-0.22	0.83				
Tree biomass index : percentage ground cover	0.13	0.08	1.56	0.13				

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3.1.2 Coral cover

Five models were identified to explain shallow (5m) coral cover, including the variables: tree biomass; percentage ground cover; shore accessibility and land use. The representative model included only land use, with watersheds containing urban areas having lower cover than nature areas(Table 5, for figures see Appendix B).

Table 5. Results from General Linear Model investigating effects of watershed vegetation on mean coral cover at 5m. n=49. Full model deviance = 32.28, df=37. Representative model deviance = 38.62, df=47. Intercept for full model set to soil type: loam; shore access: no; salina: no. Significant terms in bold.

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	Full Model AIC: 144.61				Representative Model AIC: 133.39			
	Est.	SE	t	P	Est.	SE	t	P
Intercept	3.35	1.70	1.97	0.06	**2.49**	**0.14**	**17.57**	**<0.01**
Tree biomass index	-0.56	0.55	-1.02	0.32				
Percentage ground cover	-0.01	0.03	-0.47	0.64				
Shore accessible	-0.45	0.43	-1.03	0.31				
Distance from town	<0.01	0.00	1.47	0.15				
Rocky soil	-0.36	1.24	-0.29	0.77				
Terrace soil	-1.17	1.55	-0.75	0.46				
Terrace/rocky soils	-0.12	1.92	-0.06	0.95				
Salina present	0.04	1.12	0.03	0.97				
Slope	-4.91	9.79	-0.50	0.62				
Urban use	-0.66	2.29	-0.29	0.77	-0.61	0.35	-1.75	0.09
Tree biomass index : percentage ground cover	0.04	0.04	1.00	0.32				

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Three top models were identified to explain deep (below 10m) coral cover, including variables: tree biomass index; percentage ground cover; shore accessibility; distance to town; presence of a salina; land use; and tree biomass: percentage ground cover interaction. A positive relationship was found between deep coral cover and ground cover, with a stronger relationship as tree biomass increased (Table 6 & Figure 5). Tree biomass had a negative relationship to deep coral cover, with a steeper relationship with lower levels of ground cover (Table 6 & Figure 6). Coral cover also increased where the watershed contained a salina, and where the watershed was predominantly nature areas (Table 6). A decrease in coral cover was seen with shore accessibility, as well as with increased distance from town, though the latter impact was very small (Table 6, for additional figures see Appendix B).

Table 6. Results from General Linear Model investigating effects of watershed vegetation on mean coral cover deeper than 5m. n=49. Full model deviance = 17.39, df=37, representative model deviance = 19.08, df=41. Intercept for full model set to soil type: loam; shore access: no; salina: no' land use: nature. Representative model: shore access: no; land use: nature. Significant terms in bold.

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	Full Model AIC: 114.3				Representative Model AIC: 110.85			
	Est.	SE	t	P	Est.	SE	t	P
Intercept	**4.85**	**1.25**	**3.88**	**<0.01**	**3.09**	**0.44**	**6.99**	**<0.01**
Tree biomass index	**-1.43**	**0.41**	**-3.53**	**<0.01**	**-0.77**	**0.15**	**-5.21**	**<0.01**
Percentage ground cover	-0.02	0.02	-1.33	0.19	0.00	0.01	-0.27	0.79
Shore accessible	**-0.73**	**0.32**	**-2.27**	**0.03**	**-0.71**	**0.30**	**-2.35**	**0.02**
Distance from town	**<0.01**	**0.00**	**2.47**	**0.02**	**<0.01**	**0.00**	**2.84**	**0.01**
Rocky soil	-1.67	0.91	-1.83	0.07				
Terrace soil	-1.73	1.14	-1.51	0.14				
Terrace/rocky soils	-2.00	1.41	-1.42	0.17				
Salina present	1.50	0.83	1.81	0.08	0.78	0.46	1.70	0.10
Slope	2.14	7.19	0.30	0.77				
Urban use	-1.88	1.68	-1.12	0.27	**-1.06**	**0.53**	**-2.00**	**0.05**
Tree biomass index : percentage ground cover	**0.11**	**0.03**	**3.51**	**<0.01**	**0.06**	**0.01**	**5.21**	**<0.01**

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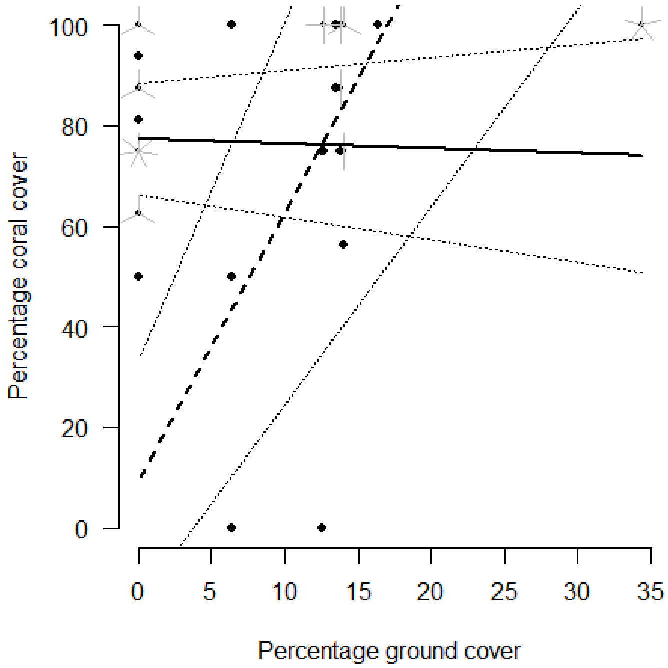

Figure 5. Change in deep coral cover with ground cover showing how this relationship was dependent on tree biomass. Dashed – Median tree biomass; Solid – Min tree biomass. Estimates with maximum tree biomass are not presented as these are not representative of the majority of locations on Bonaire. Dotted lines indicate upper and lower confidence intervals of ground cover impact.

