# Exploring patterns of coral ecological niche construction in coral reef ecosystems

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# Contributions

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Viviana Brambilla designed the chapter with help from Maria Dornelas and Josh Madin. Fieldwork and data collection were carried out by Viviana Brambilla, with the help of Maria Dornelas, Josh Madin, Oscar Pizarro, Stefan Williams, Rachael Woods, Kyle Zawada, Damaris Torres-Pulliza, Nader Boutros, Luisa Fontoura, and Wilhelm Marais. Viviana Brambilla analysed and interpreted the results, with insights and guidance from Maria Dornelas and Josh Madin.

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# Thesis abstract

Ecological niche construction is the process through which (i) organisms modify environmental states and (ii) their modifications favour the organisms' fitness in return. Ecosystem engineers are an obvious class of putative niche constructors since they produce environmental change modulating resource flow within their ecosystems. Corals, a well-established group of autogenic ecosystem engineers, are a prime example of this class since through their own skeletal structures, they create the reef habitats they inhabit. This thesis aims at investigating coral ecological niche construction patterns in coral reef ecosystems.

To understand how corals modify the reef environment (i), I show that reef quantitative surface descriptors that measure coral reef engineering affect patterns of light availability among reef habitats (chapter 2). Furthermore, I performed a coral reciprocal transplant experiment to assess to what extent coral could provide diverse habitats through plasticity. I detected that high plasticity in niche-constructing traits results in a higher ability to provide diverse habitats, under different environmental conditions (chapter 3).

To understand if coral engineering activity was favourable to their own fitness (ii), I have studied patterns of coral recruitment across differently engineered habitats. I showed an increase in settler presence on artificial tiles deployed in the field along a gradient of coral-built structural complexity, measured as surface rugosity (chapter 4). I also showed an increase of juvenile abundance across reefs characterized by small-scale high fractal dimension and large-scale high surface rugosity, both being measures of coral engineering activity (chapter 5).

With this thesis I aimed at clarifying the role of corals as ecological niche constructors, enabling a future description of coral niche construction as evolutionary agent.

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# Chapter 1. General Introduction

## 1.1 Niche construction theory framework

In the 20th century, evolutionary biology focused on merging Darwin's ideas of natural selection (Darwin, 1859) and Mendel's discoveries of genetic inheritance (Mendel, 1869) together in a mathematical and statistical framework (Mayr 1982; Wright 1942; Fisher 1930*), that served as the basis for the modern evolutionary biology studies (Mayr, 1984). In the last decades, recent discoveries in the field of ecological developmental biology (Eco-Devo, (Gilbert, 2001; Gilbert, Bosch and Ledón-Rettig, 2015), epigenetics (Goldberg, Allis and Bernstein, 2007), population ecology (Schoener, 2011) and behavioural ecology (Badyaev, 2005) highlighted the need for a new and expanded context for the study of evolution. The Extended Evolutionary Synthesis (EES) framework (Pigliucci and Müller, 2010; Laland *et al.*, 2015), proposes to replace the DNA-centric vision of evolution sustained by the Modern Synthesis since the 1930s, with one that puts the organisms - environment dualistic interaction in a central and active role, hence integrating ecology and evolution. Recognising this reciprocal causation helps to remove the boundaries between organisms and environment and considering the whole as an evolutionary unit. In this context, niche construction, *sensu* Laland et al. (Laland, Matthews and Feldman, 2016), can be considered an evolutionary force in its own right, since it systematically biases natural selection acting upon the niche constructor or the recipient populations resulting in fixation of traits that could not be otherwise fixed by natural selection alone (Laland, Odling-Smee and Feldman, 1999; Odling-Smee, Laland and Feldman, 2003; Laland, Matthews and Feldman, 2016). This definition gets back to Lewontin's idea of organisms and their environments evolving together, each one as a function of the other (Lewontin, 1983). Different concepts converge under this niche construction definition, such as the modification of the organismal environmental experience (Donohue, 2014) or the ecological inheritance (Erwin, 2008; Badyaev and Uller, 2009). The latter describes the passing on to descendants of inherited resources or conditions, left either through parental effect (Badyaev and Uller, 2009) or ecosystem engineering (Laland, Matthews and Feldman, 2016), which modify natural selection forces on the descendant. Most criticisms were focusing on the lack on novelty they were bringing on the table, as processes and concepts close to the nct already served the used (TABLE 1)

Ecosystem engineers are an obvious class of putative niche constructors (Barker and Odling-Smee, 2014; Matthews *et al.*, 2014; Laland, Matthews and Feldman, 2016) since by producing long-term environmental changes they can affect macroevolutionary paths and biodiversity (Erwin, 2008). Corals, as autogenic bioengineers (Jones, Lawton and Shachak, 1994b) are a prime example of this class since they create habitats that host other species while enhancing their own fitness. Their capacity to build structures potentially biases the evolutionary processes through modifications of environmental states - and then natural selection - both at the macro and at the micro scales. From an ecological and evolutionary point of view, it is remarkable that the structures they build persist beyond the life span of the individuals that built them and needs to be taken into account when performing modelling to consider the different time scale of the ecosystem response (Hastings *et al.*, 2007).

Traditionally, ecosystem engineering has been studied in terms of feed-forward ecological effects on other species, largely ignoring feedbacks on the agent at evolutionary scales (Kylafis and Loreau, 2008). In fact, dealing with bioengineers mainly meant joining ecosystem ecology and population biology (Lawton, 1994), an approach that already found some applications in coral reefs (Bozec *et al.*, 2013; Bosch *et al.*, 2014). Introducing bioengineers in a niche construction context means to demonstrate that they not only modify the ecosystem but also modify their selection pressures and bias their evolutionary processes. It means integrating ecology and evolution (Barker and Odling-Smee, 2014; Laland, Matthews and Feldman, 2016). For example, Erwin tracked macroevolution of benthic ecosystem engineers from the Paleozoic, arguing that their outputs persisted over geological time giving positive feedbacks to the engineering populations through niche construction (Erwin, 2008).

Matthews et al. presented three practical criteria to test whether or not an organism is a niche constructor (Matthews *et al.*, 2014; after Odling-Smee *et al.*, 2013). First, the niche constructor must change its external environment, through behavioural, physical/chemical or other metabolic processes (Donohue, 2014; Laland, Matthews and Feldman, 2016). Second, these modifications must bias natural selection upon the organism itself and/or other organisms, either positively or negatively (Zahavi, 1974; Matthews *et al.*, 2014). Third, the modifications must leave a trace in the evolutionary history of the organisms involved, in the form of an evolutionary response to the environmental modification (Matthews *et al.*, 2014). While criteria 1 and 2 can be tested in an ecological framework, criterion 3 applies to an evolutionary time scale. The first two criteria describe an ecological feedback loop that can lead to diverse consequences, ranging from the local extinction of the responding population, to triggering trait fixation (criterion 3).

The ecological mechanisms niche constriction entails deserve more attention and are the focus of what has been described as *ecological* niche construction (Kylafis and Loreau, 2008, 2011; Barker and Odling-Smee, 2014). According to Kylafis and Loreau, who first described this concept, ecological niche construction is the sum of the "activities of a species that result in niche-improving impacts" (Kylafis and Loreau, 2011). In their view, ecological niche construction could be either direct (i.e. the niche of the constructing species is improved by its activities) or indirect (e.g. the niche of competing species gets deteriorated), but mainly focused on the feedback on the acting species. Barker and Odling-Smee relaxed the concept of ecological niche construction by including the possibility of having niche-constructing populations and recipient populations that do not coincide (Barker and Odling-Smee, 2014). According to this definition, we can have scenarios where directly or indirectly, one niche-constructing population affects multiple recipient populations or vice versa. This led to the investigation of collective niche construction, where groups of species with certain sets of traits would affect whole ecological communities (Matthews *et al.*, 2014; Bråthen and Ravolainen, 2015). In the Norwegian tundra, for example, plant species of the same growth form and known to have group-specific environmental effects, act as collective niche constructors and drivers of species diversity, without interfering with orthogonal occurring environmental gradients (Bråthen and Ravolainen, 2015).

## 1.2 Corals reefs as study system

In coral reef ecosystems, hermatypic scleractinians corals, also called stony corals (phylum: Cnidaria), act as prime ecosystem engineers. These organisms develop hard skeletons to protect the soft polyps' bodies, shaping extreme complex and heterogeneous habitats that harbour one of the most biodiverse communities in the world (Veron, 1995). Most of those corals rely on an intimate symbiosis with dinoflagellate algae, the zooxanthellae (*Symbiodinium spp.)*. Given the number of other living organisms that inhabit coral built structures – both at the macro and in the micro scale – and their capacity to modify external environmental states as ecosystem engineers, there is great potential in using them to test the niche construction processes. However, the focus of coral reef research has been on detecting plastic responses to the environment and not on the active role they play in shaping it. The general trend so far has been to focus on the phenotypic response of an external (environmental) parameter viewed as an extrinsic factor from the organism. Thus, the challenge remains to go one step further and studying corals as ecological niche constructors (Figure 1.1).

Corals are structural obligate bioengineers, which means that they modify the ecosystem by their own physical structure without the possibility to do otherwise (Jones, Lawton and Shachak, 1994b, 1997; Cuddington, Wilson and Hastings, 2009; Berke, 2010). In the process, they can increase heterogeneity, modulate flow systems and sediment deposition, and enhance diversity and richness (Berke, 2010). Structures built by ecosystem engineers give a third dimension to otherwise almost flat surfaces and affect local environmental conditions, increasing in this way microhabitat diversity. Structures per se, regardless from other indirect modifications they bring to the local environment, act as an alteration and affect habitat provision patterns within the ecosystem. And the spatial distribution of environmental conditions can determine where organisms can and cannot live (Hutchinson, 1957), through a process known as environmental filtering (Keddy, 1992). Thus, direct and indirect effects can act upon the local reef community composition and relax the environmental filter that would be in place without the presence of coral individuals (C2 in Figure 1.1).

Furthermore, corals are clonal modular organisms where each module (i.e. the coral polyp) engages in persistent bioengineering activities. The results of these bioengineering activities serve as basis for the next generation, having extended temporal and spatial scale consequences (Hastings *et al.*, 2007). As the skeleton of dead corals is left behind in the reef continues to affect the environment, it can be considered ecological inheritance for the future generations, potentially having evolutionary consequences (Erwin, 2008).

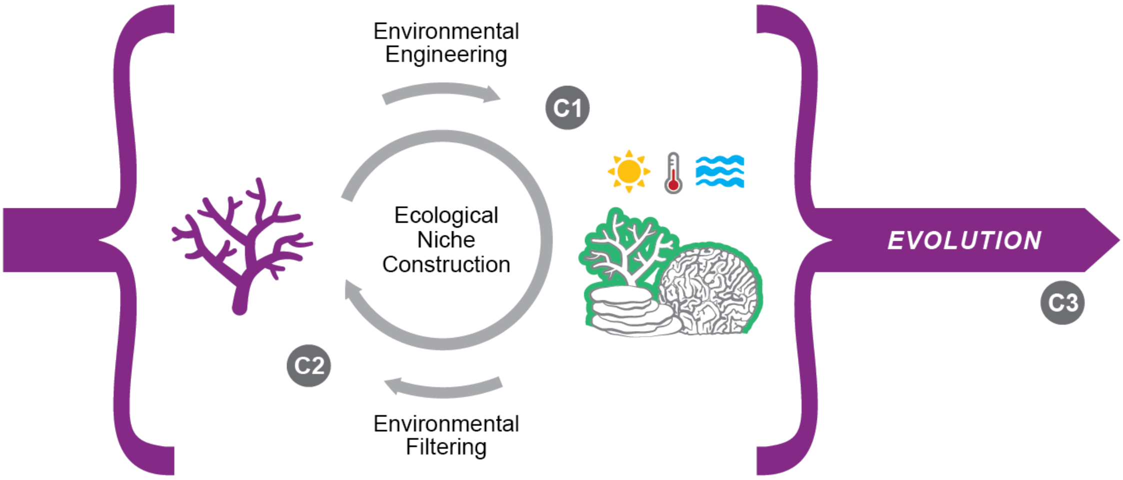

**Figure 1.1 – Evolution of coral through niche construction.** Ecological processes such us ecosystem engineering and environmental filtering, both detectable at ecological time scales, plausibly play an important role in coral evolution. Corals are obligate physical ecosystem engineers, since they create and modify the habitat around themselves. Their physical structures inherently modify the environmental conditions that the colonies themselves will experience. Transforming the 3D structure of the reef is likely to bring changes in environmental patterns (flow, light and temperature). It also creates habitat and resources that other marine species exploit and thereby impacts community composition, which in turn plausibly changes the selective pressures on the coral. Over time, these ecological processes are likely to shape coral evolution. In the grey circles, the three criteria for niche constructions outlined in the introduction are paired to the presented processes. C1 = criterion 1, C2 = criterion 2, C3 = criterion 3.

## 1.3 On the use of the niche construction framework

Since its conception, niche construction theory received criticisms (Dawkins, 2004; Scott-Phillips *et al.*, 2014), mainly for its focus on evolution through non-gene-centred mechanisms. While this thesis does not aim at resolving this apparent controversy, it uses this framework as a helpful tool to explore the dual relationship between corals and their environment, even if in a merely ecological setting.

The role of coral in coral reefs can be classified into many different ecological categories at once, but niche construction captures all the aspects of interest that come from those many definitions (Table 1.1). For example, corals are coral reef foundation species, this is species whose traits define ecosystem functioning, and that have a strong role in structuring local communities (Dayton, 1972). As such, corals are often seen as the taxon that can stabilize reef communities and define which taxa type and identity could inhabit the local reef (Knolton 1992, Glynn and Enochs, 2011). In other words, they create reef niches. In section 1.2, we saw how they do so though as ecosystem engineers (Jones *et al.* 1994,).

**Table 1.1** - Definitions of some relevant concepts and the significance they acquire under the niche construction theory framework.

| | *Definition* | *Under niche construction theory* |
|---|---|---|
| *Foundation species (Dayton, 1971)* | Species whose traits define ecosystem functioning and community structure. Traditionally studied as proxy for the response to disturbances of whole communities. | By focusing on the active role of foundation species in the ecosystem, these organisms can be studied as niche constructors with focus on the impact of their traits in stabilizing environmental states. |
| *Ecosystem engineer (Jones et al., 1994)* | Organisms that modify their physical surroundings and as result modulate the resources availability and/or energy fluxes in their ecosystem. | Ecosystem engineers are the class of organisms that can engage in niche construction through alteration of the environment. The way and if their alterations can modify selective pressures is crucial. |
| *Extended phenotype (Dawkins, 1992)* | Extension of the concept of phenotype to include biological adaptations conveyed outside of the body of the organism. Extended phenotypes are traditionally considered as genetically controlled. | The environmental states modified by extended phenotypes are viewed as fundamentally different from independent extrinsic environmental states and they can alone non-randomly bias selective pressure. As such, reefs as extended phenotypes can correspond to that subset of niche-constructing activities that are biological adaptations. |
| *Eco-evolutionary dynamics (Pelletier and Garant, 2009)* | Field that studies ecological and evolutionary processes and mechanisms that take place at overlapping time scales. It aims at describing how ecological changes affect evolution, and vice versa. | Focuses on evolution through niche construction by explicitly recognizing environmental modification by organisms, ecological inheritance, and extended phenotype as a source of modified selection and the dual link between organisms and environment. |

Additionally, they also build external skeletal structures that can persist after death of the organisms and build the reef framework, while also providing raw material for sand formation. This phenomenon falls under the definition of extended phenotype (Dawkins, 1982). Ecosystem engineering and extended phenotypes define the reef environment as created by corals. How corals and the whole reef community live in an environment that is mediated and altered by coral presence becomes then obvious. As such, using the reciprocal evolutionary causation in the relationship between corals and their environment, a setting stone in NCT, as a framework for the forthcoming analysis seems optimal. In fact, eco-evolutionary models could explore ramification of reef ecological links for coral evolutionary history.

## 1.4 Environmental variables of relevance

To tackle how corals relate to their habitat it is important to understand which parameters are relevant to them. Environmental variables such as flow, light, and temperature among others, play an important role in shaping coral morphologies, but long-term studies on how corals affect these same environmental parameters are scarce.

### 1.4.1 Flow

One of the first environmental parameters that are recognised to have a determinant effect on corals fitness and shape is flow. There are 3 main flow scales to consider in coral reefs: the coral colony flow (colony scale, up to ~1m), the boundary level flow (1 to 10m scale) and the reef-scale flow (100 to 1000m) (Monismith, 2006). At each of these scales, the organism-environment reciprocal causation is readily evident, since coral morphologic phenotypic traits both respond to and cause variations in flow (Mass and Genin, 2008; Todd, 2008; Hench and Rosman, 2013). With increasing spatial scale, the temporal scale through which corals can affect flow variation increases too. One year is enough to change a colony morphology and consequently the colony level flow; but it takes decades and even hundreds of years to change coral reef morphology and affect the reef-scale flow, apart from when major disturbances (cyclones) hit. For this reason, mainly the two smaller scales are thought to be of primary interest for the purpose of studying ecological niche construction, while broader scales may be useful for macroevolutionary studies.

At the colony level, asymmetrical growth forms are related to flow for example in the the branching coral *Pocillopora verrucosa* (Chindapol *et al.*, 2013). Under unidirectional current, colonies grew allometrically and less compacted, developing branches pointing in the upstream direction (Chindapol et al., 2013). A broad range of calcifying organism's growth (corals and sponges) has been modelled through the study of nutrients diffusion and absorbing patterns on the surface of the organism at a given flow (see Kaandorp and Sloot, 2001; Kaandorp *et al.*, 2003, and more studies from the research group). By changing growth patterns and directions, corals can induce variations in the inside colony flow that can result in localised calcification and specific preferential growth (Lesser *et al.*, 1994; Carpenter and Patterson, 2007) and modified photosynthetic efficiency (Helmuth *et al.*, 2010). It can also result in an optimised branching orientation for maximising nutrient uptake or prey capture (Sebens, Witting and Helmuth, 1997). Flow determines maximum sizes and morphological preferences since it can cause mortality through mechanical dislodgement (Madin and Connolly, 2006) and is responsible for changing diffusion and thermal boundary levels thickness, buffering heat dispersion (Jimenez *et al.*, 2008), with respiration that normally improves with rising of flow conditions (Patterson, Sebens and Olson, 1991). To what extent these modified morphologies affect other habitat variables and coral related taxa in the field is still undetermined.

Focusing on a bigger scale (up to 10m), flow is spatially very variable around and between colonies (Hench and Rosman, 2013). In fact, measuring flow with high resolution (20 to 25 cm between samples) in Moorea backreefs, they found several acceleration zones between and over coral colonies, sometimes with an increase of 50% in the flow level. In addition, turbulence dissipation rates varied a lot between upstream and downstream areas of colonies or groups of colonies, being up to 20 times more powerful in downstream dissipations. By diminishing the spacing between branches, corals minimise internal flow since they enact a buffer effect that brings the flow to follow the outside surface of the coral (Lowe *et al.*, 2008). The long term ecological and evolutionary consequences of this remain unclear.

### 1.4.2 Light

Given the photosynthetic activity of the coral symbiont and its dependence on light availability (Muscatine *et al.*, 1984), this is a very important parameter to consider. Zooxanthellate corals rely on photosynthesis outputs for up to 95% of their energetic needs (Gattuso, Allemand and Frankignoulle, 1999) Moreover, light determines the latitudinal distribution of coral reefs, as their depth occurrence (Veron, 1995). The fraction of light that matters to corals corresponds to the Photosynthetically Active Radiation (PAR, 400-700 nanometre of wavelength), only a subsample of the visible light. Light availability influences coral growth form and calcification (M. O. Hoogenboom, Connolly and Anthony, 2008), both at the macro and at the micro scale. For example, foliose corals have been demonstrated to respond to light gradients maximising the planar area of the colony (M. Hoogenboom, Connolly and Anthony, 2008) and massive ones changing the geometry of corallites (Bruno and Edmunds, 1997; Todd *et al.*, 2004) in order to harvest more light.

At the reef scale, by growing in size, on the other hand, corals may determine the availability of light for other corals or benthic organisms, such us sponges, bivalves and algae. However, although light reduction beneath table corals increases towards the stem, the coral community living behind them was found to be no different than the local community, suggesting that shading may not be of competitive advantage between corals and other benthic fauna (Sheppard, 1981). Canopies of branching corals can also reduce light availability by half just below coral surfaces (Brakel, 1979).

### 1.4.3 Temperature

Temperature is another parameter that determines coral's global distribution (Veron, 1995). Temperature affects the symbiont fitness and furthermore causes bleaching events (Brown, 1997). Corals respond very differently to this parameter depending on species, region and environmental history. By modulating the pigmentation intensity in their tissues (by controlling zooxanthellae densities), corals can control temperature microenvironments surrounding colonies at a given flow and irradiance (Fabricius, 2006). Corals disperse heat into the water through the thermal boundary level: the thicker is the boundary, the less heat is dispersed. Hemispherical morphologies have thicker layers and higher surface temperature than branching corals under the same environmental condition, both in *in situ* studies and in aquaria (Jimenez *et al.*, 2008; Ong *et al.*, 2017; Stocking *et al.*, 2018). These bottom-up controls of temperature may be particularly relevant in the context of avoiding bleaching events.

At the reef scale, differences in water temperature measured simultaneously on the bottom of an Hawaiian reef were found as high as 0.7 °C (Gorospe and Karl, 2011). Depth, relative water flow, and substrate cover and type were are not significant drivers of the temperature variation found (Gorospe and Karl, 2011), and if this temperature variation was related to local differences in coral community structure (hence habitat surface complexity) remains unknown.

When the environment is considered extrinsic and totally unpredictable, then predicting ecological (and evolutionary) consequences is problematic. In contrast, when ecosystem engineers are taken into account, environmental consequences of organismal activities on selective pressures can be quantified (Hastings *et al.*, 2007). To make this possible, mechanisms of habitat construction need to be identified and relevant coral traits that may trigger them quantified.

## 1.5 Corals as ecosystem engineers and relevant traits

Organismal shape often varies in space and across environmental gradients, because we find different organisms living in different conditions, and because organisms grow differently through phenotypic plasticity. This is true for corals as well, which as physical ecosystem engineers can bias abiotic conditions in multiple ways. In fact, their structures define habitats both *per se* (modifying habitat surface geometry) and indirectly via other abiotic modifications (such for example the modification of flow patterns through superficial drag as mentioned in the previous section). Furthermore, by increasing spatial extent and considering coral assemblages instead of individual colonies (reef scale), organismal effects on the reef environment can be cumulative and affect habitats and community structure.

Complexity is linked to biodiversity for terrestrial ecosystems (e.g. in forests with birds (MacArthur and MacArthur, 1961) and arthropods (Lassau *et al.*, 2005)), and according to Takeshi and Araki this relationship is expected to be more predominant in aquatic systems for two reasons (Tokeshi and Arakaki, 2012). First, water is more viscous and denser than air. This poses greater drag forces to organisms that live in aquatic systems, which need to be adapted to currents (Mann and Lazier, 2013). As a result, physical structures that break the flow offer refugia against highly current-efficient predators and interfere with dispersal, both particularly important mechanisms for species coexistence. Second, while in terrestrial ecosystems there's a prevalence of feeding specialists whose habitat choice depends on the availability of their food source (e.g. insects in a forest), in aquatic systems sessile particle-feeding generalists prevail. Here, the 3D structure is crucial for holding particulate food available, especially for suspension feeders such as corals and other key marine habitat engineers, such as mussels in mussel beds and polychaete tubes in soft sediments (see references in Tokeshi and Arakaki, 2012). Consequently, issues that relate to habitat complexity may be more clearly identifiable in aquatic systems, including insights on the functionality and organization of the engineering community (Tokeshi and Arakaki, 2012).

In order to detect coral engineering activities and mechanisms that can trigger niche constructing processes, it is useful to focus on the measurements of traits that simultaneously describe characteristics of the corals and the habitat they provide. Thus, because reefs result from a cumulative effort of coral colonies, we can identify traits at both the colony and at the reef scale.

### 1.5.1 Colony scale

To measure the ability to modify the reef structure, coral growth is an immediate trait to consider. Faster growing corals have faster effects on modulating habitat availability than slow growing ones. Coral growth is then essential for maintaining habitat complexity and all the bioengineering activities in general. So far, growth rates have been measured in different ways with a lack of standardised methods, even though parameters obtained with different methods are widely compared (Pratchett *et al.*, 2015). A traditional way to describe growth is through the measurement of three parameters: linear extension rate (cm $y^{-1}$), bulk skeletal density (g $cm^{-3}$), and calcification rate (g $cm^{-2}$ $y^{-1}$), the latter obtained as the product of the former two (Dodge ad Brass, 1984). These parameters allowed us to understand different patterns on coral growth (Carricart-Ganivet and Merino Martin, 2001; Carricart-Ganivet, 2004;

Crook *et al.*, 2013; Manzello *et al.*, 2015; Tambutté *et al.*, 2015), but from a bioengineering perspective, linear extension fails to describe how the habitat changes in terms of three-dimensional complexity and extend of the structures being formed. These are important reef characteristics for recipient species that inhabit the colonies and for other reef builders, such as sponges and algae, which compete with corals for space. Skeletal density affects bioerosion patterns and consequently other species distributions (Highsmith R. C., 1981) and provide information about the space holding capacity and the longevity of the coral colony (Madin, Hoogenboom, *et al.*, 2016). Yet, instead of being linked to the physical three-dimensional structure, skeletal density is rather a trait that describes resource availability, which goes beyond aspects of physical engineering.

Colony growth and size are not all that matters. The diversity in three-dimensional occupancy needs to be described to allow us to scrutinize mechanisms of habitat provision. Colony growth form (morphotype) describes the general organization of coral skeleton in space and is linked to different coral demographic traits and ecological characteristics (Glynn and Enochs, 2011; Coker, Wilson and Pratchett, 2014; Alvarez-Noriega *et al.*, 2016; Madin, Hoogenboom, *et al.*, 2016). However, the use of this trait remains highly limited by its discrete nature, which does not allow considering the different types of space occupation that each morphotype can display. In fact, it shows great variation between and within species, being highly plastic in some cases. For example, clonal fragments of *Porites sillimaniani* develop branches only when transplanted to high-light conditions but develop hemispherical colonies otherwise (Muko *et al.*, 2000). At the reef scale, morphological zonation along reef crests or depth gradients is widely recognized (Veron, 1995). Species that can adapt foliose morphologies that maximize the colony planar area usually occur in forereef deep zones, tabular ones in zones of low flow like backreefs, and so on. Although they describe the shape of the organisms, it is impossible to measure differences within categories.

Novel metrics should be used instead of discrete growth form categories for detecting differences among coral shapes in a quantitative continuous fashion. Zawada et al. identify three categories of traits that capture how corals interact with the ecosystem: volume compactness traits, surface complexity traits and top-heaviness traits (Zawada *et al.*, 2019). Volume compactness traits measure how much coral skeletons are close to a sphere in their geometric arrangements and organize colonies in a gradient that goes from massive, spherical shapes to more slender and horizontally developed shapes (i.e. tabular or arborescent colony). In terms of habitat provision, the more compact the colony, the longer the structure will persist. The less compact the colony, the more microhabitat a colony can provide to other organisms such as fishes and invertebrates (Graham and Nash, 2013; Darling *et al.*, 2017). For example, less compact colonies associate with small size fishes (Alvarez-Filip *et al.*, 2011) and provide  refuge from predators (Wilson *et al.*, 2008). Top-heaviness traits measure how colony surface area and volume are distributed vertically and organize colonies in a gradient that goes from encrusting and massive shapes to laminar and tabular ones. In terms of habitat provision, top-heavy colonies provide sheltered habitat underneath them for organisms such as large fishes including ambush predators (Kerry and Bellwood, 2015). On the other hand, bottom-heavy encrusting corals may help consolidate the reef framework by calcifying over rubble, resulting in stable conditions for other colonizers. Surface complexity traits measure convolution of skeleton surfaces and organize colonies in a gradient that goes from smooth encrusting or boulder-like shapes to convoluted and branch-packed shapes, like corymbose or tabular growth forms. In terms of habitat provision, colonies with higher surface complexity increase environmental conditions diversity (such as in light and water flow) both nearby and within the colony itself (Chamberlain and Graus, 1975; Wangpraseurt *et al.*, 2012). Microstructural surface complexity may also increase larval recruitment of corals or other species by increasing turbulence near the substratum (as hypothesized in Hata *et al.*, 2017).

Uni- or bi-dimensional traits like colony size, planar area and polyp density have been linked to demographic rates (Hughes and Connell, 1987; Hall and Hughes, 1996; Madin *et al.*, 2014; Madin, Hoogenboom, *et al.*, 2016), and only recently three-dimensional traits are being tested as more powerful proxies of demographic rates (Zawada *et al.*, 2019), still leaving behind a huge potential for their application to measure bioengineering activities.

### 1.5.2 Reef scale

Studying if and how niche-constructing colony traits scale up not only determines if there are limitations in their use but also gives an idea of the potential scale-effect of a given niche constructing trait (Messier, McGill and Lechowicz, 2010). Looking at bigger reef scales makes sense because focusing on single colonies is reductive when looking for niche-constructing patterns in coral reefs, where habitats are built by more colonies altogether. Topographic complexity at the habitat scale is the trait through which corals maintain the high associated biodiversity and its reduction generally corresponds to an increase in homogeneity and a loss of reef productivity (Graham and Nash, 2013). Corals, through the reef structure they build, affect a wide range of other taxa. A recent study demonstrated that three-dimensionally complex hard substrates sustain higher abundance and diversity of mobile invertebrates, regardless of whether the corals are alive or dead (Nelson, Kuempel and Altieri, 2016). On the other hand, for fish communities, there is evidence to suggest that their declines follow coral loss, even for fishes that do not use corals as habitats (Pratchett *et al.*, 2011; Chase *et al.*, 2014). Overall, the presence of associated fish functional group enhances the spatial resilience of coral reefs and their capacity to establish ecological feedbacks (Nyström and Folke, 2001). As result, reef traits have repercussion on corals themselves, as well as on environmental parameters and the ecosystem in general. All of these modifications can feedback to the coral engineering population.

At the reef scale, complexity was traditionally assessed visually by ranking portions of reef based on broad description of increasing complexity (Polunin and Roberts, 1993). But fractal dimension and surface rugosity have been increasingly used to capture respectively the volume filling capacity and the surface convolution of the surface and describe continuously reef habitat complexity. For instance, fractal dimension measures the scalability of surface patterns and for 3D surfaces, ranging from 2 (perfectly flat surface) to 3 (perfectly fractal surface). In nature, these extremes are virtually impossible to find, but nonetheless more intricate surfaces have higher fractal dimension than smoother ones. Surface rugosity is measured as the ratio between the actual 3D surface of the habitat and its planar projection (Friedman *et al.*, 2012), such that a flat surface would have a rugosity of 1 and R would increase with increasingly convoluted surfaces. These two variables are tied together with height range (difference between the highest and the lowest elevation of a given surface), and the three together have been found to define a surface descriptor plane that can be used to investigate the repercussions of these reef traits (Torres-Pulliza *et al.*, 2020).

Fractal dimension and rugosity have been proposed as metrics for the measure of surface complexity in coral colony as well (Zawada *et al.*, 2019; Zawada, Dornelas and Madin, 2019). When considering reef scale metrics, it looks like these two variables can contain information on the prevalence of the other colony metrics in the assemblage to analyse. In Torres-Pulliza et al., we found that different reefs around Lizard Island (Australia) were occupying different portions of the surface descriptor plane. For example, high surface rugosity and small fractal regions of the plane would correspond to assemblages with compact and relatively mid-heavy boulder-like corals, while highly fractal region portions, would predominantly have mid- to top-heavy, not compacted colonies. It looks then as if these two metrics at the reef scale would be capturing differences at the habitat scale coming from differently top-heaviness or volume compactness metrics of individual colonies as well. Furthermore, at the reef scale, top heaviness and compactness metrics would need to be rethought in the way they are measured because of the different extent considered (i.e. it does not make sense to approximate the reef to a sphere, or it would be difficult to assess compared to which vertical profile top-heaviness would need to be measured), making scaling analysis more difficult.

So far, rugosity and fractal dimension have been found to be related to coral presence, abundance, and diversity (Leon *et al.*, 2014; Burns *et al.*, 2015a, 2015b; Storlazzi *et al.*, 2016; Duvall, Hench and Rosman, 2019; Torres-Pulliza *et al.*, 2020), promising to be the right metrics for measuring how coral modifies habitat within coral demographic dynamics.

## 1.6 Corals and reef habitat: how to make the link

The interconnection between variation in coral bioengineered niche-constructing traits, the environment and coral performance remains a critical scientific gap. To overcome it, measures of structures and identification of demographic traits that can be modulated by engineering activities are necessary.

### 1.6.1 Measuring structural traits

*Colony scale*

Apart from the lack of standard methods in measuring traditional coral traits (Pratchett *et al.*, 2015; Madin, Anderson, *et al.*, 2016), when they have three-dimensional nature, measuring them is not easy. Traditional methods to estimate size parameters such as volume and surface area of a given colony or fragment require the removal of the organisms, often resulting in the organism's death (Jokiel, Maragos and Franzisket, 1978; Naumann *et al.*, 2009). Among the most common, there are for example the water displacement method (Jokiel, Maragos and Franzisket, 1978) and the paraffin dipping/wax weighting method (Naumann *et al.*, 2009). Unfortunately, by using these or similar methods, continuous observations and monitoring are impossible to obtain, because the organisms are removed from their natural environment, and even if taken back to their site of origin, stress due to manipulation can bias coral performance afterwards. Nowadays, computer-assisted modelling methods provide accurate non-intrusive means to measure coral structural parameters like volume and surface area. While laser scanning is still an expensive solution, structure-from-motion algorithms offer an easy and economically accessible way to measure coral traits from photographs without manipulation. Structure-from-motion is a photogrammetric technique that allows the reconstruction of three-dimensional structures beginning from a sequence of two-dimensional images with surface overlap. This approach allows generating semi-automatically 3D surface models from 2D imaging (Westoby *et al.*, 2012). So far, the use of structure-from-motion in this field gave acceptable results with relatively inexpensive settings, and considerable effort has already been invested in demonstrating precision and accuracy of these methods at different scales in corals and coral reefs (Bythell, Pan and Lee, 2001; Figueira *et al.*, 2015; Gutierrez-Heredia *et al.*, 2016; Ferrari *et al.*, 2017; Pizarro *et al.*, 2017; House et al. 2018; and review by Bayley and Mogg, 2020).

When studying colony morphologies, more complex surfaces are more difficult to model in three dimensions and small colonies can be modelled with better accuracy (Bythell, Pan and Lee, 2001; Lavy *et al.*, 2015). Anyway, if structure-from-motion algorithms can detect small variation in the same colony along time periods, then traditional methods as staining and tagging to measure coral growth become unnecessary. Traditionally, the linear extension rate is obtained through repeated measurements of tagged portion of colonies or through staining, which allows identifying patterns of growing when from skeleton subsamples (Pratchett *et al.*, 2015). Different stains have been used with corals (i.e. alizarin red, calcein, and oxytetracycline), and so far, calcein has been demonstrated to cause the least stress for coral calcification (Holcomb, 2013). But both tagging and staining can lead to the inhibition of the calcification process biasing the determination of linear extension rates and sometimes requiring the loss of the organisms (Pratchett *et al.*, 2015).

Having 3D models of the colonies will also enable computing the colony shape traits described in the previous section 1.4.1. When structure-from-motion cannot be applied, using two dimensional proxies for those metrics should be sought, to avoid losing information on those traits.

*Reef scale*

Photogrammetry does not help only at the colony level. In fact, it has been applied also at the habitat level, generally to have estimations of habitat complexity (Leon *et al.*, 2014; J. H. R. Burns *et al.*, 2015). It is thanks to these digital models that informative metrics as reef fractal dimension and surface rugosity can be measured. Traditionally, the proxy that was used for rugosity was the linear rugosity index measured with the chain method, which gives an idea of the substratum complexity as the ratio between the length of a chain laid linearly along all the surfaces and crevices of the bottom and transect length. With the recent introduction of photogrammetry and the use of underwater stereo cameras, measuring complexity through digitalized elevated models is considered more appropriate and allows considering surface variation instead of a one-dimensional metrics (Zawada, Piniak and Hearn, 2010; Burns *et al.*, 2015b). So far, habitat complexity obtained with structure-from-motion procedures has always been related to the benthic cover types, without any integration of environmental variables. For example, Leon et al. reconstructed a linear transect of 250m by 1.5m and tested the capacity of surface rugosity and fractal dimension to relate to different benthic categories (Leon *et al.*, 2014), but the need for a better integration of 3D model reconstructions and ecological data has already been expressed, as the possibility to then develop reliable ecosystem models (Burns *et al.*, 2015a).

Considering the multiple scales at which photogrammetry algorithms can be used, this methodology seems appropriate to deal with ecological niche construction in its multiple expressions.

### 1.6.2 Assessing coral performance: coral settlement

Assemblages comprising diverse morphologies increase growth rates in corals, relative to the when the same species are growing in monocultures (McWilliam, Chase and Hoogenboom, 2018). This means that varied habitats may increase coral primary production, in accordance with niche construction predictions. But growth is only one way of measuring coral performance (Hunt and Hodgson, 2010).

Morphological and environmental diversity can have affect coral fitness by establishing feedback loops that increases success in early stages of coral ontogeny. Corals have a planktonic life stage and larval recruitment success is key to the persistence of the reef ecosystem (Bellwood *et al.*, 2004). At the end of the planktonic stage, coral larvae need to settle on suitable substratum, metamorphose and start the benthic life. As with other benthic marine organisms, corals undergo severe early-life stage bottlenecks, and recruitment success depends on both abiotic and biotic factors (Ritson-Williams *et al.*, 2009). For example, crustose coralline algae (CCA) release chemical cues that induce the coral to settle and metamorphose (Heyward and Negri, 1999). In contrast, macroalgae can compete with corals for space and negatively affect coral recruitment (Mumby *et al.*, 2006). Coral larvae rely on micro-eddies created by small structural obstacles, such as sea urchin burrows in the field (Birkeland and Randall, 1981) or 1-cm blocks in the lab (Hata *et al.*, 2017), to be able to find suitable substratum and attach.

Once metamorphosized, post-settlement processes transform a settled polyp into a coral colony, via asexual reproduction and the production of polyp clones that results in growth of the colony. The chances of survival of corals increase as corals grow (Vermeij and Sandin, 2008). Among causes of death at this juvenile stage, there are competition, predation and disturbances such as bleaching and reef diseases (Ritson-Williams *et al.*, 2009). For example, algae prevalence may be detrimental to juvenile corals, since it reduces substratum available for coral to grow and reduce light availability at the bottom (Hughes and Tanner, 2000). While herbivory may help controlling algae prevalence, herbivore fish and invertebrates may kill small recruits while grazing, contributing to a decrease in coral recruitment overall (Doropoulos *et al.*, 2016). In this context, the habitat where corals settle play an important role in modulating their early survival. Non-exposed habitats, presumed to be with low productivity potential as of typically low light environments, protect coral recruits from stresses and disturbances common on outer reef surfaces, resulting in higher survival (Babcock and Mundy, 1996). Observational studies found also more juveniles in crevices (Doropoulos *et al.*, 2016).

As a result, settlement and post-settlement processes may be modulated by local habitat complexity. Reef fine topography, resulting from coral engineering, may thus have a sustained effect on coral fitness and systematically bias coral fitness upon natural selection and a signal on number of settlers or recruit could be detected.

## 1.7 Conclusions

This introduction highlighted critical gaps in our understanding of niche construction in corals. The study of novel traits and linkages of biotic and abiotic ecosystem factors might open the possibility to approach niche construction from a new unique perspective, enabling novel investigations in coral reefs ecosystems.

The measurements of different environmental variables along with novel three-dimensional coral traits can thus allow to: i) define relevant traits to study coral as bioengineers under a niche construction perspective; ii) assess to what extent selective patterns can be biased by bioengineering activity; iii) describe their covariance and relationships along natural gradients, and eventually iv) integrate coral engineering activities in ecological and evolutionary modelling.

Approaching ecological niche construction mechanisms in coral reef environments is a good starting point for using coral reefs as models for niche construction theory. Comprehensive monitoring along coral cover gradient can give an estimation of corals role in maintaining high heterogeneity, both in environmental variables and community composition. Which structural trait can better predict environmental heterogeneity and population performance can also be assessed. Complementary studies as transplant experiments enable niche constructor abundance manipulation and thus measuring how coral, environment and other taxa interact via niche-constructing traits in new environments. Depending on the design, these kinds of experiment also allow insights on the role of plasticity in niche constructing traits.

Overall, this general introduction focused on the aspect of the extended evolutionary synthesis most relevant for a first approach to niche construction on coral reef ecosystems. The morphological and physical approach was determined by the number of traits with potential for quantifying niche construction that were ready to use. This does not exclude the fact that other predictions could not be capable of generating further innovative research in coral reefs context. For example, evolutionary and symbiosis processes both with *Symbiodinium spp.* and total halobiont (microbiome) at the micro scale could represent the micro scale counterpart of corals niche construction, but a broader lab expertise e different literature review effort should be brought to the table.

## 1.8 Thesis overview

In my thesis, I am studying the role of corals as ecological niche constructors in coral reef system through both observational (chapter 2 and 5) and experimental (chapter 3 and 4) approaches. In particular, I will focus on corals as physical ecosystem engineers and on different aspects of the first and second criterion for coral niche construction (see section 1.1 and Figure 1.1) (Matthews *et al.*, 2014), approaching each criterion with 2 different analysis.

In chapter 2, I quantified natural light and temperature niche variation among reefs with different type of coral communities and detected the effects of reef structure on environmental niche availability. This analysis aims at clarifying the mechanisms by which corals modify the local reef environment, and identifying niche constructing traits through which corals affect environmental variables (criterion 1).