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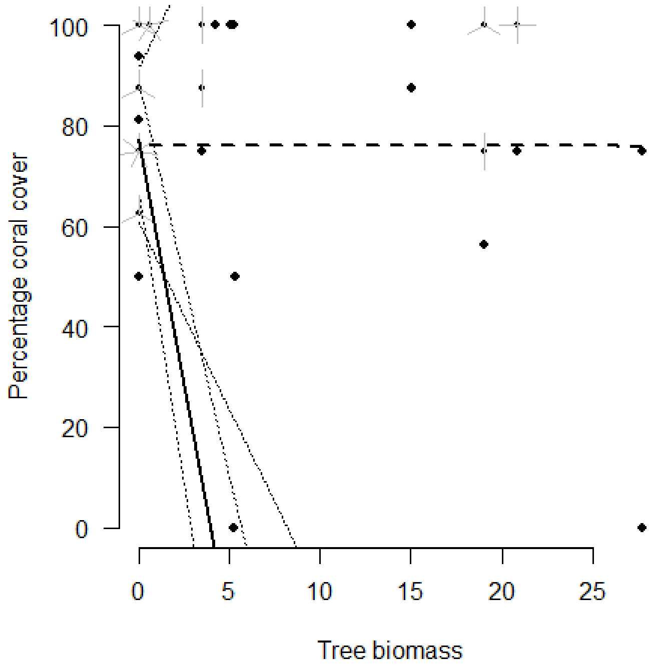

Figure 6. Relationship between tree biomass and coral cover, impacted by ground cover. Solid: min ground cover; Dashed: median ground cover. Estimates with maximum ground cover are not presented as these are not representative of the majority of locations on Bonaire. Dotted lines indicate upper and lower confidence intervals of ground cover impact.

3.1.3 Fish characteristics

Five top models were identified, including the variables: distance to town; salina presence; shore accessibility; slope; land use and predominant soil type. The representative model included: shore accessibility; soil and distance to town. Fish score increased with shore accessibility and decreased with distance to town, though this decrease was very small. Fish score decreased in terraced and rocky terraced soils (Table 7, for figures see Appendix B).

Table 7. Results from General Linear Model investigating effects of watershed vegetation on fish. n=53. Full model deviance = 0.45, df=41, representative model deviance = 0.52, df=47. Intercept for full model set to soil type: loam; shore access: no; salina: no; land use: nature. Representative model: shore access: no; soil type: loam. Data has been log transformed. Significant terms in bold.

	Full Model AIC: -75.42				Representative Model AIC: -80.12			
	Est.	SE	t	P	Est.	SE	t	P
Intercept	**2.19**	**0.19**	**11.53**	**<0.01**	**2.23**	**0.07**	**32.41**	**<0.01**
Tree biomass index	0.00	0.06	0.07	0.94				
Percentage ground cover	0.00	0.00	-0.25	0.80				
Shore accessible	**0.13**	**0.04**	**2.97**	**0.01**	**0.13**	**0.03**	**3.99**	**<0.01**
Distance from town	**<0.01**	**0.00**	**-2.39**	**0.02**	**<0.01**	**0.00**	**-3.81**	**<0.01**
Rocky soil	-0.19	0.14	-1.36	0.18	**-0.18**	**0.07**	**-2.45**	**0.02**
Terrace soil	0.14	0.18	0.81	0.42	0.09	0.06	1.56	0.12
Terrace/rocky soils	-0.11	0.21	-0.52	0.61	-0.02	0.07	-0.34	0.73
Salina present	-0.19	0.12	-1.57	0.12				
Slope	0.56	1.20	0.47	0.64				
Urban use	-0.30	0.22	-1.34	0.19				
Tree biomass index : percentage ground cover	0.00	0.00	0.12	0.90				

3.1.4 Visibility

Seven top models were identified for visibility, including the variables: tree biomass index; percentage ground cover; shore accessibility; predominant soil type; salina presence; land use;

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and tree biomass index: percentage ground cover interaction. The representative model included tree biomass index; shore accessibility; predominant soil type; and salina presence. Visibility decreased with increased tree biomass (Table 8a). Visibility also decreased in shore accessible sites, with presence of a salina on the watershed, and in rocky, terraced and combined rock and terrace soils when compared to loam soils (Table 8a).

Models were repeated excluding a single high visibility estimate, using log transformed data. Five models were identified, including the variables: percentage ground cover; salina presence; shore accessibility; and slope. The representative model included slope and shore accessibility, with both reducing visibility (Table 8b, for figures see Appendix B).

Table 8a. Results from General Linear Model investigating effects of watershed vegetation on visibility. n=. Full model deviance = 792.16 df=37, representative model deviance = 890.61, df=42. Intercept for full model set to soil type: loam; shore access: no; salina: no; land use: nature. Representative model: shore access: no, soil: loam; salina: no. Significant terms in bold.

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	Full Model AIC: 301.42				Representative Model AIC: 297.16			
	Est.	SE	t	P	Est.	SE	t	P
Intercept	**21.79**	**8.44**	**2.58**	**0.01**	**33.01**	**2.80**	**11.80**	**<0.01**
Tree biomass index	4.84	2.74	1.77	0.08	-0.14	0.09	-1.51	0.14
Percentage ground cover	0.06	0.12	0.44	0.66				
Shore accessible	**-5.34**	**2.15**	**-2.48**	**0.02**	**-4.81**	**1.54**	**-3.13**	**<0.01**
Distance from town	<0.01	0.00	-0.88	0.39				
Rocky soil	-2.57	6.16	-0.42	0.68	**-10.36**	**2.96**	**-3.50**	**<0.01**
Terrace soil	4.93	7.70	0.64	0.53	**-8.76**	**2.45**	**-3.58**	**<0.01**
Terrace/rocky soils	5.33	9.52	0.56	0.58	**-5.74**	**2.83**	**-2.03**	**0.05**
Salina present	**-11.93**	**5.57**	**-2.14**	**0.04**	-2.98	2.47	-1.20	0.24
Slope	47.23	48.50	0.97	0.34				
Urban use	-0.53	11.33	-0.05	0.96				
Tree biomass index : percentage ground cover	-0.37	0.22	-1.72	0.09				

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Table 9ab Results from General Linear Model investigating effects of watershed vegetation on visibility with outlier removed. n= 48. Full model deviance = 1.05 df=36, representative model deviance- = 1.2, df=45. Intercept for full model set to soil type: loam; shore access: no; salina: no. Representative model: shore access: no. Significant terms in bold.

	Full Model (Outliers removed) AIC: -21.25				Representative Model (Outliers removed) AIC: -31.50			
	Est.	SE	t	P	Est.	SE	t	P
Intercept	**3.64**	**0.33**	**11.19**	**<0.01**	**3.20**	**0.05**	**59.41**	**<0.01**
Tree biomass index	0.01	0.11	0.08	0.93				
Percentage ground cover	0.00	0.00	-0.91	0.37				
Shore accessible	**-0.35**	**0.08**	**-4.34**	**<0.01**	**-0.26**	**0.06**	**-4.63**	**<0.01**
Distance from town	<0.01	0.00	-0.47	0.64				
Rocky soil	-0.07	0.23	-0.31	0.76				
Terrace soil	-0.30	0.30	-1.00	0.32				
Terrace/rocky soils	0.17	0.35	0.49	0.62				
Salina present	0.09	0.23	0.39	0.70				
Slope	-2.87	1.98	-1.45	0.15	-1.09	0.59	-1.85	0.07
Urban use	0.53	0.43	1.23	0.23				
Tree biomass index : percentage ground cover	0.00	0.01	-0.30	0.77				

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4. Discussion

Coral reef health is impacted by terrestrial ecosystems through sediment run-off. Sediment run-off can be altered by changes to watershed characteristics, including vegetation ground cover and tree biomass. We modelled the impacts of these on coral cover, fish communities, and visibility, using the small island of Bonaire as a case study. Bonaire's coral cover (below 10m) showed a positive relationship with ground cover and a negative relationship with tree biomass. When considering reef health across all attributes, the impact of watershed vegetation was smaller than that of shore accessibility. Shore accessibility is related to increased suspended marine sediment due to presence of a sandy shelf, and divers coming into contact with the reef when entering and exiting the site, and had a significant impact on all reef attributes. Soil type,

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salina, and slope, all of which may impact the amount of sediment which can enter the coral reef, had small impacts, influencing reef score, deep coral, and visibility respectively.

Composite reef score was impacted by both watershed soil type and presence of salina on the watershed, with terrace soils associated with a reduced reef score, highlighting the importance of watershed characteristics to overall coral reef health on Bonaire. Reef score was comprised of percentage coral cover, fish community index and visibility. Whilst this does not capture all of the variation in reef health on Bonaire, these are reported to be reliable indicators of reef health, and have been used in a range of studies (DeMartini et al., 2013; Fabricius, 2005; Pollock et al., 2014; Risk, 2014; Rogers et al., 2014; Rogers, 1990; Schep et al., 2013; Uyarra et al., 2009). Our results therefore indicate the importance of the watershed to coral reef conservation, and may be used to suggest that sediment levels are impacting additional reef attributes not tested here. It is important to note the large errors associated with this model, which indicates further analysis of individual reef attributes is important to fully understand the relationship.

The relationship between watershed characteristics and coral cover varied with depth. Shallow coral cover varied only with land use, being lower in urban areas. This is likely due to the watersheds associated to urban areas experiencing higher reef use and boat traffic, which may damage shallow corals in particular. The lack of relationship with other watershed characteristics seen to impact deep coral may be a result of shallow corals experiencing multiple stresses not felt by deeper corals, masking the impacts of watershed. Shallow coral was measured at 5m, whilst divers were carrying out their safety stop. This stop occurs for three minutes at the end of each dive, and is therefore carried out in areas of high diver traffic, or near to mooring buoys, both of which may reduce coral cover. Shallow coral may also be more vulnerable to collisions from boats, snorkelers, novice divers and other water sports. This study did not allow us to discern the main factors determining coral cover at shallow depths, however

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further study would be warranted to identify factors, such as restrictions on divers or other water sports, which could be incorporated into coral reef management plans.

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Deep corals, below 10m depth, showed a positive relationship with ground cover, with relationship increasing as tree biomass index increased. Increases in ground cover are associated with increased root systems within the soil, as well as creating surface complexity. Areas with high ground cover therefore slow water flow, reducing energy available to dislodge sediment.

In contrast to existing literature, a negative relationship was seen between deep coral cover and tree biomass index, though review studies have indicated that ecological context is important in determining impacts of tree biomass on sediment run-off (Brown et al., 2005; van Dijk and Keenan, 2007). Increased tree biomass index would be expected to reduce sediment run-off, and therefore increase coral cover, through tree roots anchoring soils, and creating pools of water, increasing water seeping into the soil. However Bonaire's dry forest is characterised by very low rainfall. Dry-forest tree species therefore have deep root systems, which may have little impact in anchoring surface sediments susceptible to transport, or in increasing surface complexity, rather acting to reduce water levels in the water table (van Dijk and Keenan, 2007). In dry-forest such as Bonaire sediment transport through the water table is of limited impact to sediment levels when compared to surface run-off (Bartley et al., 2014). The negative relationship observed may arise from increased tree litter associated with trees with higher above ground biomass, which would increase sediment available for transportation. In overgrazed systems disruption of leaf litter has been suggested to be linked to increases in sediment run-off (van Dijk and Keenan, 2007). The highly degraded nature of Bonaire's dry-forest may also contribute to the negative relationship observed, with positive impacts of afforestation observed only in studies which increased tree abundance in over 20% of the catchment (Brown et al., 2005). The low tree density on Bonaire may therefore limit the impact these have on reducing sediment run-off. This relationship is reduced where ground cover increases, suggesting this reduces transportation of this sediment.

Salina presence is associated with an increase in deep coral cover. This may result from salinas acting as a sediment traps, therefore reducing sediment run-off. Building of salinas may therefore also perform a role in reducing sediment run-off into the reef, but have a smaller impact than increasing ground cover. Shore accessibility decreased coral cover, probably because it is associated with increased suspended sediment. Both of these impacts are small at the scale of deep coral cover, though shore accessibility is larger with regard to whole reef ecosystem health, in comparison to the impact of watershed vegetation. Sites with watershed dominated by urban areas also showed reduced coral cover. This could be attributed to higher run-off associated with concrete in urban areas, but may also be a result of increased reef use in locations close to residences and hotels.

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Composite fish score did not show significant variation with watershed vegetation, though did vary with soil type. Unlike coral, fish are mobile throughout the reef, and may therefore move between areas of high and low sediment. In addition to direct impacts on sediment on fish (Goatley and Bellwood, 2012; Hess et al., 2015; Wenger et al., 2014, 2013, 2011), large impacts arise through their relationship with coral (DeMartini et al., 2013; Edmunds and Gray, 2014; Jones et al., 2015; Rogers et al., 2014; Rogers, 1990), therefore the coral declines seen in Bonaire may not have reached levels high enough to impact fish communities. In this study we have not accounted for the reef reliance of the species recorded. Impacts of sediment run-off on reef dependent species may therefore be masked by responses of less restricted species, though the ten most common species recorded in surveys across Bonaire are all reef dependent. Further studies should address impacts on sensitive species in particular to identify declines.