In chapter 3, I performed a reciprocal transplant experiment among 4 differently related species of corals to study plasticity in coral niche-constructing traits. This analysis aims at clarifying how coral plasticity can affect habitat provision (i.e. niche constructing patterns) depending on the local environment and how much of that is linked to coral evolutionary history and/or previous environmental filtering (criterion 1).

In chapter 4, I looked at the effect of coral structure and adult presence on local coral settlement in an experimental setting during the transplant reciprocal experiment described in chapter 3. This analysis aims to quantify feedback on the early stages of coral recruitment (settlement) and at evaluating the effects of local cumulative niche constructing traits in increasing chances of coral settlement (criterion 2).

In chapter 5, I looked at the effect of adult abundance and coral structure at different scales on natural patterns of coral juveniles among shallow reefs. This analysis aims at detecting the effects of cumulative niche construction as found on reefs on the success of coral post-settlement processes and evaluate the impact of reef traits at different scales (criterion 2).

In chapter 6, the general discussion, I bring together findings from the different analysis and discuss possible future research.

With this thesis I hope to clarify the role of corals as ecological niche constructors, enabling a future description of coral niche construction as evolutionary agent.

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** I acknowledge Fisher's contribution to the genetical theory of natural selection, but I want to disclose that I do not endorse his personal views on eugenics nor his political and racist pursues.*

# Chapter 2. Relationship between habitat geometry and environmental niches on coral reefs

The distribution of microhabitats across a landscape, mediated by the shape of its surface, is an important determinant of species occurrence and abundance. Smooth flat surfaces are expected to have more homogenous environments, whereas convoluted, complex surfaces have more variable environments. Here, I investigated the effects of habitat geometry on fine-scale environmental conditions. In particular, I quantified the relationship among patch-scale environmental variables (i.e., tide phase, light at the surface, depth), continuous surface descriptors (i.e., fractal dimension, surface rugosity, height range and angle of solar irradiance), and variation in light and temperature simultaneously sampled at 30 to 50 locations within reef patches. Remarkably, temperature differences across reef patches were less than the temperature logger margin of error (0.5 degrees C), regardless of where loggers were placed in amongst the complex reef structure. However, light varied greatly across patches and 37.5 – 43.3% of variation was explained by the environmental and surface descriptor variables. This chapter showed that quantitative surface descriptors, especially surface rugosity, can affect patterns of light availability. While meteorological and tidal-phase-linked variables also have an effect, structure-mediated environmental variation is important for environmental niches variability among reefs. In fact, while the former variables are much more temporally and stochastically variable (i.e. they depend on weather conditions or sun and/or tidal phase), reef geometry of the reef can consistently bias local environments, affecting habitats in ways that are likely to accumulate and eventually interfere with ecological processes of the reef.

## 2.1 Introduction

The spatial distribution of environmental conditions can determine where organisms can and cannot live (Hutchinson, 1957). Mechanistically, environmental conditions can regulate local species occurrence and abundances by influencing biological and ecological processes such as physiological status (Bradford and Hsiao, 1982), recruitment (Underwood and Denley, 1984), competition (MacArthur and MacArthur, 1961), and predation (Huffaker, 1958). The distribution of microhabitats within a landscape should be mediated by the shape of its surface. Smooth flat surfaces are expected to have more homogenous environments, whereas convoluted, complex surfaces have more variable environments. A recent advance on the quantification of habitat structure (Torres-Pulliza et al 2020) allows testing these hypotheses for highly complex habitats such as coral reefs. Here, the effect of surface structure on local environmental conditions across coral reefs is investigated.

Surface complexity is an important regulator of coral reef ecology and influences reef productivity (Graham and Nash, 2013), metabolism (Long *et al.*, 2013), species distributions (Darling *et al.*, 2017; Torres-Pulliza *et al.*, 2020), and more. Many biological and ecological processes that are linked to local environmental conditions often display patchiness in the field (e.g., coral bleaching and mortality; Glynn, 1996). Environmental conditions are affected by the local physical structure of the reef habitats (Shashar *et al.*, 1996; Lowe *et al.*, 2005). Coral reef structures are mainly built by hard corals, colonial organisms that secrete calcium carbonate as sessile exoskeleton than can have many different morphologies (Veron & Stafford-Smith, 2000). As a result, reef complexity can vary tremendously, depending on the coral species present and the ecological and geological history. Individual colony morphologies can affect the local environmental variables, such us flow (Hench and Rosman, 2013), temperature (Jimenez *et al.*, 2008; Ong *et al.*, 2017) and light (Brakel, 1979; Fabricius, 2006). However, the collective effect of structure on the environment at the reef scale remains poorly understood. Here I quantify the effects of coral reef scale habitat complexity on local environmental conditions by focusing on light and temperature.

For corals, the foundational taxa for coral reefs, light and temperature are two particularly important environmental variables. Corals rely on photosynthesis by unicellular algae (zooxanthellae) for energy supply and need the right environmental conditions to have an efficient symbiosis (Muscatine, 1973). Zooxanthellate corals rely on photosynthesis outputs for up to the 95% of their energetic input (Gattuso, Allemand and Frankignoulle, 1999) and comprise most reef-building species. If local light and temperature increase too much, the zooxanthellae get expelled from the coral causing bleaching, a starving condition that can lead to coral mortality (Brown, 1997).

Water temperature affects coral growth (Buddemeier and Kinzie, 1976), reproduction (Ritson-Williams *et al.*, 2009) and survivorship (Hoegh-Guldberg et al., 2007). Temperature and solar radiation thresholds for coral bleaching have been experimentally defined for several species and vary across taxa (van Oppen and Lough, 2009) and high sea water temperatures have been shown to increase bleached coral coverage in the field (Hoegh-Guldberg, 1999a). However, the cause for small-scale patchiness in bleaching spatially on reefs remains unclear. Boundary layer thermal profiles of individual colonies show that different morphologies (Jimenez *et al.*, 2008; Ong *et al.*, 2017) and colours (Fabricius, 2006) can have a different effect on the temperature of the coral living tissue. These studies controlled for irradiance and flow, since these parameters affect temperature and modify the boundary layer shape. For example, hemispherical massive morphologies have thicker layers and higher surface temperature than branching corals under the same light and flow condition, both in *in situ* studies and in aquaria, with differences up to 1°C (Jimenez *et al.*, 2008). Corals are morphologically plastic when exposed to different environments (Todd, 2008) and this may be particularly relevant in the context of avoiding bleaching events or increase individual fitness (Hoogenboom and Connolly, 2009). The combined effect of multiple coral colonies (i.e. a reef habitats) should cause water temperature to vary within reefs. For example, since temperature is linked to flow (Jimenez *et al.*, 2008), we can imagine that stagnant portions of water bodies may heat up more than where there are currents. Yet, the effects of reef structure on the surrounding water temperature is not well understood. Differences in water temperature measured simultaneously on the bottom of an Hawaiian reef could be as high as 0.7 °C (Gorospe and Karl, 2011). Depth, relative water flow, and substrate cover and type were are not significant drivers of the temperature variation found (Gorospe and Karl, 2011), and if this temperature variation was related to local differences in habitat complexity remains unknown.

Light is another important variable for corals and coral reefs. For instance, light availability determines the latitudinal distribution of coral reefs and their depth (Kleypas, McManus and Meñez, 1999). The fraction of light that coral zooxanthellae, and plants in general, use for photosynthesis corresponds to the Photosynthetically Active Radiation (PAR) wavelengths (400-700 nanometre), a subset of the visible light. The integral of PAR over time (µMol/m$^2$) is a measure of the energy per area that corals can receive to photosynthesize and coral colonies have been shown to optimize their energy acquisition through morphological organization (M. O. Hoogenboom, Connolly and Anthony, 2008). With morphology being an extremely plastic trait in corals, light plays a big role in determining realized coral colony morphologies (Todd, 2008). The daily PAR integral available to a reef location at any given day is determined by: (1) light reaching the ocean surface, which is a function of sun angle and atmospheric conditions; (2) its attenuation with increasing water column height, which is in turn function of reef depth and tidal phase; and (3) physical structures of the local reef that may cast shadows. Thus, when considering local reef habitats, canopies of branching corals can reduce light availability by half just below coral surfaces (Brakel, 1979). Table corals of the species *Acropora hyacynthus* also shade understory colonies with consequences for their demography (Stimson, 1985). While some studies focused on the effect of single colonies, much less is done when considering reef habitats.

Traditionally, coral colony morphological complexity was measured either qualitatively (morph type) or with simple unidimensional metrics (branch length, branch tips spacing, maximum diameter). With the possibility to digitalize coral surfaces (through laser scanning or photogrammetry) coral morphology can now be quantified through a set of continues variables that capture different aspects and functions of the geometric organization of the colonies (Zawada et al., 2019). The same applies to coral reefs and reef habitat complexity. Traditionally, reef complexity was measure either qualitatively (visual assessment) or with simple metrics with the aid of field equipment (Graham and Nash, 2013). For example, a rugosity index was used as proxy for complexity and was commonly measured with chain and transect tape in the field. With the possibility to digitalize reef surfaces (through side-sonar or simultaneous-location-and -acquisition mapping) reef complexity can now be defined through a set of variables that capture different aspect of the geometric features of the reef (Burns *et al.*, 2015b; Torres-Pulliza *et al.*, 2020). For example, surface rugosity can be computed as the ratio between the 3D actual surface of a certain portion of the reef and its planar projection on the horizontal plane (Friedman *et al.*, 2012). There are diverse quantitative surface descriptors that can capture diverse aspects of habitat complexity.

Fractal dimension (D), surface rugosity (R) and height range (H) altogether describe unique habitat structural conditions (Torres-Pulliza *et al.*, 2020). Fractal dimension (D) is a measure of scalability of surface patterns and can be used as a measure for volume filling capacity of a certain habitat surface. For 3D surfaces, D ranges from 2 (perfectly flat surface) to 3 (perfectly fractal surface). In nature, these extremes are virtually impossible to find, but nonetheless more intricated surfaces have higher fractal dimension than smoother ones. Surface rugosity (R) is measured as described above, such us that a flat surface would have a rugosity of 1 and R would increase with increasingly convoluted surfaces. While D focuses on self-similarity of the surfaces among scales, R tends to capture changing in elevation distributions. Height range (H) captures the elevation range of an area and is computed as the difference between the highest and the lowest elevation of a given surface. For example, high surface rugosity is expected when there are reef boulders or massive colonies. With multiple relatively small boulders at a given area, you can have high R and low H. With only a big one in the same area, you would have high H and high R. Because massive colonies have a smooth surface, D in the previous cases would be quite low. Tall fine-branching colonies would result in high H, R and D.

These three continuous variables may have consequences on local light and temperature availability. For example, the ability of branching colonies to break the flow and have thinner thermal boundary layer, may lead to a decrease in local temperature with increases in D. When big boulders are present, water can stagnate (Hench and Rosman, 2013), and portions of reefs can be shadowed, leading to an increase or decrease of temperature and light depending on sun exposure. In these scenarios, consequences on temperature and light would be bigger with higher H. Sun exposure would be relevant for local temperature and light niches as well. A surface exposure towards the sun (North in the southern hemisphere and South in the northern one) would catch more irradiance, with obvious consequences for light and temperature regimes. The inclination of a reef surface on the North-South plane (here referred as 'northing') can influence light and temperature niches. Lateral inclination of surfaces (i.e. towards East or West, here referred as 'sloping') would play a role as well, since it decreases the window of exposure to the sun by restricting exposure time only in the morning or the evenings.

Because reef structures determine reef habitats, understanding how reef structural traits can modify the environment in a quantitative framework can make us go full circle understanding the dual relationship of coral and environment. In this Chapter, the extent to which structural geometric traits affect light and temperature variation within reef patches will be determined. In particular, I used environmental variables (tide phase, light at the surface, depth) and local reef structural traits (fractal dimension, surface rugosity, height range, sloping and northing) obtained from reef digital elevation models to predict local variation in light and temperature within reef patches. At the scales analysed, I expect structural traits to play a role in defining light and temperature availability, as explained above and summarised in Table 2.1.

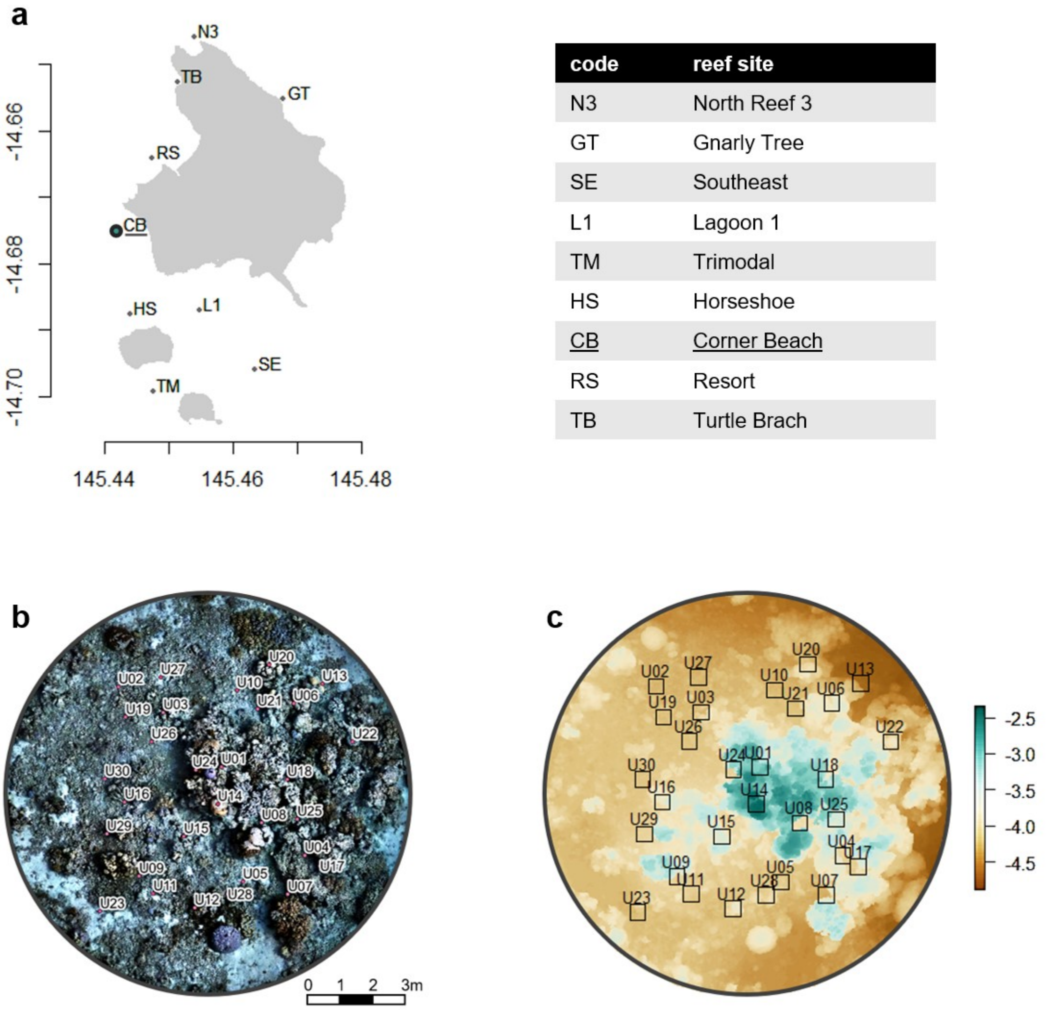
**Table 2.1 - Predicted relationship between light and temperature availability and reef geometric and weather predictors.** While positive or negative relationships among most pairs of variables were predicted, relationship with some surface descriptors are unsure. (NP = no prediction)

| | Predicted relationship | |
|---|---|---|
| | Light | Temperature |
| Fractal dimension (D) | NP | Negative |
| Surface rugosity (R) | Negative | NP |
| Height range (H) | Negative | NP |
| Sloping (a) | Negative | NP |
| Northing (b) | Positive | Positive |
| Mean water column height | Negative | Negative |
| Water column height at noon | Negative | Negative |
| Surface PAR | Positive | Positive |
| Mean temperature at -0.6m | - | Positive |

## 2.2 Methods

### 2.2.1 Data collection

I collected data in 9 shallow reef flat sites at Lizard Island (Great Barrier Reef, Australia, Figure 2.1) in November and December 2017,2018 and 2019. Sites were about 130 m$^2$ and have been chosen to capture a range of habitats and structural conditions.



| code | reef site |
|---|---|
| N3 | North Reef 3 |
| GT | Gnarly Tree |
| SE | Southeast |
| L1 | Lagoon 1 |
| TM | Trimodal |
| HS | Horseshoe |
| CB | Corner Beach |
| RS | Resort |
| TB | Turtle Brach |

**Figure 2.1 – Reef sites and 3D models of a site.** a) On the left, the map shows the reef study sites around Lizard Island (Australia). On the right, codes for reef sites table. b) and c) are example of datalogger unit locations within Corner Beach (CB, highlighted and underlined a) in 2018. c) shows the position of each unit as annotated on the orthomosaic of the reef site. c) is the digital elevation model, where every pixel of the map represents elevation (depth) data. 50-cm side rectangles highlight the respective areas used for computing surface descriptors of the local reef for each unit at this scale (i.e. explanatory variables).

### 2.2.2 Response variables

Every year, 9 sampling events on different days, one per site, were performed. Environmental variables were simultaneously sampled at 30 to 50 locations of each site on each sampling event. I used underwater dataloggers (HOBO Onset pendant) and recorded light (lux) and temperature (°C) values every 5 minutes for 24-h continuous periods (i.e. the sampling event). For 2017, temperature and light were recorded together, with a single datalogger, provided with both sensors. As later calibrations demonstrated (Appendix A), light exposure was causing overheating of air within the housing and the temperature sensor, biasing the temperature recorded for that year in ways that do not reflect water temperature variation. So, records from 2017 were discarded and in 2018 and 2019, temperature was measured by a separate datalogger wrapped in aluminium foil to reflect solar radiation and minimize heat absorption (Appendix A). According to year, one or a pair of dataloggers was attached to underwater weights to form logging units and units were deployed haphazardly within the sites. The positions of these units were then annotated on colour photomosaic maps of the sites (Figure 2.1b), printed on underwater paper. Some units changed position and inclination during the sampling (i.e. they were not in the same position in the map when they were picked up at the end of sampling) and were excluded from the analysis.

Light as response variable was computed as the daily integral (6am-6pm) of photosynthetic active radiation (PAR, µMol/m2/s) at the reef location. For more meaningful values, light measured in lux with the dataloggers was converted into PAR (µMol/m2/s) using the coefficient in Thimijan and Heins 1983 (Thimijan and Heins, 1983). The use of this conversion has been criticized in other studies as absolute value, but for the purpose of this analysis, it is likely that the rank order of light values measured within sites in either currency would be maintained.

Because I was interested in detecting variation within sites, temperature as response variable was computed as mean residual temperature at each sampling event; that is, the difference between the mean temperature of each unit and the mean temperature across units deployed at the same sampling event. This way, differences due to daily variation of water conditions among the various days did not contribute to the variation recorded.

### 2.2.3 Geometric variables

To compute geometric variables, digital elevation models of each site, each year, were obtained following the spiral method described in Pizarro et al. (Pizarro *et al.*, 2017), and the digitalization pipeline described in Torres-pulliza et al. (Torres-Pulliza *et al.*, 2020). More than 3000 stereo-pair overlapping images were captured and through simultaneous location and mapping algorithms I used GPS, stereo-camera images and altitude information to estimate an initial pose of the cameras. I then used Agisoft Metashape (Agisoft LLC, 2018) to produce a georeferenced 3D dense cloud. Since field conditions such as cloud cover or sunlight inclination on each particular sampling event affect the ability of the algorithm to approximate overhangs (Bryson *et al.*, 2017), I export DEMs with one depth value for coordinate pairs. DEMs had resolutions varying from 1.6 to 2.3 mm/pixel. Reef site alignment among years was done visually using multiple landmarks in ArcMap (ESRI, 2019) and corrected using the 'update georeference' tool. For 2018, only DEMs for 5 sites were obtained.

Locations of the logging units were annotated on orthomosaic maps printed in underwater paper in the field, then digitized to store geographic coordinates of each unit in shapefile format with QGIS (QGIS Development Team, 2019).

Geometric traits of the reef, this is the surface descriptors, were calculated for square patches centred on each data logger for three different sizes: 0.25 m, 0.5 m and 0.75m. The 0.5 m patch was chosen to represent a medium to large coral colony size, and the smaller and larger patches were chosen to see how sensitive my results were to the selection of patch size. Because the geometry of reef below where light loggers are deployed does not influence light readings, surface descriptors for the light analysis were calculated on DEM patches where all depth values greater than where the logger depth were transformed to the logger's depth; thereby flattening the DEM at the point of the logger (for examples, see Figure B.1). For temperature, no transformation of the DEM was required.

For each patch area and response variable, I computed:

- Surface rugosity (R), with the 'surfaceArea' function in the package 'sp' (Pebesma and Bivand, 2005).

- Height range (H), as the difference between the maximum and minimum elevations registered in the areas.

- Fractal dimension (D), using the formula from the geometric theory for habitat complexity by Torres-Pulliza et al. (Torres-Pulliza *et al.*, 2020)

$$D = 3 - \frac{\log\left(\frac{H}{\sqrt{2}\, L_0 \sqrt{R^2 - 1}}\right)}{\log\left(\frac{L}{L_0}\right)}$$

where L is the extent (i.e.,0.25 m, 0.5 m or 0.75 m) and $L_0$ is the resolution of the model (i.e., between 0.0016 to 0.0023 m, depending on the DEM resolution). To make sure that this formula would hold with the smaller areas considered in this analysis, I compared D obtained from the theory to D computed empirically with the variation method (Zhou and Lam, 2005). For this, each area was divided into square grids small enough to capture at least 2 order of magnitudes with the square grids division necessary to apply this method (Zawada and Brock, 2009). For D, flattening the surface for the light analysis was not possible because it would break patterns of self-similarity necessary to compute D. So D was computed on the unmodified DEM surface for light as well (see Figure B.1).

- Sloping (a), i.e. the lateral inclination of the surface, as absolute value of the slope respects the longitude axis of the surface best fit (Figure B.1c and d). To compute the best fit plane on the surface, I fit a linear model to elevation and spatial coordinates.

- Northing (b), i.e. the inclination of the surface with respect to the sun direction, as slope respect the latitude axis of the best fit plane on the DEM elevations (Figure B.1c and d) To compute the best fit plane on the surface, I fit a linear model to elevation and spatial coordinates.

All the analysis of the DEMs were carried out with R, version 3.6.0 (R Core Team, 2018), using the ‘raster’ and ‘sf’ packages (Pebesma and Bivand, 2005; Hijmans, 2020) where not specified otherwise.

### 2.2.4 Meteorological variables

To capture different weather conditions, I used surface Photosynthetic Active Radiation recorded at the weather station in Lizard and available online at the Australian Institute of Marine Science Data Centre (AIMS, 2020). Data were recorded every 10 minutes, and I used the daily integral over the sampling time as a predictive variable in both the models. Temperature at a depth of 0.6m was also available, and daily means were used as explanatory variable in the temperature model.

To account for differences of tidal regimes (hence daily mean depth of the unit, or water column height), depth of unit location was corrected by the tidal phase of each sampling event. Tide prediction at each round hour and maximum and minimum tide time were available from the Queensland Government website (Maritime Safety Queensland and Department of Transport and Main Roads, 2019). To predict continuous tidal regime for the whole sampling event duration, I used the 'TideHarmonics' package (Stephenson and Stephenson, 2017) and interpolated the available data with 37 harmonics, as suggested for mixed semidiurnal tide regimes (i.e. the tidal regime of Lizard Island). As such, mean water column was computed as the difference between the daily mean tide and the elevation of the logger unit.

Because interested in the daily PAR integral measured in each site location and light intake is higher at noon, water column height at noon was included in the model to account for the fact that tide and natural light daily variations are phasal and oscillate with different patterns. In fact, with a cloud-free sky, sun light hits sea surface at a low angle from sunrise, increases intensity until the sun is perpendicular to the surface (noon) and the decreases as the sun inclination decreases towards sunset time. When considering the integral, the light at noon will represent most of the daily light intake value. Tides follow circles with varying phases, depending on the moon cycle and the geographic position of the location of interest. Along time, the tide and light cycles can be in phase (high tide when light is high), in counterphase (tide is low when sun light is high) or in any combination between these two extremes. The interaction between these two variables may play an important role in affecting light and temperature patters. The two extremes depicted above would result in a lower reef daily integral and a higher one respectively, because tide can buffer the effect of the light that can penetrate to the reef, and vice versa. For this reason, I decided to account for the water column height effect on niches during the peak surface PAR availability and computed it as tide at noon minus the elevation of the logger unit.

### 2.2.5 Analysis

Because temperature differences across units fell within the precision limits of the temperature loggers used (0.52 °C), models for temperature were not fitted.

To model light, 10 predictors were considered: the five surface descriptors, the four meteorological variables and included site as a random factor to account for spatial autocorrelation. R and H were log-transformed before fitting the models.

I fit a model separately for each of the patch sizes that were used to compute surface descriptors (25cm-, 50cm-, 75cm-side squares). To account for spatial autocorrelation expected with the environmental variables (Gorospe and Karl, 2011), latitude and longitude were included as predictors in the models. I fitted general additive models (GAMs) with the function 'gam' in the package 'mgcv' (Wood, 2019). Coordinates were included in all the models with a Gaussian process smoothing basis and allowing latitude and longitude to interact (implemented by specifying 'bs = "gp", m=2' in the smooth function). All the other variables were included with a smoothing effect leaving a default of 10 smooths (k=10) as bases number (models sc). Models with variables as linear predictors were fitted as well (model lc). As sensitivity analysis for accounting for spatial autocorrelation, I refit the two models without the effect of coordinates, but with site as random effect specifying a ridge penalty type for each level as smoothing basis (model lr and sr, implemented by specifying 'bs = "re"' in the smooth). All analysis were made with R, version 3.6.0 (R Core Team, 2018).

## 2.3 Results

### 2.3.1 Variation in light, temperature and structure

Light in lux and temperature in °C were obtained (see Figure B.3 for an example) and transformed to daily light integral and sampling event temperature residual (Figure 2.2). A total number of 903 units for light and 302 for temperature were considered. Overall distributions can be seen in Figure B.4, together with pairwise comparisons of the distributions.

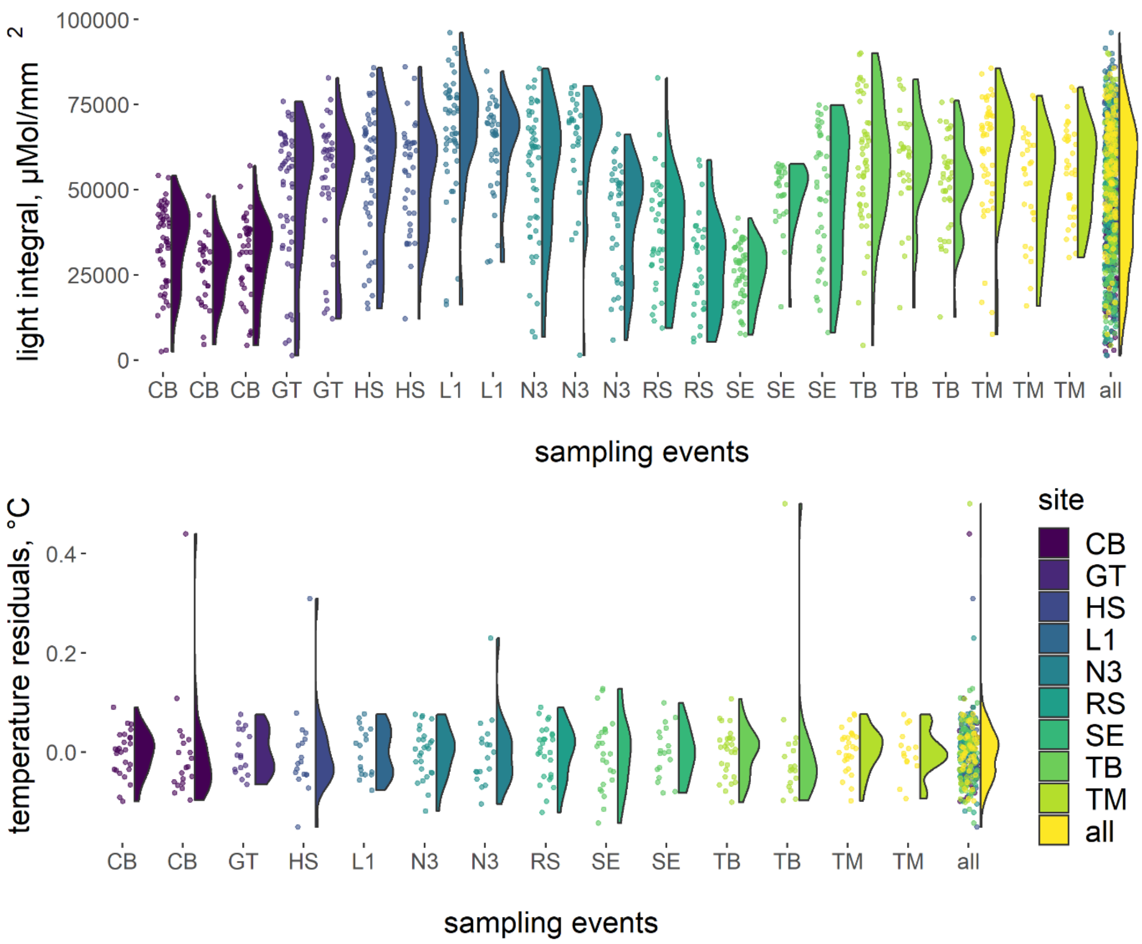


**Figure 2.2 - Light daily integrals and temperature residuals distributions among sampling events.** Samplings are color-coded by site. On the right, in yellow, the overall variable distributions. Most temperature residuals are within temperature sensor precision.

Light integrals varied from a minimum of 1260 µMol/mm$^2$ to a maximum of 96133 µMol/mm$^2$, spanning almost 2 orders of magnitudes. The daily integral distributions varied greatly among sampling events within same site (Figure 2.2). Despite differences in mean temperature registered among sampling events, temperature residuals at each site fell within the precision limit of the logger used, so models for this variable were not fitted.

Fractal dimension obtained by the theory closely mirrored values obtain empirically at the 3 scales considered (Figure B.3), so I used D from the theory in the models. All the other variables considered in the models were reasonably approximated by a normal distribution, after log transforming H and R (Figure B.4).

### 2.3.2 Explaining variation in light

Depending on the area considered for the surface descriptors, the model allowing a smoothed relationship with the predictors (models sc) including coordinates for spatial autocorrelation explained 42.2% – 43.3% (adjusted $R^2$: 0.403 – 0.414, Figure 2.4, Table 2.3) of the light variance, while including variables as linear predictors explained from 35.7% to 37% (adjusted $R^2$: 0.345 – 0.358, Table 2.2). Considering site as random effect instead of coordinates produced qualitative similar models (Figure B.5) which explained 35.6% to 38.8% of the variance in case of linear predictors (Table B.1a), and 42.0% - 43.0% in case of smoothed terms (Table B.1b). All the models show that spatial proximity (either when considering coordinates or reef site) significantly affected reef light niches (Table 2.2, Table 2.3 and Table B.1a-c).

Light integral decreases with increasing surface rugosity (Table 2.2, 2.3 and Figure 2.4) across all models considered. Fractal dimension and height range do not have a detectable effect in most cases. The exception is at the smallest scale, where I detect significant effect of both variables when used smoothed albeit affecting light in ways contrary to expectations (light integral increase, Figure 2.4). Therefore, in the two primary models fitted (lc: Table 2.2 and sc: Table 2.3), I could detect different effects of the geometric predictors on light at the smallest scale, while the bigger scales were more consistent (Figure 2.4 and 2.5, and Figure B.6).

When focusing to the meteorological variables, increased surface PAR integral consistently increased predicted light daily integrals among all models and areas considered (Table 2.2 and 2.3, Table B.1). Water column at noon is the only parameter related to tidal phase for which I could detect a significant effect across scales when using smoothed predictors (models sc: Table 2.3 and Figure 2.5 and sr: Table B.1a). As expected, the higher the water column, the lower the daily integral. For the bigger area considered in model sc, mean water column height also played a role, with an effect that is contrary to expectations: overall, higher mean water columns corresponded to higher light integrals.

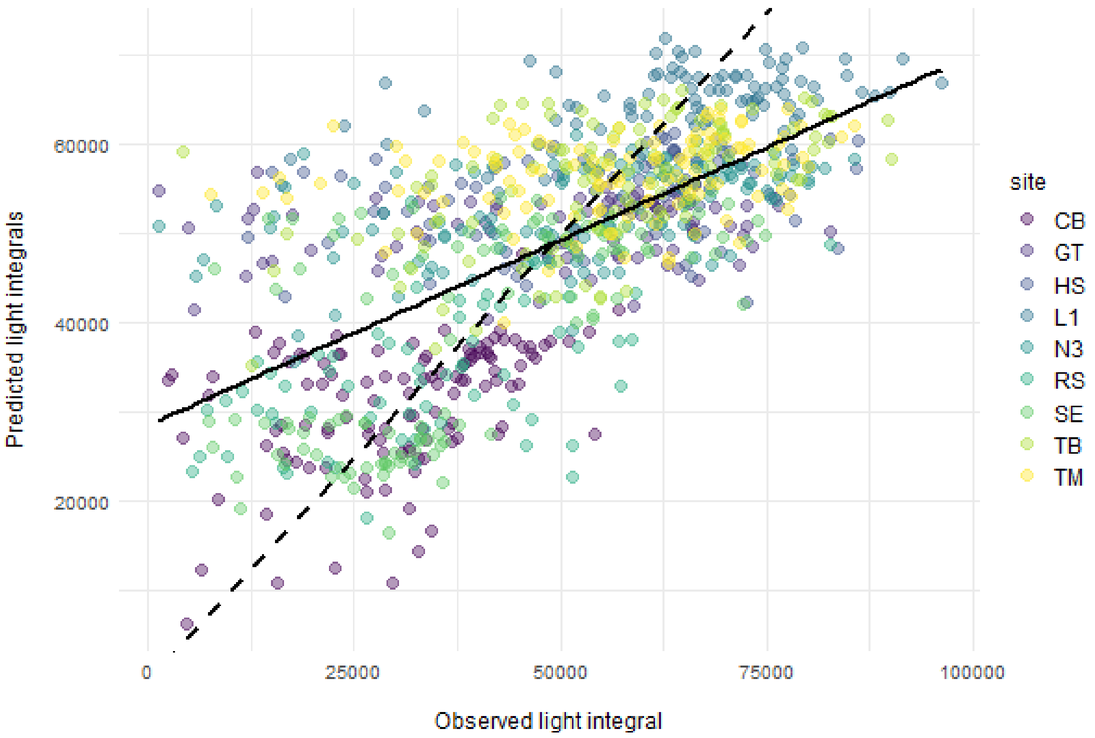


**Figure 2.3 - Model accuracy.** Light predictions as function of the observed values for models fitted with smoothed predictors and using 50-cm side areas to compute surface descriptors. The black solid line shows the best fit linear regression. The dotted line shows the identity (i.e. where predicted values would be the same as the observed). Dots are color-coded by site. For accuracy across all models and areas considered, see Figure B.5.

**Table 2.2 - Linear predictors and smoothed coordinates (lc) model coefficients.** Model coefficients, adjusted $R^2$ and deviance explained for the GAM model fitted with a smooth term for latitude and longitude for each of the area considered to compute surface descriptors. Statistic shows the T statistic for the linear predictors and the F statistic for the smoothed terms.

| | **25-cm side predictors** | | | **50-cm side predictors** | | | **75-cm side predictors** | | |
|---|---|---|---|---|---|---|---|---|---|
| *coefficients* | *estimates (SE)* | *statistic* | *p-value* | *estimates (SE)* | *statistic* | *p-value* | *estimates (SE)* | *statistic* | *p-value* |
| intercept | **50709.47<br>(19322.63)** | **2.62** | **0.009** | **85796.07<br>(21950.39)** | **3.91** | **<0.001** | **67513.22<br>(23804.11)** | **2.84** | **0.005** |
| fractal dimension | 12152.68<br>(8839.07) | 1.37 | 0.170 | -9234.34<br>(9896.94) | -0.93 | 0.351 | -2715.94<br>(10330.19) | -0.26 | 0.793 |
| surface rugosity | **-39367.63<br>(8248.04)** | **-4.77** | **<0.001** | **-27348.38<br>(9437.98)** | **-2.90** | **0.004** | **-26427.91<br>(10698.08)** | **-2.47** | **0.014** |
| height range | 4949.27<br>(2592.19) | 1.91 | 0.057 | -364.43<br>(2987.78) | -0.12 | 0.903 | -1683.73<br>(3410.59) | -0.49 | 0.622 |
| northing | 1839.38<br>(1276.97) | 1.44 | 0.150 | 3124.26<br>(1962.48) | 1.59 | 0.112 | 4418.46<br>(2687.54) | 1.64 | 0.101 |
| sloping | -42.50<br>(2119.92) | -0.02 | 0.984 | -3663.19<br>(3422.81) | -1.07 | 0.285 | -2832.56<br>(4779.92) | -0.59 | 0.554 |
| mean water column | -3956.09<br>(2794.12) | -1.42 | 0.157 | -2618.45<br>(2849.42) | -0.92 | 0.358 | -2218.47<br>(2934.38) | -0.76 | 0.450 |
| water column at noon | -144.42<br>(1993.05) | -0.07 | 0.942 | 59.30<br>(1996.49) | 0.03 | 0.976 | 143.55<br>(2013.05) | 0.07 | 0.943 |
| surface PAR integral | **3472.35<br>(625.51)** | **5.55** | **<0.001** | **3467.08<br>(627.27)** | **5.53** | **<0.001** | **3449.26<br>(631.14)** | **5.47** | **<0.001** |
| s(lon,lat) | **8.70** | **23.31** | **<0.001** | **8.77** | **22.72** | **<0.001** | **8.71** | **21.59** | **<0.001** |
| Observations | 903 | | | 903 | | | 902 | | |
| Adjusted R2 | 0.358 | | | 0.355 | | | 0.345 | | |
| Deviance explained | 37% | | | 36.7% | | | 35.7% | | |

**Table 2.3 – Smoothed predictors and coordinates (sc) model coefficients.** Model coefficients, adjusted R2 and deviance explained for the GAM model fitted with a smooth term for latitude and longitude for each of the area considered to compute surface descriptors. Statistic shows the T statistic for the linear predictors and the F statistic for the smoothed terms.

| | **25-cm side predictors** | | | | **50-cm side predictors** | | | | **75-cm side predictors** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *coefficients* | *estimates* | *statistic* | *p-value* | *edf* | *estimates* | *statistic* | *p-value* | *edf* | *estimates* | *statistic* | *p-value* | *edf* |
| intercept | **48696.07** | **96.07** | **<0.001** | **873.25** | **48696.07** | **95.66** | **<0.001** | **873.31** | **48714.61** | **95.16** | **<0.001** | **871.94** |
| s(fractal dimension) | **1.58** | **3.24** | **0.036** | **6.16** | 1.00 | 0.37 | 0.546 | 5.89 | 1.00 | 1.17 | 0.280 | 5.85 |
| s(surface rugosity) | **2.12** | **9.04** | **<0.001** | **1.01** | **3.11** | **3.03** | **0.014** | **1.00** | **3.73** | **2.71** | **0.019** | **1.01** |
| s(height range) | 1.01 | 4.82 | **0.029** | 2.84 | 1.00 | 0.25 | 0.616 | 2.66 | 1.00 | 2.81 | 0.094 | 2.38 |
| s(northing) | 1.00 | 3.01 | 0.083 | 2.73 | 1.00 | 3.11 | 0.078 | 3.96 | 1.00 | 2.72 | 0.099 | 4.69 |
| s(sloping) | 1.00 | 0.11 | 0.745 | 1.99 | 1.01 | 1.21 | 0.271 | 1.01 | 1.01 | 0.49 | 0.492 | 1.00 |
| s(mean water column) | 4.97 | 2.06 | 0.056 | 1.01 | 4.73 | 2.03 | 0.069 | 1.01 | **4.69** | **2.22** | **0.046** | **1.03** |
| s(water column at noon) | **2.22** | **4.59** | **0.005** | **9.20** | **2.08** | **3.98** | **0.011** | **9.29** | **1.87** | **4.26** | **0.010** | **9.28** |
| s(surface PAR integral) | **6.63** | **11.49** | **<0.001** | **7.68** | **6.48** | **11.19** | **<0.001** | **7.54** | **6.46** | **11.72** | **<0.001** | **7.53** |
| s(lon,lat) | **8.21** | **13.96** | **<0.001** | **1.01** | **8.28** | **13.55** | **<0.001** | **1.01** | **8.28** | **13.61** | **<0.001** | **1.01** |
| Observations | 903 | | | | 903 | | | | 902 | | | |
| Adjusted R2 | 0.414 | | | | 0.409 | | | | 0.403 | | | |
| Deviance explained | 43.3% | | | | 42.8% | | | | 42.2% | | | |

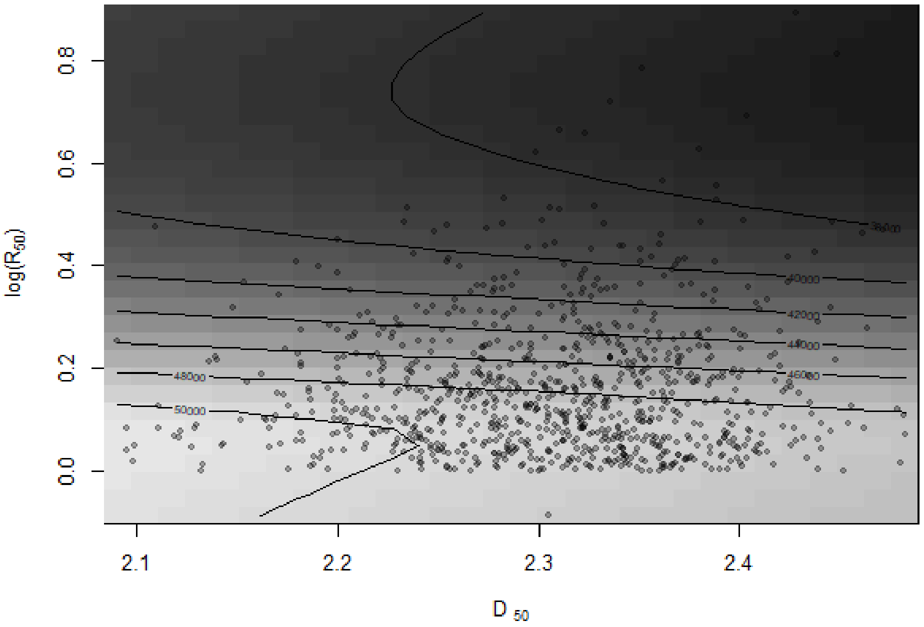


**Figure 2.4 – Light prediction on the habitat complexity plane.** Predictions of light among the space defined by two of the 50cm patch habitat complexity surface descriptors (D – fractal dimension, R – surface rugosity), obtained with the smoothed predictor fit. Dots are observed data. For predictions across all models and areas considered, see Figure B.6 and B.7.