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Fish score was improved in sites accessible from shore, and increased with increased distance from town. Shore dive sites are characterised by sandy flats, leading to the reef. This may provide larger variation in habitat for fish species, a result observed by Pattengill-Semmons (2002) on Bonaire using the REEF database. Fish may also be more easily identified on sandy areas when compared to the reef itself, leading to inflated estimates.

Once a single outlier was removed, a negative relationship between watershed slope and visibility was found. Increased slope is associated with higher sediment run-off (Boer and Puigdefábregas, 2005; Millward and Mersey, 1999; Renard et al., 2000), and would therefore be expected to relate to reduced visibility. Shore accessible sites also show reduced visibility, due to the presence of sandy flats from which sediment may be disturbed by divers, waves or currents.

The overall weak relationship between reef characteristics and watershed vegetation is in line with existing literature (Ramos-Scharron et al., 2015; Rodgers et al., 2012), and is a consequence of the multitude of threats to coral reef ecosystems (Hughes et al., 2003). However, the largely uniform nature of threats impacting the coral reef on Bonaire's west coast has enabled us to identify degradation of vegetation ground cover as decreasing composite reef score and coral cover below 10m depth. Through the use of multivariate analysis we have intended to capture the biotic and abiotic factors impacting reef characteristics. However in a complex system, such as coral reefs, these models remain limited. Though the low currents on Bonaire are likely to mean that sediment transport on entering the coastal ecosystem is limited, we have not explicitly tested this assumption, and there is potential that sediment entering from one watershed may be impacting in other locations. We have also not considered the impacts of sediments originating from other locations. Though these sediment inputs would be expected to be small in comparison to those directly from Bonaire, large changes in sediment inputs into the Caribbean sea may have impacts on coral cover. Though we have estimated coral cover and fish

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abundance, this has not accounted for species or community structures, which could also be expected to be impacted by sediment run-off. As a result the negative impacts of sediment run-off may be under represented by the models. Similarly due to the need to keep methods simple for volunteer data collectors coral cover estimates were assigned to one of four ranges (Under 25%, 26-50%, 51-75%, and over 75%). This limits the power of the model to estimate impacts on coral cover, and a more accurate understanding would be achieved through detailed coral cover surveys. Additionally we have not considered factors influencing the reef on regional or global scales, such as lionfish abundance, or ocean temperatures. While it is unlikely that large variations in such occur at the small scale of Bonaire, the influence of regional and global factors should be accounted for when applying such models to management decisions.

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It is important to recognise when considering the relationships described within this thesis that though sediment run-off is found to have a negative impact on coral cover, this is expected to be small when compared to global factors, such as coral bleaching. At the local scale Bonaire's shallow and deep corals are recognised as having undergone bleaching events, linked to changes in water temperature (Bak et al., 2005; Steneck et al., 2015; Stokes et al., 2010), though some recovery is suggested (Steneck et al., 2015). However though climate change may be a more significant threat than the local threat of sediment run-off, local managers have little power to tackle global climate change. Recognising actions which can be taken at the local level would therefore still be expected to improve reef health, and increase resilience of coral reefs to these global threats (Maina et al., 2013; Risk, 2014). Though the impact of vegetation cover is small across reef characteristics measured, it is within the capacity of reef managers to improve watershed ground cover through terrestrial restoration (for example, by reducing grazing pressures, or supplementary planting). It is also valuable to note that the terrestrial ecosystem on Bonaire has already undergone significant environmental damage, resulting in limited variation in vegetation. Modelling the effects of management using links established here can therefore help to target conservation efforts to achieve the highest impacts. Long-term

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monitoring of both reef health and watershed vegetation would improve understanding of this relationship, and enable joint management of the terrestrial and marine ecosystems on Bonaire, and across the tropics.

5. Conclusions

The analysis presented in this paper illustrates, in situ, the relationship between watershed vegetation and coral reef health, in particular coral cover at depths below 10m. As coral reefs are in decline worldwide (Kennedy et al., 2013; Wilkinson, 1999), understanding the scope of threats is important for conservation management decisions. Whilst local managers are limited in their ability to address threats at the global and regional scales, reductions in local level threats can increase reef resilience to outside threats (Birrell et al., 2005; Maina et al., 2013; Risk, 2014). Our models show that where all other threats, such as recreation, fishing, or invasive species, are equal, improvements to watershed vegetation can lead to improvements to reef health.

Bonaire's economy is highly reliant on dive tourism, therefore reef protection is high on the agenda of Government and dive operators. However, until now, reef conservation has, excepting the creation of a sewage treatment plant, largely focused on only marine-based actions. Here we show that low ground cover decreases coral cover at depths below 10m, where the majority of recreational diving occurs. Reef managers may therefore expect to see improvements in coral cover following terrestrial conservation actions, which may include fencing of areas to exclude grazers, control or eradication programs for invasive grazing species, or replant of natural vegetation. The models presented in this paper provide reef managers on Bonaire with tools to estimate impacts that actions to improve ground cover will have on coral cover. In utilising the models managers would therefore be better equipped to compare alternative management options for their effectiveness. Where these estimates were used alongside cost estimates in decision making cost-effectiveness of environmental management actions could also be

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improved. These findings highlight the need for the island to integrate terrestrial and marine conservation to further preserve the island's valuable coral reef.

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8. Appendix A

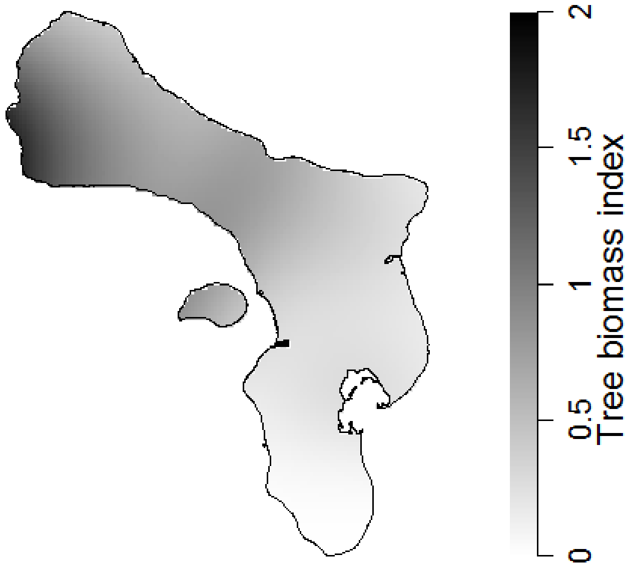

Figure A1. Spatial variation in tree biomass index across Bonaire

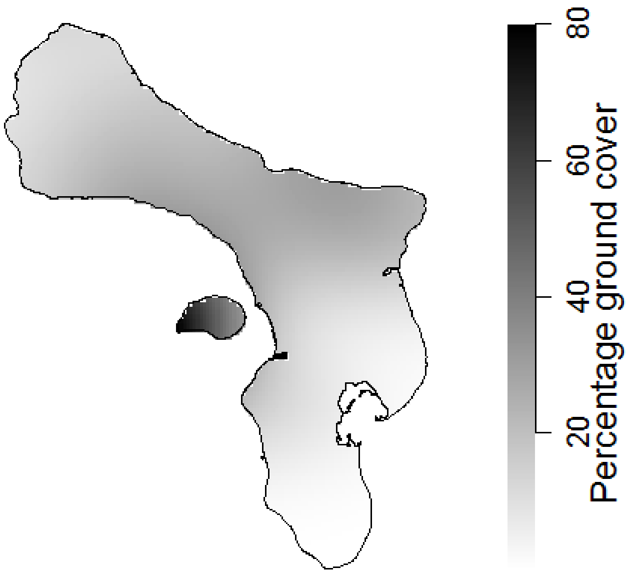

Figure A2. Spatial variation in percentage ground cover across Bonaire.

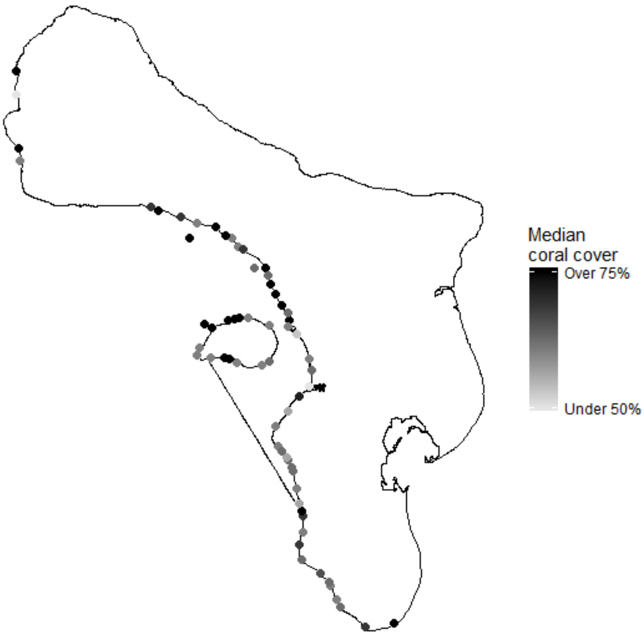

Figure A3. Median coral cover recorded at Bonaire's dive sites

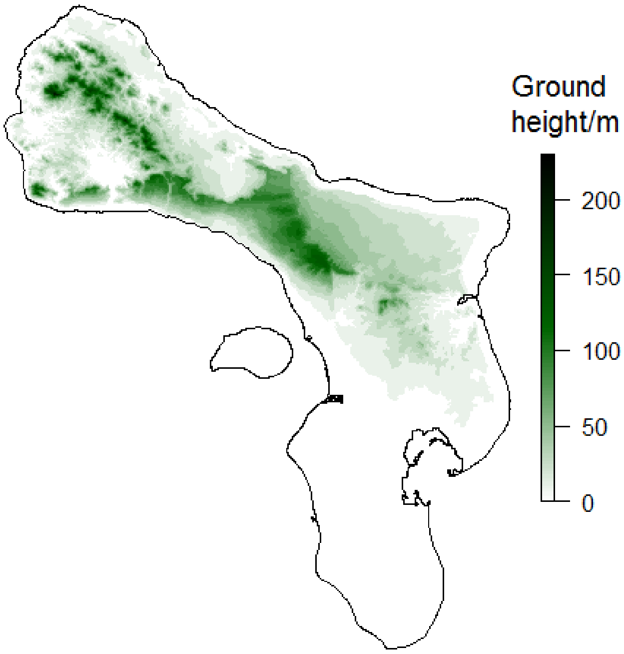

Figure A4. Topographic map of Bonaire

9. Appendix B

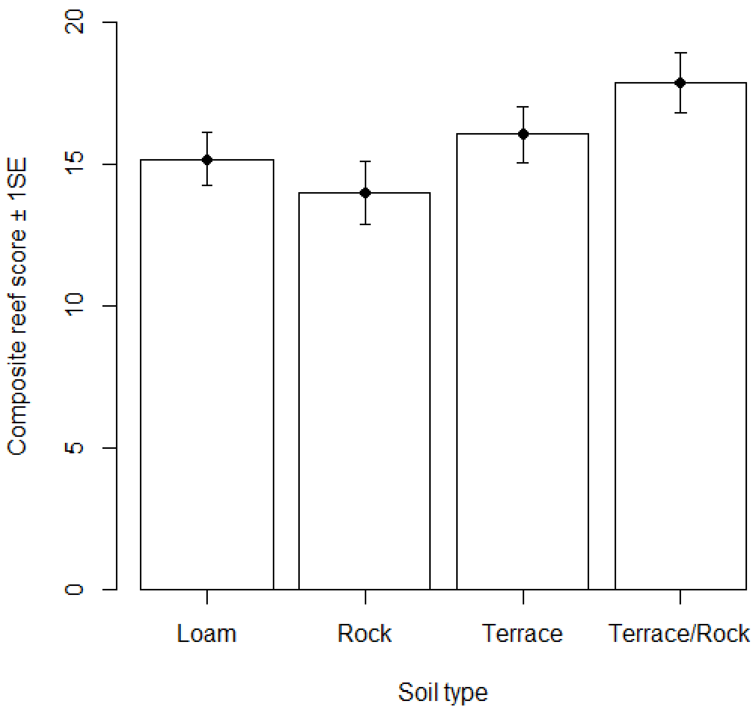

Figure B.1 Impact of soil type on composite reef score, with standard error bars.