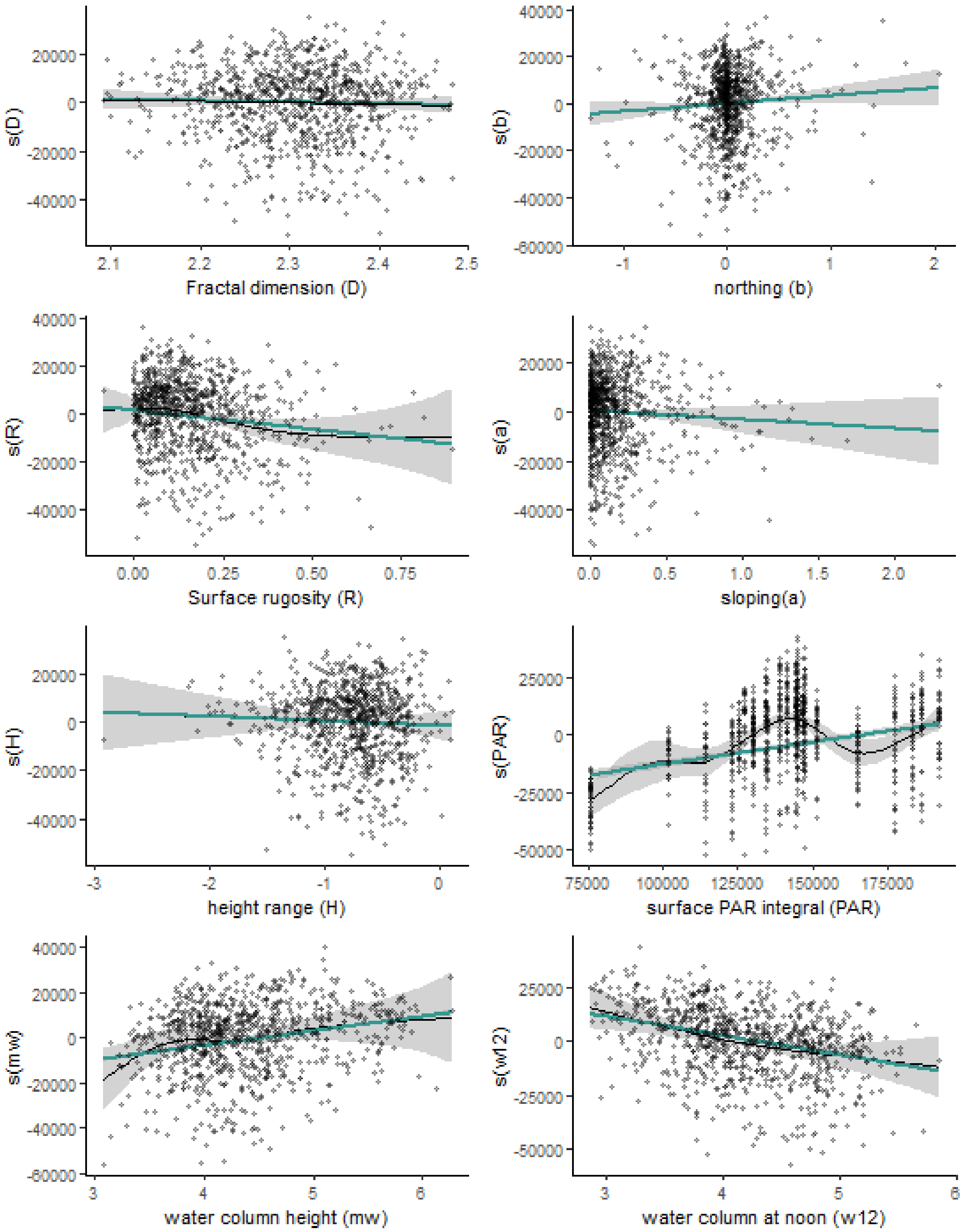


**Figure 2.5 – Smooth and linear effect plots when computing variables with 50-cm side areas**. In black the fitted smooth effects, in green the linear fits. Confidence intervals are shown for the smooth effects in grey.

## 2.4 Discussion

Among geometric variables, surface rugosity (R) was found consistently significant among areas, with light values decreasing with R. This means that more than height range *per se*, the local distribution of reef elevations mattered the most. High R means that there is a protuberance that can cast a shadow at some point during the day. Since neither northing nor sloping had significant effects on light integral, sun direction in underwater environment may be a poor predictor for light daily integrals at this scale. Statistically an effect of fractal dimension was not detected, probably due to the scale dependency of this variable. In fact, the variable considers self-similarity of structural patterns that are at a much smaller scale than the sensor size (mm vs. cm) and that are unlikely to produce shadows, and maybe rather refract and scatter light around. Nonetheless, there is a noticeable effect when rugosity is very low (Figure 2.4). Remarkably, temperature differences across reef patches were less than the temperature logger margin of error (0.5 degrees C), regardless of where loggers were placed in amongst the complex reef structure.

As predicted, there was a clear effect of light availability at the surface and of water column at noon in some models across all the scales. While depth is a constant variable for each location, water column height varies accordingly to tidal phase. Thus, water height accounts for temporally variable parameters, which are not constant through time as the surface descriptors were. Water column at noon seemed to best predict the interaction between daily light availability and tidal phase. Coral tissues temperatures have been found to peak when tide is low at noon (Jimenez *et al.*, 2008), hinting at the importance of this variable. Furthermore, from looking at the raw readings of light (Figure B.2), most of the light intake occurred around noon and considering water column at this time in the day seems like a good way to consider interactions among the sun and the tidal phases across different sampling days.

Among the scales considered, light variation was qualitatively consistent across the 50-cm and 75-cm scales; whereas, they differed at the 25-cm scale. At the smaller scale, predictions of light among the surface descriptors considered contrasted with expectations. Height range and fractal dimension coefficient estimates are positive when fitted as linear predictors and are significant when fitted with a smooth basis, still showing an overall positive trend (particularly evident in Figure B.6). A change in the response in all the three variables at once might be expected because of how they are inherently tied together. Nonetheless, this may suggest two things: i) small-scale local light refraction may increase with high fractal dimension, or 2) the irregularity of the reef surfaces caused this size to be too small to catch structural features which influence light patterns in the area.

Depending on the model, 37.5 – 43.3% of light variation was explained, which is quite impressive considering that for the predictions I assumed a flat-water surface. For instance, the sea surface is almost constantly changing its shape, breaking the assumption of vertical direction of light penetration enabling the use of depth to account for water light adsorption. This may explain why models tended to overestimate low daily integrals as shown by the difference between the sparse points locations on the top left of the plots in Figure 2.3 and the identity dotted line. This pattern can also be due to limitations posed by the nature of the surface model used. In fact, lower daily integrals were usually observed in crevices and close to overhangs which get simplified to vertical surfaces when producing 2.5D elevation models. Higher observations were made either at the bottom of very flat areas or at the top of an elevated structural feature, which experience very different environmental conditions, but had similar R, a, b and H, since the surface for computing those traits was flattened at the observation depth (Figure B.1). Since environmental variables are likely to be highly spatial and temporally correlated (Currie, Pétrin and Boucher-Lalonde, 2019), spatial location (either as coordinate pairs or site) explained differences among sampling events, as expected (Gorospe and Karl, 2011).

Contrary to expectations, the data did not detect spatial differences in temperature within reefs. This finding is surprising because different temperature regimes have been described at both larger and smaller scales (Bainbridge, 2017; Ong *et al.*, 2017). If water temperature is pretty much spatially constant at the reef patch scale, then morphological traits of each colony may play a primary role in defining niche regimes at which the coral tissues are exposed. Reef processes that display patchiness, such us bleaching and mortality, may be thus linked primary to light patterns differences and its interaction with temperature, rather than temperature *per se*. In particular, the present results suggest that more patchiness could be expected in relatively flat reefs (low surface rugosity) and especially if characterized by high fractal dimension. The lack of difference of temperature within reef location as measured in this study (daily temperature regimes) may also be overlooking variation through time or variation between sites, which are not the object of the present study but affect reef community dynamics (van Oppen and Lough, 2009). For example, mean water temperature may be different when considering longer time scales, with different tidal conditions and specific weather. Or differences may exist in mean temperature among sites (Bainbridge, 2017), rather than within site at a smaller scale, but the nature of this data does not allow to investigate this further.

This study focuses on the effects of reef habitat complexity on environmental niches using a quantitative continuous framework. By capturing different aspects of complexity, fractal dimension, surface rugosity and height range allow making different predictions and understanding different functionalities reef structures have. Adult coral colonies can reach sizes that are comparable to the areas considered to compute surface descriptors in this analysis. This means that major disturbances that alter coral communities (Madin *et al.*, 2018) can also lead to a considerable reshuffle of light niche variability in reef habitats. In nearly any ecosystems, living organisms create, modify or maintain habitats in which they live (Lewontin, 1983). Corals, as ecosystem engineers (Jones, Lawton and Shachak, 1994b), for instance modify habitat resources for themselves and other reef species, with consequences on their and other population and community dynamics (Laland, Odling-Smee and Feldman, 1999; Matthews *et al.*, 2014). Understanding the mechanisms behind ecological niche construction processes (Barker and Odling-Smee, 2014), for example investigating the link between habitat structures and habitat environmental variables, may benefit management and conservation of ecosystems (Boogert, Paterson and Laland, 2006). This would be particularly needed for coral reefs management since reefs are one of the most threatened ecosystems in the world. For example, coral bleaching often results from an interaction of environmental factors that increases coral metabolic stress (Fabricius *et al.* 2006). Irradiance is one of these factors and understanding how light niches correlate with geometric features of the reefs may help designing optimal areas for coral restoration projects.

In this chapter, I showed that quantitative geometric variables, i.e. the surface descriptors, can affect light niches in a quantitative framework. While meteorological and tidal-phase-linked variables also have an effect, structure-mediated environmental variation can still be important for environmental niches variability among reefs. In fact, while the former variables are much more temporally variable (i.e. they depend on weather conditions or sun or tidal phase), surface descriptors of the reef can consistently bias local environments, constantly effecting habitats in ways are likely to accumulate and eventually interfere with ecological processes of the reef.

# Chapter 3. Shaping coral traits: environment and genes

Physical ecosystem engineers are organisms that create and modify habitats via their own physical structures, thereby influencing all the taxa that are associated with those habitats. Understanding how plasticity and local environment determine the variation in their physical structure is necessary to understand their role in ecosystem dynamics and evolution, since they define the habitats available in the ecosystem. Here, I explore the morphological plasticity of corals in coral reef ecosystems, focusing on traits that describe habitat provision. To do so, I conducted a reciprocal clonal transplant experiment in which branching corals from the genus *Porites* and *Acropora* were moved to and from a deep and a shallow site within a lagoon in the Maldives. Survival and trait analysis showed that the transplant destination, which is the environment of exposure during the experiment, consistently induced different degrees of change in morphologies, particularly among the *Acropora spp*.. The origin of the corals (i.e. where the coral developed in the reef before transplantation) only affected some of the traits marginally and independently from whether the coral changed site of destination. As common in coral transplant experiments, there was genotype by environment interactions and intra-specific variation, showing that traits linked to habitat provision are phenotypically plastic. The results provide evidence that different local environmental conditions may consistently induce differently varied habitat availability in reef ecosystem, explaining how reef zonation and community structures are sustained on the long term by coral phenotypic plasticity.

## 3.1 Introduction

Ecosystem engineers are organisms whose presence or activity alters their physical surroundings or changes flow of resources within the local populations (Jones, Lawton and Shachak, 1994). Plants, for example, modify habitats within a forest with their structures (Callaway and Walker, 1997) and act as chemical engineers altering soil nutrients patterns with their root system for the whole soil ecosystem (Rovira, 1964). In the marine realm, some organisms act as physical ecosystem engineers through the accumulation of bio-constructed carbonate calcium structures. For example, some algae deposit calcium carbonate formations, some bivalves build shell beds, and coral have hard aragonite skeletons that shape reef substratum (Jones, Lawton and Shachak, 1994).Structures built by ecosystem engineers give a third dimension to otherwise almost flat surfaces and affect local environmental conditions, increasing in this way microhabitat diversity. Thus, habitat availability on an ecosystem depends on the shape of the organisms that build it. Understanding what determines variation of ecosystem engineers shape is important to understand ecosystem dynamics and evolution (Miner *et al.*, 2005). Organismal shape often varies in space and across environmental gradients, because we find different organisms living in different conditions (environmental filtering), and because organisms grow differently (plasticity). Here I investigate the relative role of environmental filtering and plasticity on coral morphology.

Plasticity and environmental filtering are important drivers of engineers' morphologic variation. Environmental filtering is a macroecological concept that describes a form of natural selection, that is when environmental conditions filter out some genotypes from a community pool, preventing them from being present under certain circumstances (Keddy, 1992). If applied to engineering species, it means that the environment favours the presence or absence of different habitat constructors. Through phenotypic plasticity, individuals of the same genotype may be present under a wide range of environmental conditions when they develop different phenotypes depending on the environment they are exposed to (Bradshaw, 1974). Consequently, local habitat conditions result from both a bottom-up process (habitat construction via ecosystem engineers), and a top-down process (natural selection and environmental filtering). This is particularly evident in coral reef habitats, shaped by hard corals.

Coral reefs rely on hard coral to accumulate calcium carbonate through skeleton accretion, which is the basis for the reef matrix. On the one hand, reef zonation, (i.e. the prevalence of certain forms of corals depending on environmental condition (Chappell, 1980)), is very evident along depth or wave exposure gradients. On the other, corals can respond to environmental factors by changing their shape in ways that are often found convenient for their fitness. For example, they can maximize physiological efficiency (Hoogenboom, Connolly and Anthony, 2008) or particle capture (Sebens, Witting and Helmuth, 1997) and be present under different environments but developing different structures. Yet, how much of this variation in shape is driven by environmental filtering vs. plasticity, and how this balance differs across species remains poorly understood.

To disentangle the drivers of variation in coral shape we need to quantify it. Scleractinian corals' morphologies are traditionally divided into growth forms based on discrete qualities of their shapes. For example, the presence and structural organization of branches, the tendency to "encrust" substrata, or the build of bulging shapes. Depending on the categorization (Wallace, 1999; Veron and Stafford-Smith, 2000), a branching coral can be divided into arborescent, corymbose or digitate, depending on branches organization (respectively with secondary branches stemming at random steep inclinations; with branches stemming from a constrained basal area and pointing up and outwards with slightly different angles; and with branches stemming all directly from a broader basal area and pointing upwards; Veron and Stafford-Smith 2000; Wallace 1999). But using categories does not allow to capture intraspecific variation in shape, nor how these different shapes translate into physiologically and ecologically relevant variation (Zawada *et al.*, 2019; Zawada, Dornelas and Madin, 2019). Instead, the use of quantitative continuous variables that capture defined ecosystem function is then necessary. For instance, colony compactness promotes reef stability, surface complexity promotes microhabitat diversity and recruitment facilitation and top heaviness provide large fish refuge (Zawada *et al.*, 2019). Each one of those variables can be measured continuously by focusing on the geometric aspects that define that property. As an example, compactness can be quantified with the circularity index, which measure how close to a circle an area is arranged in space (1 for circles and getting closer to 0 as the shape margin becomes more convoluted). Here, I quantify the drivers of variation across multiple axes of coral morphology, including those along these niche constructing traits.

Clonal transplant experiments provide a powerful method to investigate phenotypic plasticity (Sultan, 2015). Exposing clones (same genotype) to different environments allows comparing differences in traits that arose under different environmental conditions (Schlichting, 1986). The alternative phenotypes encoded by a given genotype under different environmental conditions define the norm of reaction of a specific trait (Woltereck, 1909). In naturally evolved populations, there is often individual trait variation because of genotype by environment interaction. Using clones allows to control for individual variation in trait response to different environmental conditions (Pani and Lasley, 1972; Sultan, 2015). When clonal transplant experiments are reciprocal, then sites with different environmental conditions are chosen and clones of individuals found in each site are transplanted both back in the site of origin and to the other sites. This allows comparing trait variation within and between individuals that developed under the same conditions (i.e. same origin). Thus, clonal transplant experiments enable us to detect the effects of both the experimental environmental exposure (transplant destination site) and the developmental environment (origin site), while taking into account individual variation in response to the environment (genotype by environment interaction, Figure C.1). Furthermore, by taking into account the interaction between site of origin and destination, it is possible to detect whether the individuals can locally adapt through plasticity in the new environment.

Corals as colonial organism are particularly suitable for such experiments because fragments from the same colony act as clones of the same individual (same genotype). Further, corals are relatively easy to manipulate under different environmental conditions. Numerous reciprocal transplant experiments to tackle coral phenotypic plasticity have been carried out to show the different extent of plasticity among coral species and along different environmental gradients (Todd 2008). Since most corals rely on light for energetic intake through photosynthesis, and photosynthesis is tightly linked to calcification, morphological differences are particularly evident along light gradients (Dustan, 1975; Jaubert, 1977; Gattuso, Allemand and Frankignoulle, 1999; Todd, 2008; Hoogenboom and Connolly, 2009). In nature and for a number of species, flattened and horizontally developed morphology would develop in deep environments, possibly to minimize tissue that has to be sustained for any given light flux (Stambler and Dubinsky, 2005; Hoogenboom, Connolly and Anthony, 2008). To look at coral morphological plasticity though, it is necessary to follow transplants' phenotypic development within generational time and draw phenotypic reactions (Sultan, 2015). Transplant experiments paired with continuous morphological traits that translate in ecological function allow understanding whether reef habitat availability depends on environmental conditions or is genetically driven.

Coral reciprocal transplant experiments focus on measuring intra- and interspecific variation of a wide range of traits, from physiological features (Bongaerts *et al.*, 2011; Mayfield *et al.*, 2012) to gene expression (Mayfield *et al.*, 2012; Kenkel and Matz, 2016), from symbiosis plasticity (Baker, Milburn and Tennant, 1988; Bongaerts *et al.*, 2010) to corallite structure (Bruno and Edmunds, 1997; Hoogenboom, Connolly and Anthony, 2008). When growth is the focus of the experiment, it is usually measured either as weight gain or linear extension (Todd, 2008), which provide different functions to the ecosystem. Focus on variation in colony morphological features is rare, especially when compared to the much more investigated changes in corallite structures, possibly due to the challenge posed by measuring colony complexity and structural self-organization in 3D. As an example, complexity in *Acropora cervicornis* has been measured as number of daughter branches and branch bifurcation ratios (Mercado-Molina, Ruiz-Diaz and Sabat, 2014, 2016), which are discrete values that do not capture alone information about how the individuals are occupying and shaping reef space. This type of trait overlooks at modularity and similarity in branch organization, making inter-specific comparisons based on these traits of little interest in terms of ecosystem dynamics. For instance, it is easy to imagine how a caespitose and an arborescent colony with the same branch number or bifurcation ratio may provide different function for the ecosystem. When looking at phenotypic inter-specific variation, species were often selected based on different morphotype or availability, while there were not clear investigations along coral phylogenies. Furthermore, to gain insights on the benefits of evolving plasticity, comparison among taxa structured in the phylogenetic tree with quantitative traits that continuously characterize colony shapes within and across species are needed.

The aim of this chapter is to understand how coral shape variation is driven by environmental conditions among differently related species. To achieve this aim, a reciprocal transplant experiment was performed using taxa of the same broad category of morph type (branching) but belonging to two different genera. I test if: i) coral colonies from different environments differ in their change in shape (evidence of environmental filtering); ii) different environments consistently induce different structural morphologies (evidence of plasticity);

iii) differences in the direction of the transplantation, this is pairs of origin and destination sites, induced different morphologies (evidence of local adaptability); and iv) genus, species or genotype affect change in coral shapes (evidence of evolutionary constrain and genotype x environment interaction).