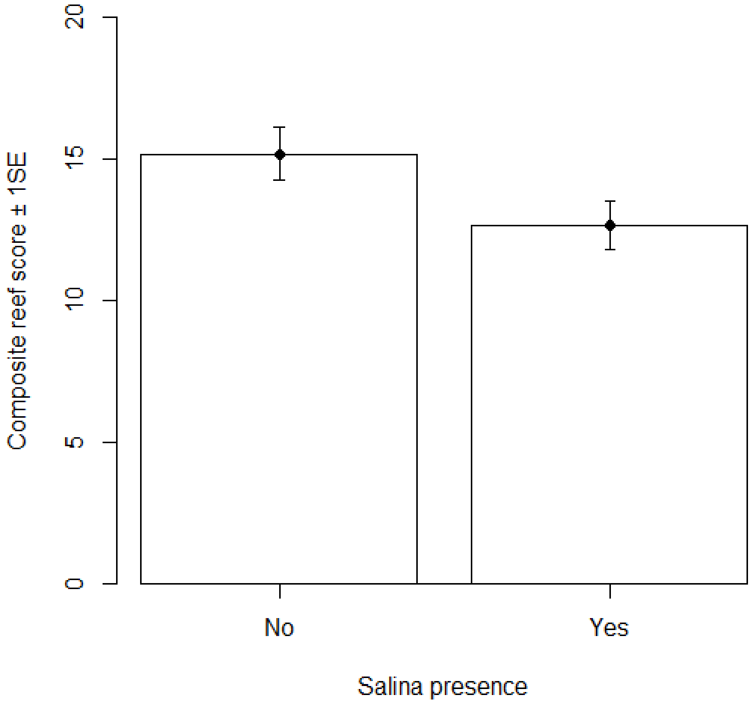

Figure B.2. Change in composite reef score with saline presence.

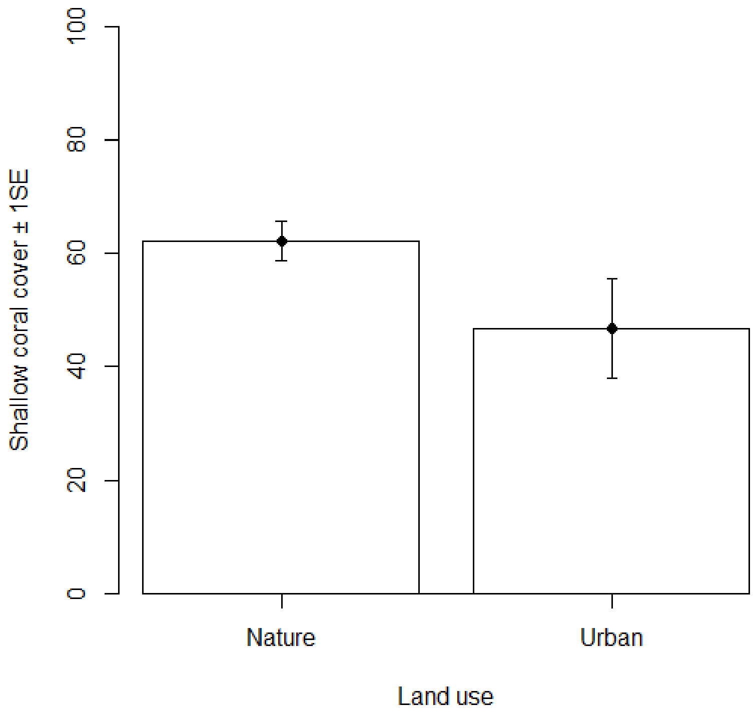

Figure B.3 Impact of land use on watershed on coral cover at 5m.

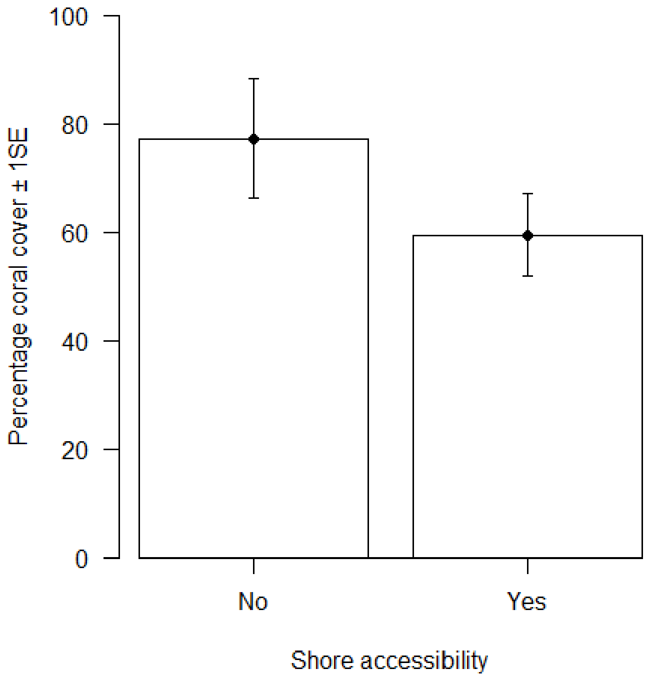

Figure B.4 Impact of shore accessibility on coral cover at 10m.

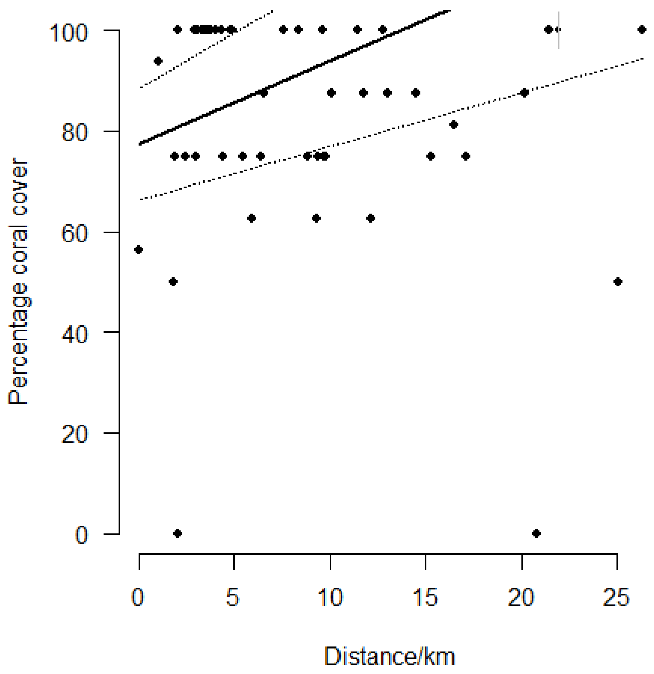

Figure B.5 Impact of distance from urban area on coral cover below 10m. Dotted lines upper and lower confidence intervals of impact of distance. Due to the unbounded nature of the model estimates exceed 100%, but are not displayed here.