## 3.2 Methods

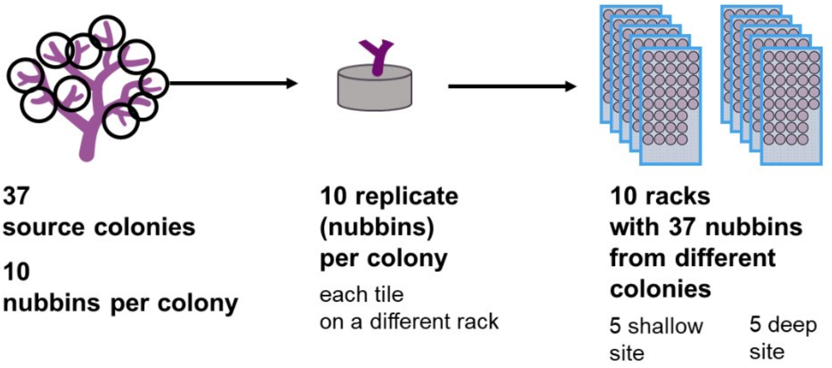
### 3.2.1 Site, species and transplant

A coral reciprocal transplant experiment was set up in the South-East lagoon of Maghoodoo Island (3°04′N, 72°57′E, Republic of Maldives) from January 2017 to May 2018. Transplants were made between a shallow (S) high-light site at 5-6 m depth and a deep (D) low-light site at 16-18m depth. Five replicate racks for coral samples were built and fixed to the reef at each site.

Coral samples were collected at the two sites from four coral species with different branching morphologies. The species were *Acropora divaricata* (arborescent/corymbose), *Acropora muricata* (arborescent), *Porites rus* (encrusting/digitate), and *Poritis cylindrica* (digitate) (Figure 3.1). Species were chosen from two genera to test the prediction that plasticity is similar across evolutionary lineages. All species were common along the depth gradient, were easy to identify, and had relatively high growth rate (Madin, Anderson, *et al.*, 2016).

For each species, 4-5 source colonies were collected at each of the shallow and deep sites, for a total of 37 colonies (Figure 3.1). To avoid collection of colonies with the same genotype (clones), a minimum distance of 10 m between source colonies of the same species was maintained. This is the minimal distance to allow confidence of genetic independence among colony sampled (Smith *et al.*, 2008). After collection the colonies were transported to the lab and were kept in aerated tanks. Colonies were only removed from the tanks for measurement and for selecting the nubbins. Each source colony provided 10 genetically identical nubbins: 5 to go back to the source site (transplanted within site as a control), and 5 to go to the other site (transplanted between sites). Nubbins were cemented to a concrete disk tile (7x2,5cm) with reef cement (NYOS © reef cement). The maximum basal diameter (D, cm), minimum basal diameter (d, cm) and length (L, cm) of each nubbin was measured with callipers. Wet weight (i.e. the weight of the nubbin on the tile as it was taken out of the tank,

**January 2017**



| Source colony breakdown | Species code | from shallow site | from deep site |
|---|---|---|---|
| *Acropora divaricata* | AD | 5 | 4 |
| *Acropora muricata* | AM | 5 | 5 |
| *Porites cylindrica* | PC | 5 | 4 |
| *Porites rus* | PR | 5 | 4 |
| | | **20** | **17** |

**May 2018**

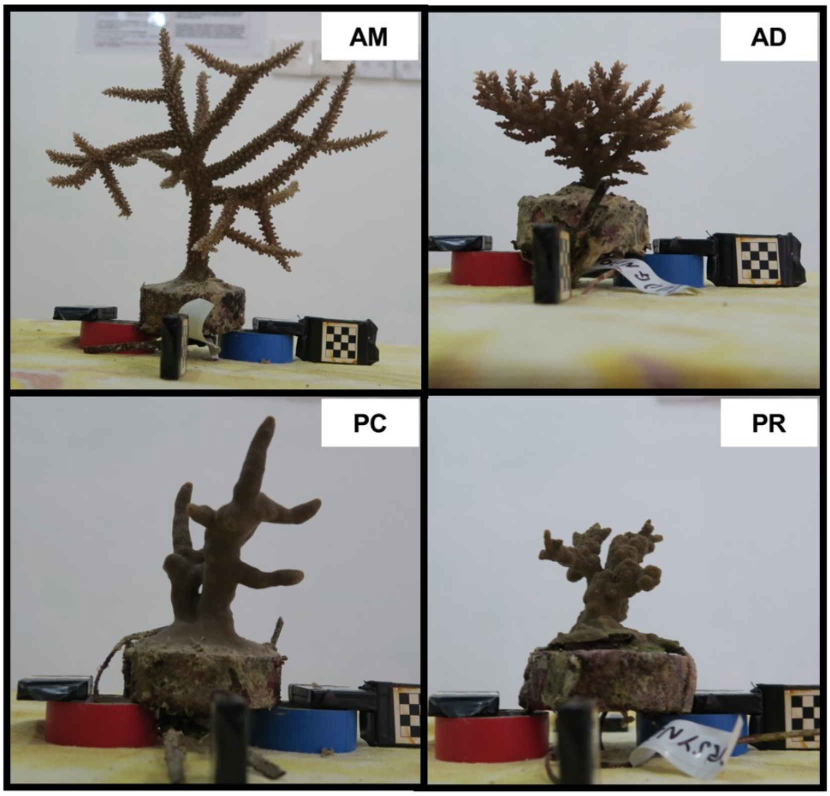


**Figure 3.1 - Reciprocal transplant experiment schematic and species transplant pictures.**

in grams) was measured at the closest 0.5g. Volume (mL) was measured with the water displacement method with graduated cylinders. Additionally, photographs of the nubbins were taken from above at a fixed distance with a scale bar. Each source colony was processed and transplanted back to the reef within 16 hours. Each nubbin from each source colony was attached to a different rack. All the samples were collected, processed and transplanted in 6 days. In total 5 racks holding 37 fragments each per site were used. I used 185 nubbins per site, of which 100 of colonies from the shallow site and 85 of colonies from the deep site, for a total of 370 nubbins.

At the end of the experiment, all the racks were brought to the lab, where the status of each nubbin (alive or dead) was recorded and the same set of measurements and photographs were repeated as outlined above.

### 3.2.2 Environmental data collection

Environmental data—sediment, temperature, flow and light—were measured at each site. Sediment traps were built and deployed as per English et al. (1997) in April 2017. Three replicates per rack were deployed for 10 days (9th to 19th of April) and checked to make sure there was no overgrowing on their top.

Flow was measured with the gypsum balls method that is based on the fact that gypsum dissolves in water directly proportionally with flow velocity (Fulton and Bellwood, 2005). The gypsum balls were shipped directly from the lab that calibrated them and were left to dry in a low-humidity room at 25°C for two days. The gypsum balls were weighted before being deployed in the field for a 24-h period (+/-20 min). At each site (i.e. shallow and deep), I allocated 3 gypsum ball replicates, resulting in 6 replicates per depth. After retrieval, each ball was left to dry again for two days in the low-humidity room at 25°C and then weighted again. A proxy for flow states was obtained as the weight lost during deployment.

I also allocated HOBO temperature and light dataloggers (Onset) to each rack. These were collected at the end of the experiment. At least two loggers for depth were deployed at all times and they were replaced three times along the experiment. Since loggers became overgrown with organic matter, only the first month of each deployment was used to measure light treatment per site. Since temperature loggers tend to accumulate heat when exposed to light (Appendix A), only the last month of each deployment (i.e. when the logger was covered with a biofilm protecting the logger from solar radiation) was used to estimate temperature.

### 3.2.3 Photograph processing and morphological traits

Nubbin photographs were processed using the image analysis software ImageJ (Rasband, 2014). A graphics tablet (medium Intuos, Wacom) was used to draw the outline of the planar projection of the nubbins on the horizontal plane. Using the scale bar present in the picture as a reference, the contours were then saved as XY coordinates to calculate planar area (PA, in cm2) and perimeter (p, in cm) with the 'pracma' R package (Borchers, 2019). Furthermore, 2D metrics to reflect three aspects of coral morphology (top-heaviness, surface complexity and shape compactness) were calculated. To measure top-heaviness, the log-ratio between the radius of the best fit circle to the outline of the nubbin and the mean basal diameter was computed (T, cm). To measure shape compactness (C, nondimensional), the circularity formula was used:

$$C = \frac{4\pi(area)}{perimeter^2}$$

To measure shape complexity, two nondimensional indexes were used. Rugosity index (R), measured as the ratio between the outline perimeter and the perimeter of a circle with the same area as the outline. And Fractal dimension (F), measured with the 'fractaldim' package (Sevčíková and Percival, 2015) and specifying 'box counting' as method.

To visualize how traits changed collectively during the experiment, a principal coordinate analysis (PCA) considering all the observed combination of traits (i.e. pooling nubbins from time 0 and time 1) was performed with the 'prcomp' function. The multidimensional space was used to inspect how different groups of nubbins were occupying different portions of the morphospace.

## 3.3 Analysis

To analyse probability survival, nubbin status (alive - 1 or dead- 0) was used as response variable (and modelled as binomial distribution). To measure change in morphological variables, log-ratios (lr) of the variable between the end and the start of the experiments were used. To measure change in the morphospace, the geometric distance between final and initial position of each nubbin in the space defined by the first two principal coordinates of the multidimensional trait space was used (deltaPCA).

Generalized and linear mixed models were used to examine the effect of coral Origin, transplant Destination and Genus on the variables of interest, following the AIC based model selection approach described in Zuur *et al*. (2009). Effects of coral Origin, transplant Destination and Genus were interpreted as effects of environmental filtering, phenotypic plasticity and taxonomic group respectively. Genus was used as taxonomic grouping factor because each pair of species is visibly more similar morphologically within Genus groups. Full models included a triple interaction of the three factors of interest because: (i) taxa were expected to be affected differently by the environment, and (ii) I was interested in detecting the interaction between Origin and Destination as signal of local adaptability. Species, genotype and rack were all initially included as random effects to account for differences in lower taxonomic groups, genotype and experimental racks. To select the appropriate combination of random effects, full models comprising every possible combination of random variables were fitted with restricted maximum likelihood and the random effect structure corresponding to the full model with the lowest AIC was selected (Zuur et al. 2009). For each response variable and maintaining the selected random effect structure, 18 models comprising every possible combination of fixed effects and interactions were fitted and selected based on the lower AIC. A binomial generalized linear model with logit link function was used for survival. Linear models were fit to trait variables, which were log-transformed in case of non-normality. Model assumptions, such us normality of error distributions and homogeneity of variances, were evaluated graphically.

To validate results, I also report significancy of each factor of each full model, with significance levels adjusted to account for multiple comparisons (Bonferroni correction, n = 8). Statistics were performed with R version 3.3.2 (R Core Team, 2018) and the 'lme4' package (Bates *et al.*, 2015).

## 3.4 Results

### 3.4.1 Environment

Both temperature and light at the shallow site were characterised by higher daily variability, with respect to the deep site. While mean temperature differences between depth were not significant ($n = 25$, $df = 23$, F value = 0.524, $p = 0.477$), light values were higher at the shallow site ($n = 25$, $df = 23$, F value = 19.56, $p < 0.001$), where light was 2.2 times higher than at the deep site.

Even though sediment rate was not significantly different ($n = 10$, $df = 8$, F value = 2.773 , $p = 0.134$) between sites, the trend showed a higher sediment rate at the shallow site (mean = 0.031 g/d, sd = 0.017 g/d) than at the deep one (mean = 0.015 g/d, sd = 0.013 g/d). Gypsum dissolution varied significantly between depths ($n = 12$, $df = 10$, F value = 16.24, $p = 0.002$), characterising the shallow site as the one experiencing higher flow. However, the amount of gypsum dissolved during the deployment was smaller than the minimum recorded by Fulton and Bellwood during the calibration procedure (Fulton and Bellwood, 2005), suggesting that overall, the conditions were of very low water motion at both sites (close to 0 cm/s). This was expected since the lagoon is protected by a high outer reef and as result, only the tidal variation is the main source of water motion, affecting the shallow site more than the deep one.

### 3.4.2 Survivorship and survival model results

Overall, the 58.9% of the transplanted nubbins survived (Figure 3.2). I failed to detect an effect of site of origin on probability of survival, however, there was a significant interaction between genus and destination (Figure 3.2b and c). This indicates that transplanted nubbins were less likely to survive in the shallow site. This difference was more prominent for the genus *Acropora* (Figure 3.2c).

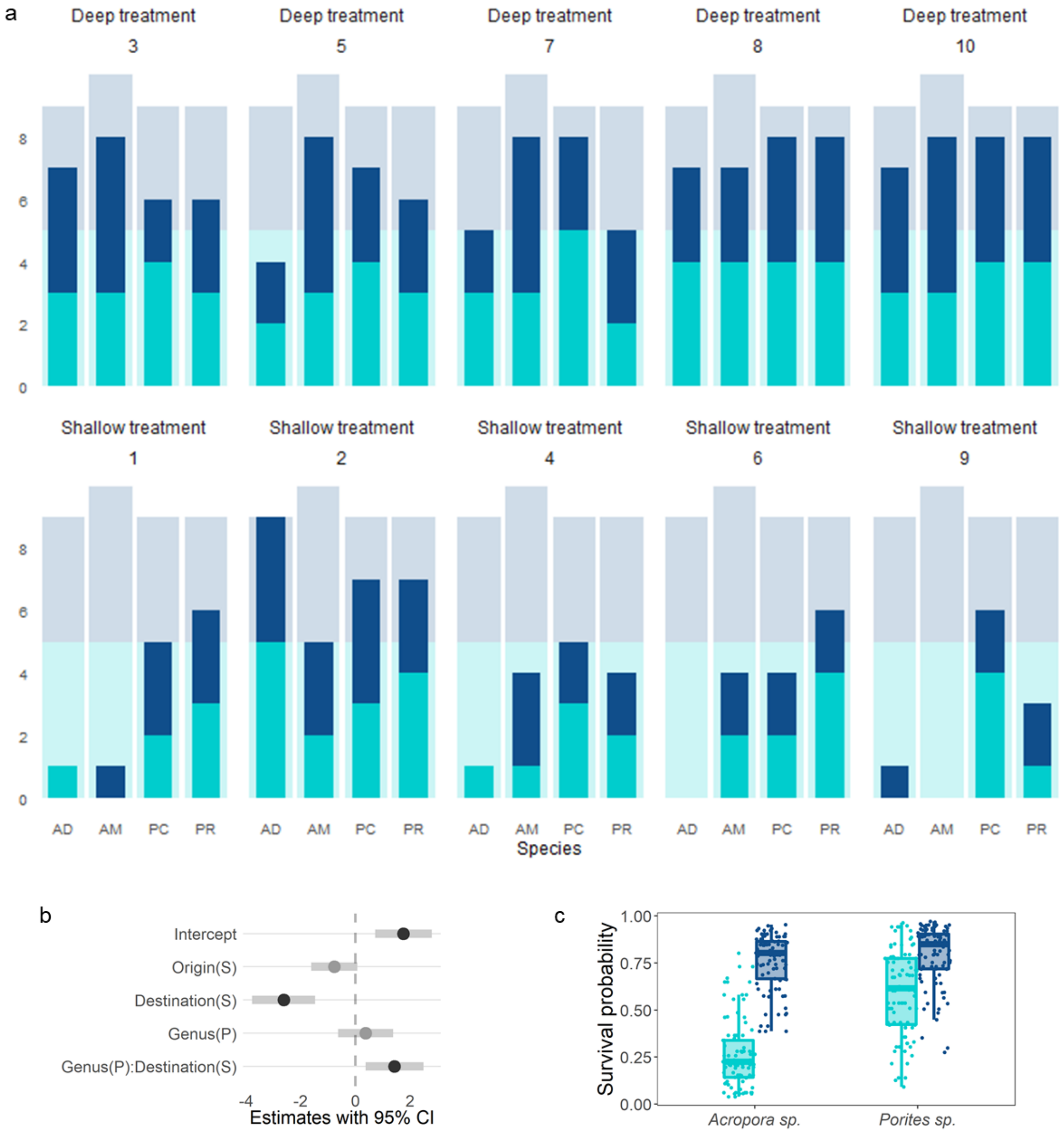


**Figure 3.2 - Nubbin survival and model results.** *a)* Counts of survived transplant divided by species (AD = *Acropora divaricata*, AM = *Acropora muricata*, PC = *Porites cylindrica*, PR = *Porites rus*) and color-coded by site of Origin (light blue = shallow site, dark blue = deep site). On the top, survivorship among racks deployed at the deep sites (Rack 3,5,7,8, and 10). On the bottom, survivorship among racks deployed at the shallow sites (Rack1,2,5,6, and 9). Bulk-colour bars represent counts of the nubbins survived. Shaded in the background, counts of the nubbins originally transplanted on each rack. Differences between the bulk and the shaded columns represent nubbin deaths. *b)* Effect size estimates for fixed factors and interactions for the selected model. Dots represent the estimated effects of each fixed variable and bars represent 95% confidence intervals. An effect is detected (black dots) when bars do not overlap 0, the vertical dotted line. *c)* Survival probability distributions across Genera and Destination (light blue = shallow site, dark blue = deep site).

### 3.4.3 Trait changes, reaction norms and morphospace

The morphological traits considered changed in different fashion during the experiment among species and treatments (Figure 3.3 and Figure C.2). Traits measured in situ (Figure 3.3a-e: Maximum basal diameter D, Minimum basal diameter d, nubbin height L, unit volume V, Unit wet weight W) were obtain for all the 218 nubbins survived, while traits derived from the nubbin outlines (Figure 3.3 f-l: Planar area A, Rugosity Index R, Fractal dimension F, Compactness C, Top-heaviness) were obtained for 217 individuals (Figure C.2).

All the morphologic traits have been used to build the morphology trait space (morphospace). The first two principal coordinates of the continuous morphospace explained 81.1% of the variation in nubbin shape (Figure C.3), which is considered satisfactory. Nubbins at the beginning and at the end of the experiment were occupying different areas of the space (Figure 3.4 and Figure C.4). The initial area occupied was much smaller than the final one, as fragments transplanted at the beginning of the experiment were as similar as possible across all experimental nubbins.

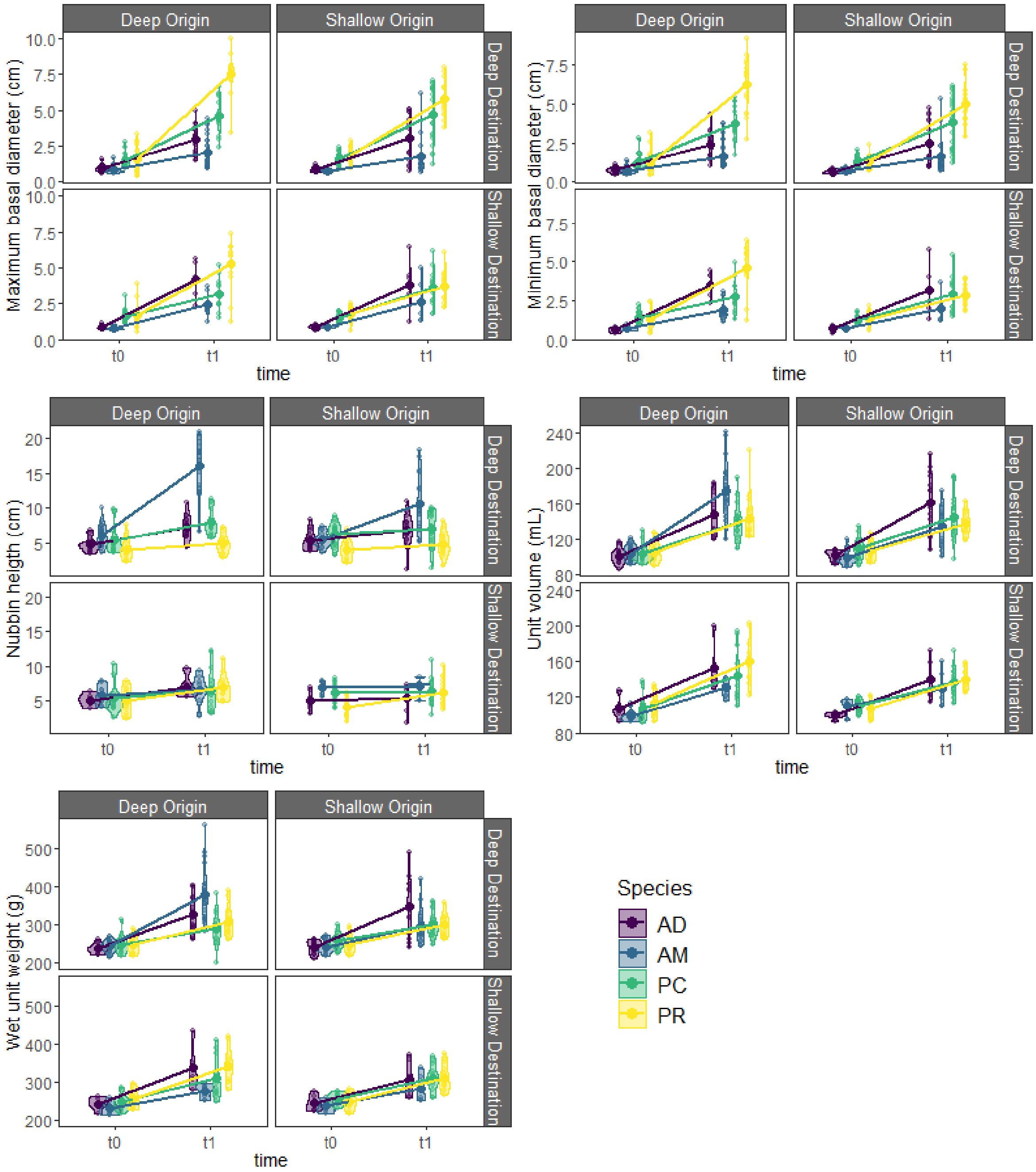


**Figure 3.3 Species trait distributions at the beginning and at the end of the experiment for the traits measured *in situ (n=218)*.** Values of each trait are represented color-coded by species at the beginning (t0) and at the end (t1) of the experiment. Both values (dots) and distributions (violins) are shown. The coloured lines link the means of the trait values of each species before and after the experiment under each experimental treatment. For every trait, data is divided by site of Origin of the source colony (deep and shallow Origin, as different columns in each panel) and site of Destination (deep and shallow Destination, as different rows). If slopes are consistent among trait panels, then the nubbins did not display morphological plasticity, nor showed an effect of the Origin on the genotype of the colonies. If patterns of the lines change among columns, then there is a strong determination of the morphs based on the Origin of the colony. If patterns of the lines change among rows, then the environment affected the trait values that changed due to morphological plasticity.  For example, in the graph for maximum basal diameter (a), while the 2 columns have almost the same lines pattern (i.e. the response did not depend on the Origin nor the Destination), the two *Porites spp.* (PC and PR) show different pattens when comparing between rows and among columns (i.e. the Destination seems to affect this trait).

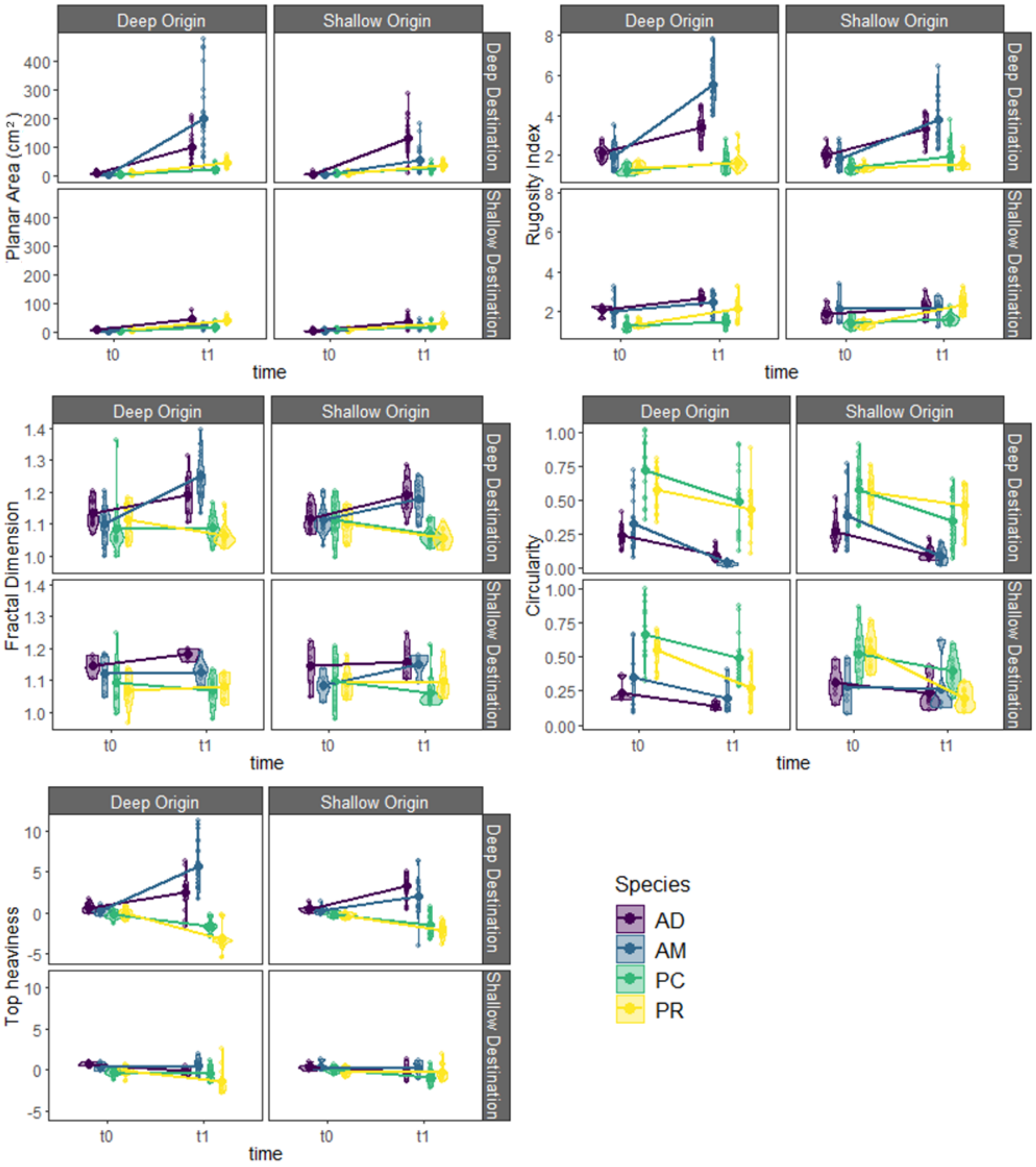


**Figure 3.3 (continuation) - Species trait distributions at the beginning and at the end of the experiment for the traits derived from the nubbin outline (n = 217).** Values of each trait are represented color-coded by species at the beginning (t0) and at the end (t1) of the experiment. Both values (dots) and distributions (violins) are shown. The coloured lines link the means of the trait values of each species before and after the experiment under each experimental treatment. For every trait, data is divided by site of Origin of the source colony (deep and shallow Origin, as different columns in each panel) and site of Destination (deep and shallow Destination, as different rows). For interpretation, see previous page.

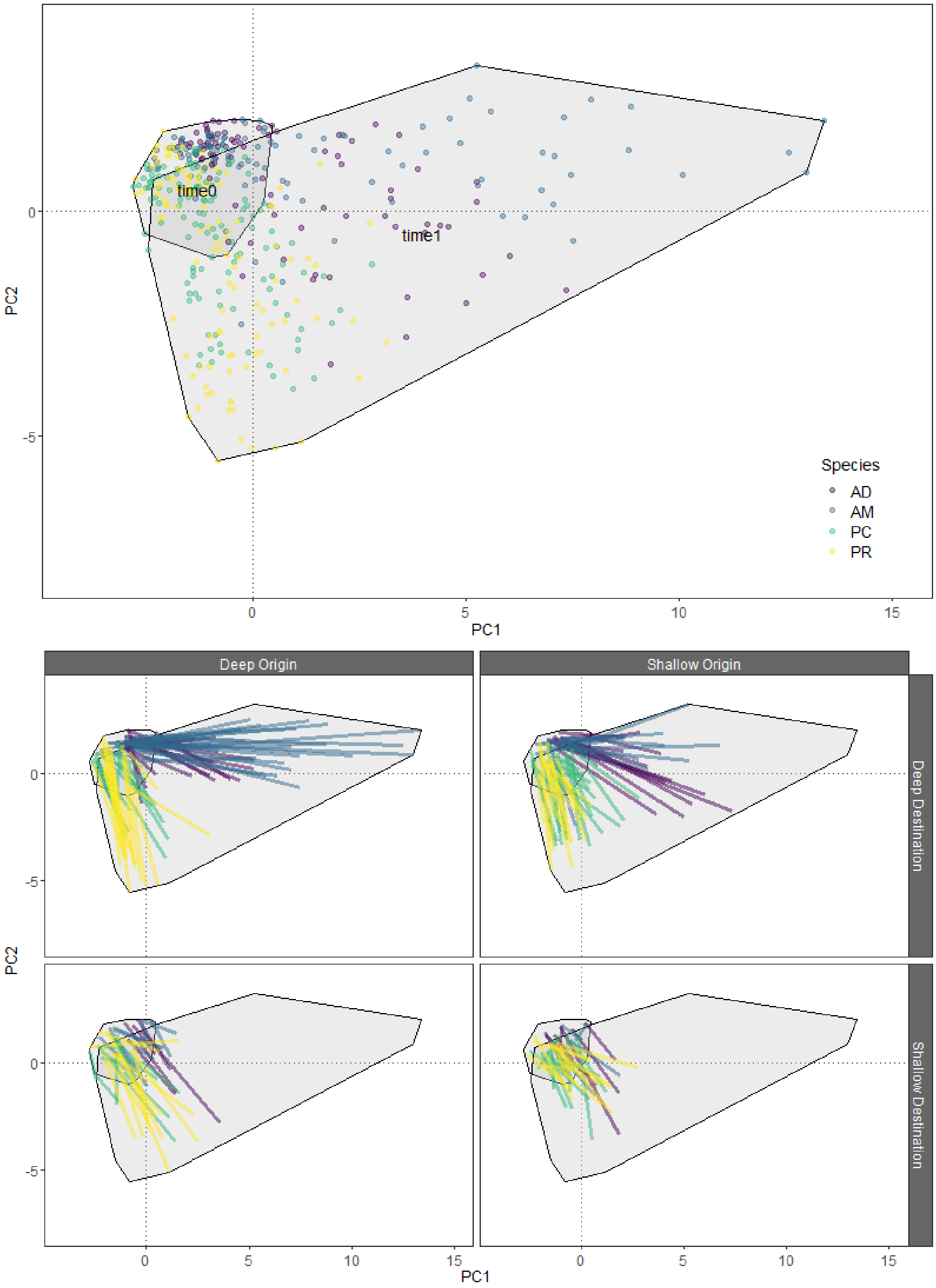


**Figure 3.4 - Morphological traits space plot.** A) Dots are color-coded by species (AD = *Acropora divaricata*, AM = *Acropora muricata*, PC = *Porites cylindrica*, PR = *Porites rus*). In the space, the 2 polygons represent the space occupied by the nubbins at the beginning of the experiment (time0) and at the end (time1). b) Segments represent the distance travelled by each transplant during the experiment, color-coded by species. The data is shown divided by Origin (columns) and Destination (rows). Trait loadings are shown in Figure C.3.

### 3.4.4 Trait models results

All the models selected but one included a significant interaction between Destination and Genus (Table C.1, C.2 and Figure 3.5). This shows how the two taxonomic groups respond differently to the environment they are exposed to (Figure 3.6). In other words, most traits changed differently when comparing changes between Genera and Destination. For all traits but the basal diameters, trait changes between sites were greater among individuals of the genus *Acropora*. A small effect of Origin was found in changes in nubbin length, planar area and morphospace occupancy. The interaction between Origin and Destination was never significant, suggesting that differenced in traits did not depend on the transplant direction.

For instance, maximum and minimum basal diameter models showed that the diameters increased slightly less at the deep site in *Acropora spp*., but consistently more for *Porites spp*., regardless of Origin (Figure 3.6a-b). Nubbin length and planar area differences across sites were more prominent in *Acropora spp*., which had higher increases in the deep site (Figure 3.6c and f). They were also affected by the coral Origin: genotypes from the deep site population expanded more across the two genera, than genotypes from the shallow site (Figure 3.5). Volume and weight differences between Destinations were particularly visible in the *Acropora* genus. Nubbins of *Acropora* transplanted into the deep site showed greater increase in the above traits (Figure 3.6d-e). Compactness decreased more at the deep site in *Acropora spp*., regardless of Origin (Figure 3.6g). Differences in rugosity and top-heaviness qualitatively mirrored the nubbin volume and weight patterns (Figure 3.6h and i). While differences between genera were smaller within the shallow site, they were greater in the deep site, where *Acropora spp.* had much higher log ratio responses than *Porites spp*. Model selection for fractal dimension showed that this variable is strictly dependent on Genus with changes *Acropora spp*. being greater regardless of destination and origin (Figure 3.5).

When looking at the change in the position of the nubbins in the multidimensional morphospace (deltaPCA, Figure 3.6m), each species tended to occupy different portions of the space. The distance travelled by each individual depended on the interaction between environment of exposure and Genus, and was minorly affected by Origin of the transplant. Differences were particularly visible in the *Acropora spp*., when comparing Destination sites (higher distance travelled in the deep site), while differences between the *Porites spp.* were smaller. They were also affected by the coral Origin, showing that genotypes from the deep site population were moving more across the morphospace.

Results show a neat difference in mean responses along axis of morphological variation between genera. The random effect structure resulting from model selection included Genotype for all the models and never included rack. Species was selected only for seven models (maximum and minimum diameter, nubbin length, compactness, surface rugosity, top-heaviness and delta PCA), for which intra-specific variance across genotypes was comparable or greater than variance due to species identity for most cases (Figure 3.7). This suggests that while there was individual plasticity in the way each genotype responded to the environment (GxE interactions), variation in the response occurred among species, as confirmed by the reaction norm plots (Figure C.2).

Bonferroni corrected significancy of the fixed effects in the full models fitted for each response variables are qualitatively consistent with model selection results (Table C.3 and Figure C.5).

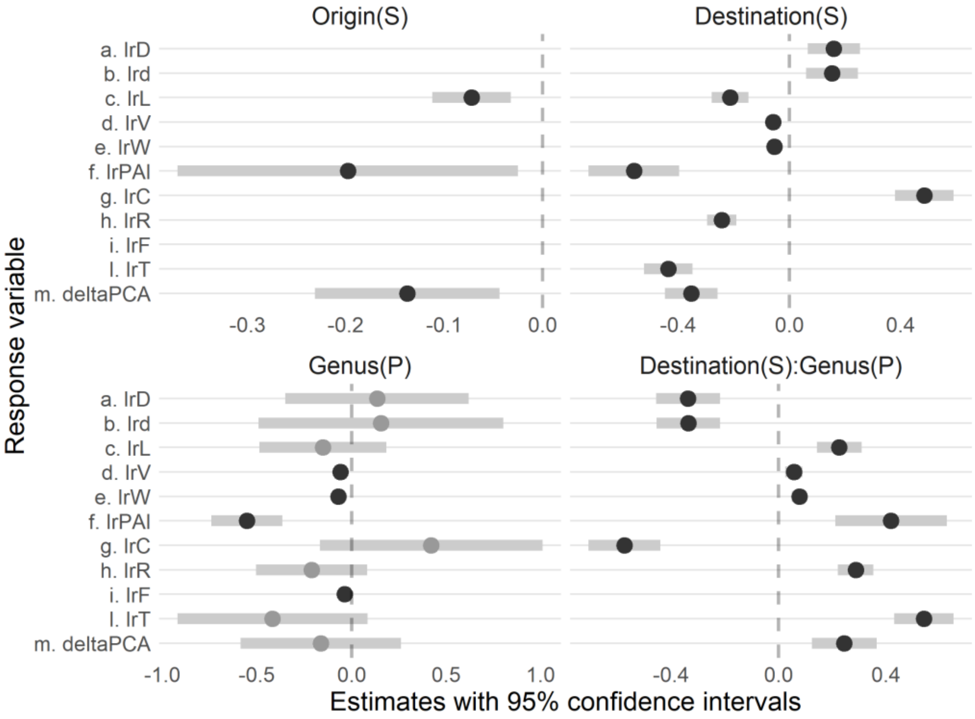


**Figure 3.5 - Effect size estimates for fixed factors and interaction terms included in the selected models.** Dots represent the estimated effect size of each fixed term in each model and grey bars represent the 95% confidence intervals. Effects are significant (black dots) when bars do not overlap 0 ,the vertical dotted line in the plots.

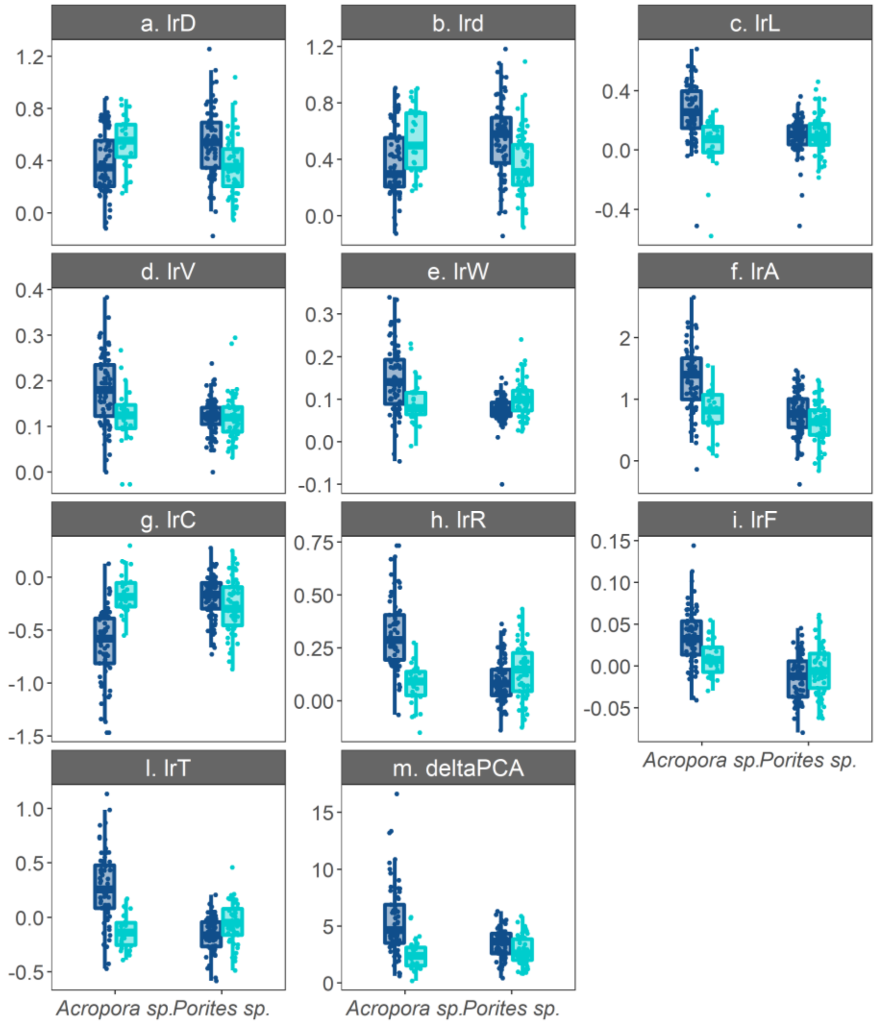


**Figure 3.6– Genus and Destination interaction plots for significant interactions.** Boxplots of trait distributions across genera and transplant destination, with raw data (dots) superimposed. Darker blue represent data transplanted to the Deep site, while lighter blue represent data transplanted to the shallow site.

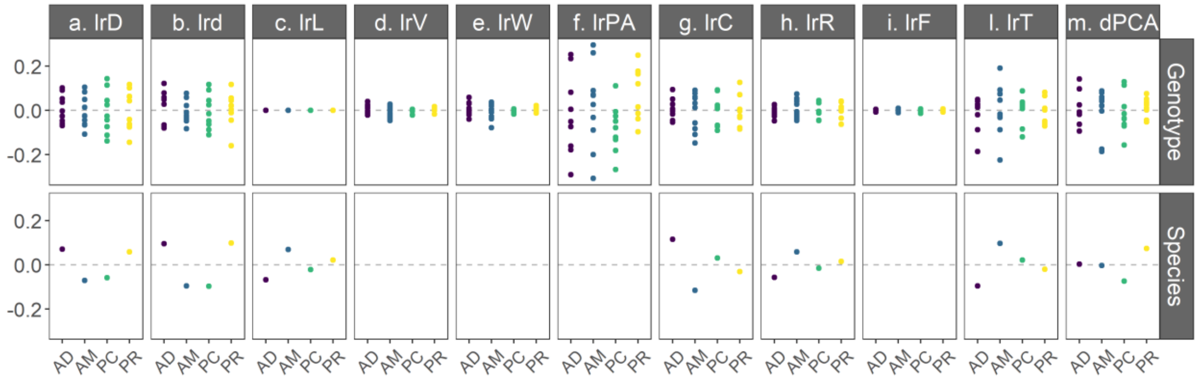


Figure 3.7 – Random effects in selected models. Points correspond to Genotype and Species effects in the models selected. Models without effects of Species do not have this variable in their selected random effect structure. AM = *Acropora muricata*, AD = *Acropora divaricata*, PC = *Porites cylindrica*, PR = *Porites rus*.