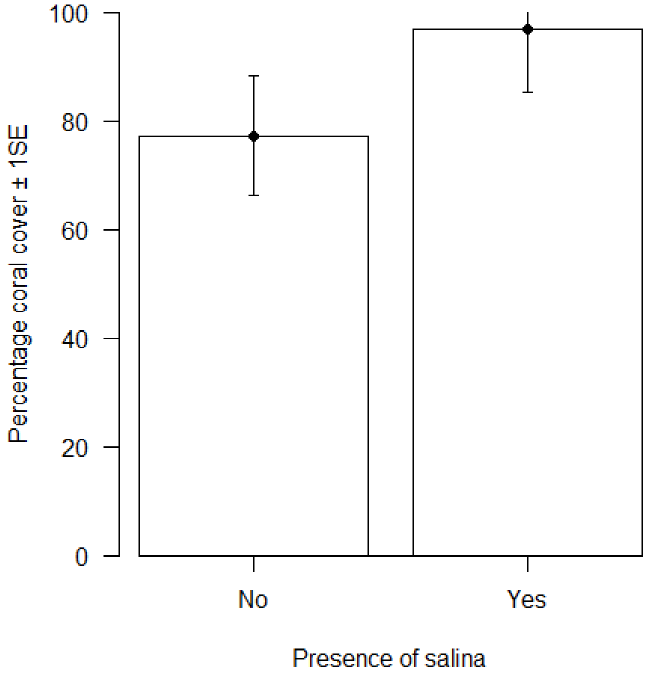

Figure B.6 Impact of salina presence on percentage coral cover below 10m

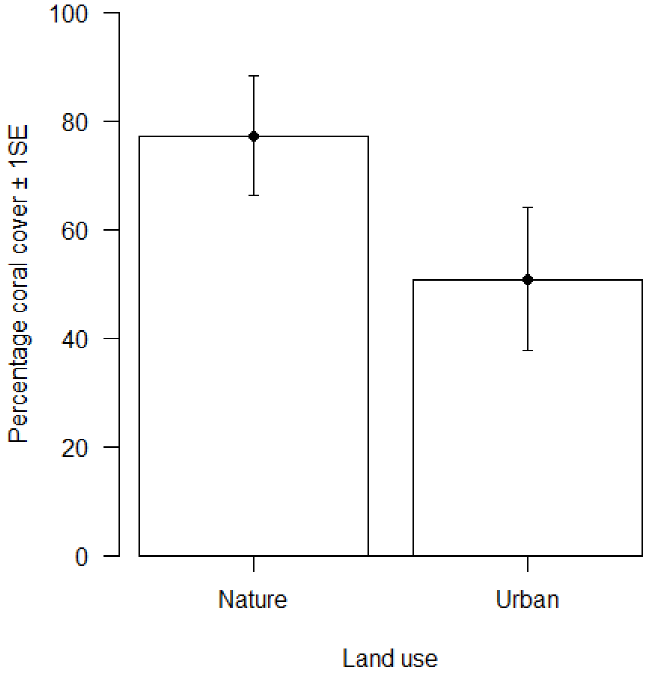

Figure B.7 Impact of land use on percentage coral cover below 10m

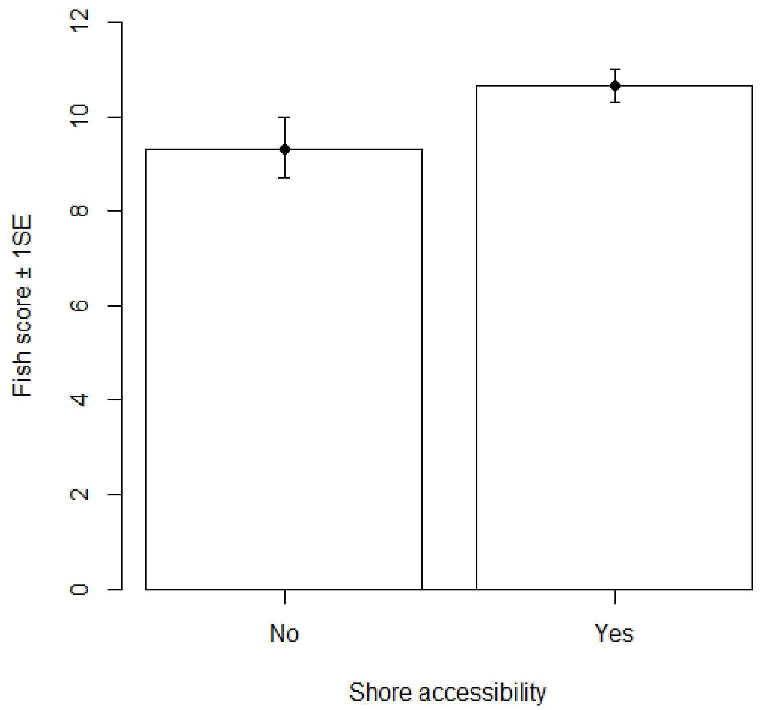

Figure B.8 Impacts of shore accessibility on fish community.

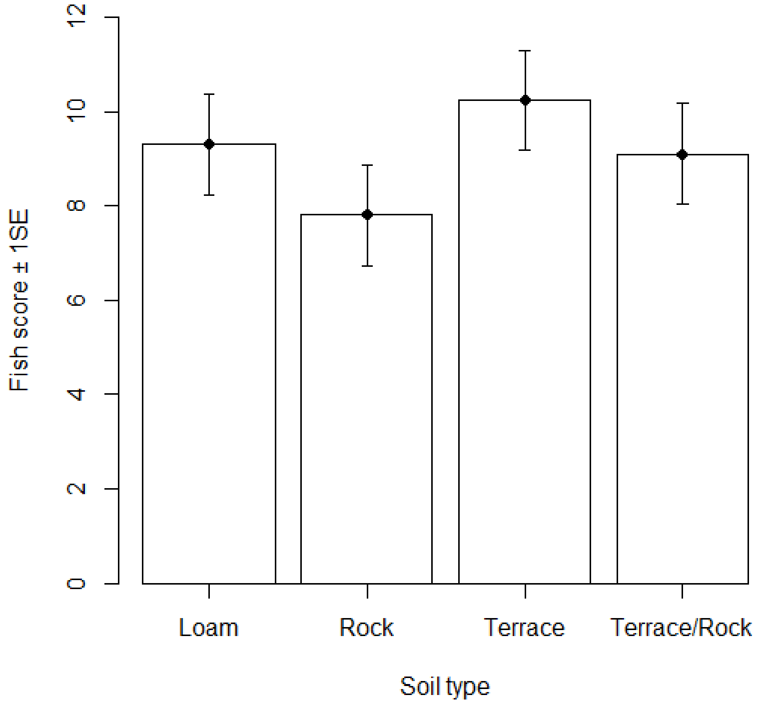

Figure B.9 Impacts of soil type on fish score

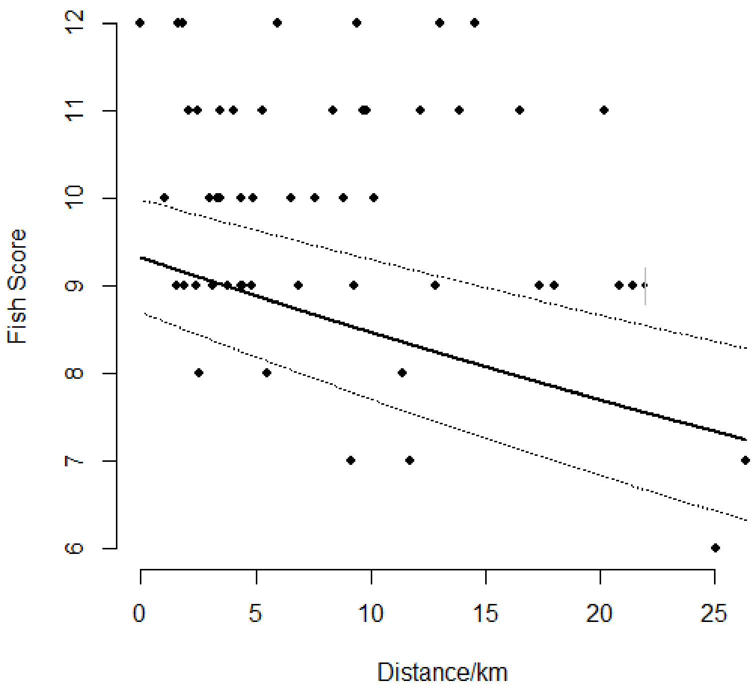

Figure B.10. Change in fish score with increasing distance from town.

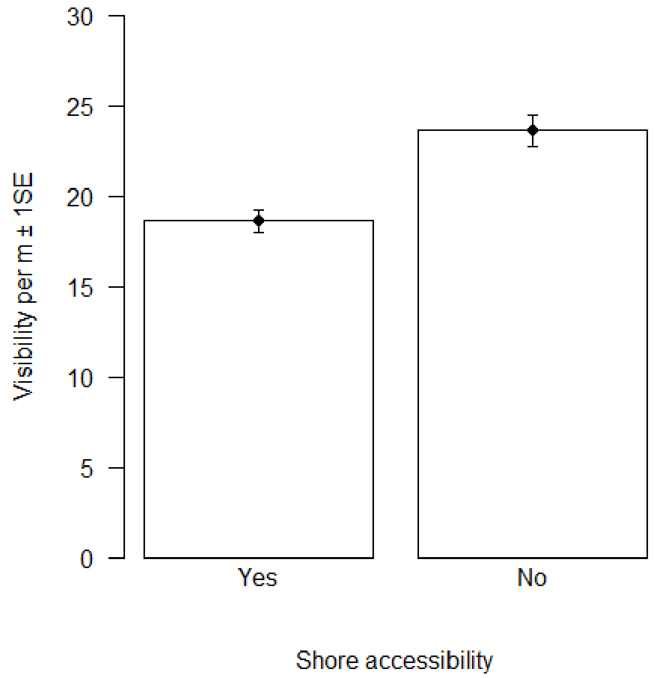

Figure B.11 Impact of shore accessibility on visibility at 18m depth. Outlying point (visibility <35m) removed.

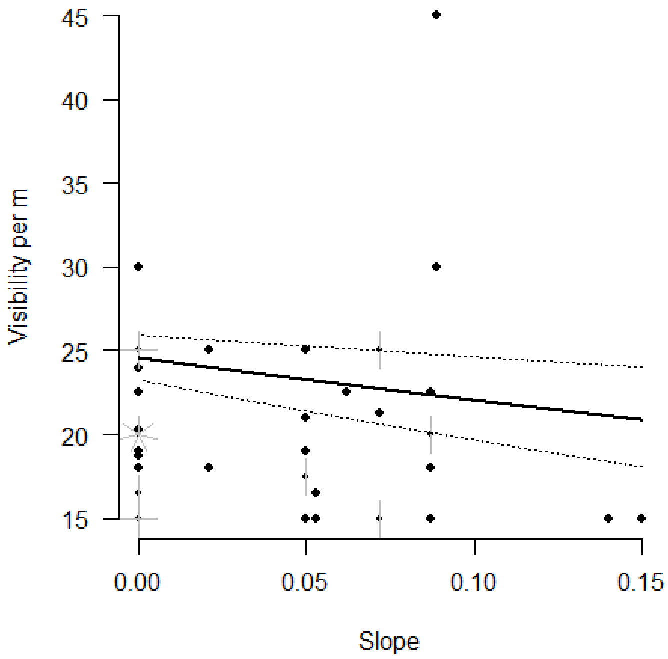

Figure B.12 Impact of watershed slope on visibility at 18m. Outlier at 45m removed from model estimate. Dotted lines upper and lower confidence intervals of impact of slope