## 3.5 Discussion

This study showed how a set of morphological variables that capture biologically relevant features of coral shape variation change when corals are exposed to different environmental conditions. The environment of exposure (i.e. the destination) consistently induced different degrees and directions of change when comparing differently branching species, with the highest differences among *Acropora spp.* (Figure 5). The origin of the corals, i.e. the site to which corals where exposed before transplantation, had smaller effects on some morphological trait change, including on changes in the multidimensional trait space (Figure 5). I did not detect a significant interaction between origin and destination, suggesting that local adaptation do not depend on if the environment of previous exposure was different or the same. As for other previous transplant experiments (Todd, 2008), GxE interactions (intraspecific variation) were detected, and because of the small effect of Origin and the overall results and uniformity of the reaction norms, the results suggest that the morphological variability found in reefs may be more due to plasticity than by environmental filtering.

When comparing environmental conditions of the two experimental sites in the lagoon, the shallow site had higher mean light (more than double), higher (though overall negligible) water motion, and higher daily variability of temperature and light. These conditions are quite common in shallow reefs and can be quite stressful for corals (Glynn, 1996). As a result, this possibly caused the decrease in survival rate, especially among the *Acropora spp.* (Figure 3.2), which are particularly sensitive to high temperature exposure (Hoogenboom *et al.*, 2017). Apart from survival, a less stressful environment (i.e. a deeper site) also promoted higher diversification in morphologies, as shown by the bigger morphospace occupied by corals transplanted at the deep site (Figure 3.4a, Figure C.4), although it is possibly because the corals grew more at this site. The shallow site covered a smaller extent of morphologic traits combinations, as showed by the restricted portion of the morphospace occupied by the shallow site at the end of the experiment (Figure C.4a).

Looking at differences between genera and pooling together survival and morphological traits results, *Porites spp.* and *Acropora spp.* had different responses. Once taken into account remarkable differences between genera (Figure 5), variation among species was small (Figure 7), suggesting that plasticity in the traits analysed may be evolutionarily genetically channelled. *Porites spp.* grew less (except at the base of the skeleton) and had smaller changes in complexity and compactness, but higher survival rate. *Acropora spp.*, on the other side, had higher changes in traits, especially in the deep site where there was higher survival rate. Since corals are ecosystem engineers, they promote habitat diversification with their shapes, but firstly for just being there (i.e. surviving attached to the substratum). Taken together, these results indicate that survival and habitat diversification ability do not have a trade-off relationship, but it is rather synergistic: the higher the survival chances, the higher trait changes, and the higher the habitat diversification ability for the ecosystem. Corals transplanted in the shallow site Destination survived less and displayed less variation in traits (less-steep slopes in Figure 3, log ratios closer to 0 in Figure SM2 and trait space occupied closer to the PCA axis origin in Figure SM4a), which in a reef may result in less varied habitat provision.

Origin had a small effect only in some of the morphologic traits considered and no effect on survival rate. The fact that the experiment was carried out in an enclosed lagoon needs to be considered, as this may facilitate gene flow between deep and shallow populations, compared to less connected exposed reef crests and slopes depths (Benzie, Haskell and Lehman, 1995). Thus, high connectivity may partly explain the minor effect of Origin in this experiment, even though the two sites were approximately 150m apart within the lagoon. The fact that trait changes were marginally higher in genotypes selected from the deep sites, that there was no effect of the direction of transplant, and that there was no effect on survival might be reassuring for conservation reasons. In fact, a common practice is to transplant coral fragments from other sites in reefs that need restoration and wait for corals to attach and grow (Barton, Willis and Hutson, 2017). If origin and direction of transplantation do not affect coral growth, but the environment does, we may expect that after some time the same shape patterns may appear in the reef. In the long term though, following corals along generations would be necessary do detect if there might be an adaptive response that will benefit restoration, as other lines of research are currently investigating (van Oppen *et al.*, 2015).

Because of their ecosystem engineering nature, corals affect local conditions all along their life span, and to different extent according to size and traits development. More information about how the morphological traits used in this analysis change along with coral growth would be useful to understand if functions are sustained all along coral life or if they are modulated by colony size or life stage. Furthermore, upon death coral skeletons are left behind as ecological legacy, so that knowing how they are ultimately linked to the environment (and not only how they change after 15 months) may better inform prediction of reef ecosystems dynamics, since reef productivity, biodiversity and competition strongly depend on reef structure (Graham and Nash, 2013; Brandl, Hoey and Bellwood, 2014; Torres-Pulliza *et al.*, 2020).

The methods used can help transitioning towards quantifying morphologic traits in a continue quantitative frameworks for detecting variation in shape complexity. In fact, in addition to applying the present findings to future research, a significant benefit of using functional morphologic traits derived from planar area representations is that they can be applied to archived images taken during other transplant experiment, making a generalization of these findings possible. Additionally, improved understanding of the relationship between the traits computed here and the 3D morphologic traits described in Zawada et al. (2019) could help us move further forwards in understanding the ecological consequence of plastic coral morphologies.

Overall, this analysis showed that traits linked to habitat provision are phenotypically plastic with some differences among genera. The environment of exposure during the experiment consistently induced different degrees of change in morphologies, and particularly among the *Acropora spp*. The origin of the corals (i.e. coral before transplantation), only affected some of the traits and only marginally. The results provide evidence that different local environmental conditions may consistently induce differently varied habitat availability in reef ecosystem, explaining how reef zonation and community structures are sustained on the long term by coral phenotypic plasticity.

# Chapter 4. Coral recruitment increases along a coral-built structural complexity gradient

Niche construction is the process through which organisms modify environmental states in ways favourable to their own fitness. Here, I test experimentally whether scleractinian corals can be considered ecological niche constructors. In particular, I demonstrate a positive feedback involved in corals building structures which facilitate recruitment at the early ontogenetic stage. Coral larval recruitment is a key process for coral reef persistence. Larvae require low flow conditions to settle from the plankton, and hence the presence of colony structures that can break the flow is expected to facilitate coral recruitment. Here, I show an increase in settler presence on artificial tiles deployed in the field along a gradient of coral-built structural complexity. Structural complexity had a positive effect on settlement, with an increase of 15,7% of settler presence probability along the range of structural complexity considered. This result provides evidence that coral-built structural complexity creates conditions that facilitate coral settlement, while demonstrating that corals meet the second criteria for ecological niche construction.

## 4.1 Introduction

Niche construction is the process by which organisms modify their surrounding environment in ways that may affect their evolution, and/or the evolution of other organisms that experience the modified conditions (Matthews *et al.*, 2014; Laland, Matthews and Feldman, 2016). Niche constructor organisms must meet three nested criteria, the first two characterizing niche construction, and the third determining whether niche construction generates an evolutionary response (Matthews *et al.*, 2014). First, the niche constructor must change its external environment, through behavioural, physical/chemical or other metabolic processes (Donohue, 2014; Laland, Matthews and Feldman, 2016). Second, these modifications must bias natural selection upon the organism itself and/or other organisms, either positively or negatively (Zahavi, 1974; Matthews *et al.*, 2014). Third, the modifications must leave a trace in the evolutionary history of the organisms involved, in the form of an evolutionary response to the environmental modification (Matthews *et al.*, 2014). While criteria 1 and 2 can be tested in an ecological framework, criterion 3 applies to an evolutionary time scale. The first two criteria describe an ecological feedback loop that can lead to diverse consequences, ranging from the local extinction of the responding population, to triggering trait fixation (criterion 3).

Ecosystem engineering species are a class of putative niche constructors (Matthews *et al.*, 2014; Laland, Matthews and Feldman, 2016) since by producing long-term environmental changes they can affect macroevolutionary patterns and biodiversity (Erwin, 2008). Scleractinian corals, as autogenic bioengineers (Jones, Lawton and Shachak, 1994a), are a prime example of ecosystem engineering since they physically create reefs that harbour some of the most biodiverse communities in the world (Hughes *et al.*, 2017). Yet, there are no explicit tests of their niche construction capability. Here, I focus on the effects of skeletal three-dimensional structures on corals themselves, examining whether this trait facilitates recruitment, thereby establishing a positive ecological feedback. I aim to advance understanding of coral niche construction by testing whether corals meet the second criterion of niche construction (Figure 1.1).

Scleractinian corals build complex and heterogeneous environments, which harbour some of the most biodiverse and threatened communities in the world (Hughes *et al.*, 2017). Corals have a planktonic life stage and larval recruitment success is key to the persistence of the reef ecosystem (Bellwood *et al.*, 2004). At the end of the planktonic stage, coral larvae need to settle on suitable substratum, metamorphose and start the benthic life. As with other benthic marine organisms, corals undergo severe early-life stage bottlenecks, and recruitment success depends on both abiotic and biotic factors (Ritson-Williams *et al.*, 2009). For example, crustose coralline algae (CCA) release chemical cues that induce the coral to settle and metamorphose (Heyward and Negri, 1999). In contrast, macroalgae can compete with coral for space occupancy and negatively affect coral recruitment (Mumby *et al.*, 2006). Once metamorphosized, post-settlement processes transform a settled polyp into a coral colony, which through its hard skeleton modifies the topography of the reef. Coral colonies modify the overall complexity of reef habitats both when alive and after death, when they leave behind their hard skeleton (Richardson, Graham and Hoey, 2017) as ecological inheritance (Odling-Smee *et al.*, 2013). Reef structural complexity is a measure of how corals engineer the environment, and is important for ecosystem function and maintenance from an ecological perspective (Graham and Nash, 2013; Zawada *et al.*, 2019). For example, reef structural complexity provides microhabitats and determines fish assemblage structure (Nash *et al.*, 2014). Furthermore, heterogeneity in coral colonies change the local environmental conditions, such as light (Brakel, 1979) and water flow (Hench and Rosman, 2013) to create a range of microhabitats and niches. All this demonstrates that corals meet the first niche construction criterion suggesting that coral niche construction may might be one process influencing the evolution of this diverse and productive ecosystem (Laland *et al.*, 2015).

Moving to the second criterion, positive ecological feedbacks to niche-constructing populations have been identified in other organisms (Matthews *et al.*, 2014), but not in corals. In the tundra, for example, plant species of all growth forms (i.e. forbs, grasses, sedges, deciduous shrubs and evergreen shrubs) collectively modify niches independently of local environmental conditions, increasing taxonomic diversity (Bråthen and Ravolainen, 2015). These environmental modifications bias natural selection upon the niche constructor and other associated species with important evolutionary consequences (Laland *et al.*, 2015). Another example is the sediment bioturbation and thickness of shell beds in paleoecological records, which increased over geological time as result of increased ability of the organisms to modify ecosystems (Erwin, 2008). This process resulted in greater evolutionary diversification of benthic niche constructors and ecosystem engineers as well (Erwin, 2008). In modern coral reefs, we can focus on how corals increase their own fitness modifying the environment in predictable and favourable ways. Identifying coral traits that capture these modifications and feed back to coral fitness would allow us to show that the second criterion for coral niche construction is met.

Settlement success plays a key role in coral fitness, because this is the life stage with lowest success rate. There is evidence that millimetre-scale rugosity of the substratum enhances settlement success (Birkeland and Randall, 1981; Hata *et al.*, 2017). However, the extent to which coral settlement is affected by increased habitat complexity (at the centimetre to meter scale) built by coral colonies remains unclear. Coral larvae are poor swimmers, and often rely on eddies created by small structural obstacles, such as sea urchin burrows in the field (Birkeland and Randall, 1981) or 1-cm blocks in the lab (Hata *et al.*, 2017), to be able to find suitable substratum and attach. On coral reefs, these flow conditions can be built by adult coral colonies with different structural complexity (Zawada *et al.*, 2019; Zawada, Dornelas and Madin, 2019). Areas of flow recirculation and of reduced current created by the presence of structural 3D complex coral assemblages (Hench and Rosman, 2013; Zawada, Dornelas and Madin, 2019) can play an important role in creating ideal hydrodynamic conditions for settlement and attachment of the larvae. Thus, high structural complexity built by corals is predicted to be favourable for coral settlement and recruitment.

Here, I show that assemblages of higher coral 3D complexity structures have higher probability of settlement of coral larvae. Specifically, I measured settlement on tiles used to hold either dead or alive corals during a reciprocal transplant experiment. I predicted that tiles in more complex coral assemblages (coral-built structural environments) will have greater probability of having coral settlers than tiles in less complex assemblages. Dead skeleton persisting over generational time as ecological inheritance can affect the evolutionary trajectories of the niche constructor as well. As such, I further investigate the effect of the status of the coral on tile (alive or dead) on recruitment success.

## 4.2 Material and methods

A coral reciprocal transplant experiment (see chapter 3) was set up in the South-East lagoon of Maghoodoo Island (3°04′N, 72°57′E, Republic of Maldives) in January 2017 (Figure 4.1). The experiment used 370, ~10 cm long fragments of colonies belonging to four species of branching corals commonly found in the lagoon (*Acropora divaricata*, *A. muricata, Porites* *rus*, *P. cylindrica*). Each fragment was cemented with reef cement (NYOS © reef cement) to a concrete disk tile (7x2,5cm) and then attached to one of 10 racks in either a shallow (5 racks, 5-6 m) or a deep (5 racks, 16-18m) site. At the start of the experiment, each rack had 37 concrete tiles with same-size same-species living fragments attached (Figure 4.1). All the racks had similar structural complexity in January 2017, but each one of them was left in different experimental conditions (deep site = low light, shallow site = high light) for 15 months (Figure 4.1). As a result, coral growth rate and mortality were different among racks, reflecting different environmental conditions experienced by the coral fragments. By the end of the experiment (May 2018), each rack had a different number of living fragments that grew into colonies (Figure 4.1), while the dead ones had different sizes and shapes depending on the time of death. Thus, the complexity of each rack increased during the experiment, but each rack displayed a different degree of structural complexity at the end.

A significant coral spawning event was observed in the Maldives on April 1st 2017 (Inga Deinhert, personal observation). The coral larvae pool was expected to be approximately the same for all the racks, since they were in the same enclosed lagoon. Given the coral assemblage present on the island (Montano *et al.*, 2012), more than just the species used in the experiment were spawning simultaneously in the lagoon. All the racks were retrieved and brought in the lab for tile analysis in the second week of May 2018 (6th and the 11th of May 2018). Settlers were found on the bottom and lateral surface of the concrete tiles used for the transplant experiment (Figure 4.1). Crustose coralline algae (CCA), bryozoans, molluscs, and sponges were also observed on the tiles, but cover was not quantified. The status (alive or dead) of the fragment attached to every tile was recorded. 26 to 37 tiles per rack were analysed, corresponding to a total of 214 tiles with a live coral attached, and 125 with a dead coral attached. Tiles were bleached overnight in a 10% commercial bleach solution, rinsed and dried, and then examined under microscope as per Babcock *et al.* (2003). Bigger settlers (> 2 mm) were considered juvenile corals that settled in 2017 and left out of the analysis (Babcock *et al.*, 2003). Smaller settlers (< 2mm, Figure 4.1) provided an estimate of settlers from the larval supply of 2018 (Babcock *et al.*, 2003) and were used as a measure of fitness (Hunt and Hodgson, 2010).

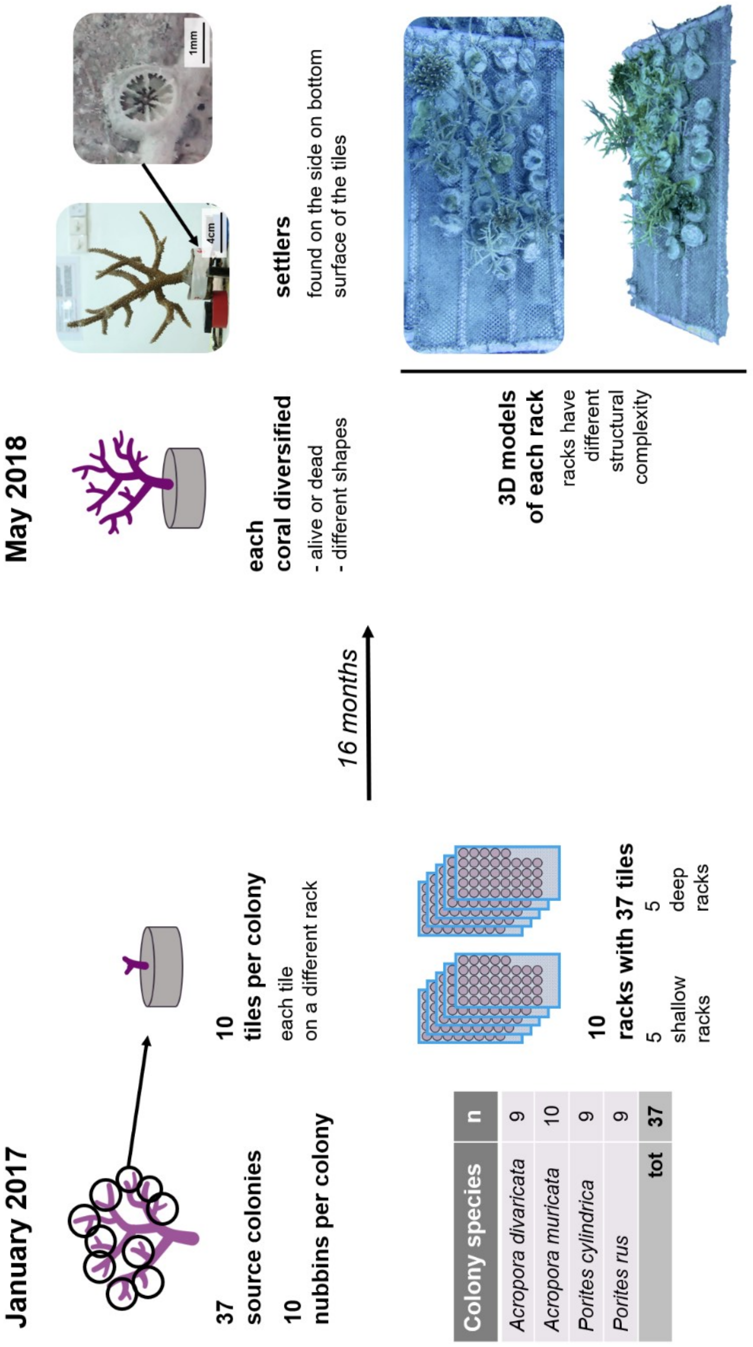


**Figure 4.1 - Timeline of experimental setup, from January 2017 to May 2018.**

Given the slow growth rate of corals it is plausible to assume that the rugosity of the racks did not change significantly in the last month of underwater permanence. I used surface rugosity (SR) of the rack at the end of the experiment as a measure of local structural complexity at time of settlement, which occurred less a month before racks were retrieved.

SR was estimated as the ratio between the 3D surface area and its planar orthogonal projection of the surface on the horizontal plane (Friedman *et al.*, 2012), with values that range from 1 (perfectly flat surface) to infinity. 3D digital models of each rack surface (Figure 4.1) were obtained through structure-from-motion photogrammetric techniques (Westoby *et al.*, 2012). A total of 160 to 190 pictures were taken of each rack from different angles underwater (House *et al.*, 2018) with a Powershoot camera (Canon 5X). Pictures were then analysed in Agisoft Photoscan Professional (Agisoft LLC, 2018). The surface area of each rack was computed with the built-in function and used to calculate SR. The values of SR were mean standardized for analysis.

Binomial Bayesian generalized linear mixed models were fitted to examine the effect of SR on explaining the presence of settlers. To control for the effect of the status of the fragment attached to the tile (i.e. alive or dead) and the depth of the rack (i.e. shallow or deep), I fitted a total of 7 models: a model including SR, depth and the status of the fragment; 3 models with any combination of 2 of the variables, and 3 models including the effects of one variable at the time. Rack ID was included in all models as random effect to account for unexplained environmental differences between experimental racks. All the priors were left as default values, and for each model four chains for 20000 iterations were run, with a warm-up period of 1000 iterations and a thinning rate of 10 iterations. I ensured that R^ values were almost 1 and goodness of fit was assessed by visual inspection of the chains. I used the Widely Applicable Information Criterion (WAIC) to evaluate the relative goodness of the fit (Vehtari, Gelman and Gabry, 2017), and check consistency of best fit with the leave-one-out cross-validation (LOOic) (Vehtari, Gelman and Gabry, 2016). All analyses were performed in R (version 3.3.2, (R Core Team, 2018)). Models were fitted with the probabilistic language RStan using the 'brms' (Bürkner, 2017) and 'loo' (Vehtari, Gelman and Gabry, 2016) packages.

## 4.3 Results and discussion

Racks surface rugosity (SR) ranged from 1,85 to 3,66 (Fig 4.2). Some corals died before the end of the experiment, and some of these had begun to erode. Therefore, as expected, lower levels of coral fragment mortality led to more structurally complex racks. Values of SR were well distributed along the range, which is representative of a healthy Indo-Pacific reef. Similar SR values were found on Australian reefs (Bryson *et al.*, 2017) and the presence of grown branching corals with convoluted shapes led to higher SR values on the most complex racks (Figueira *et al.*, 2015).

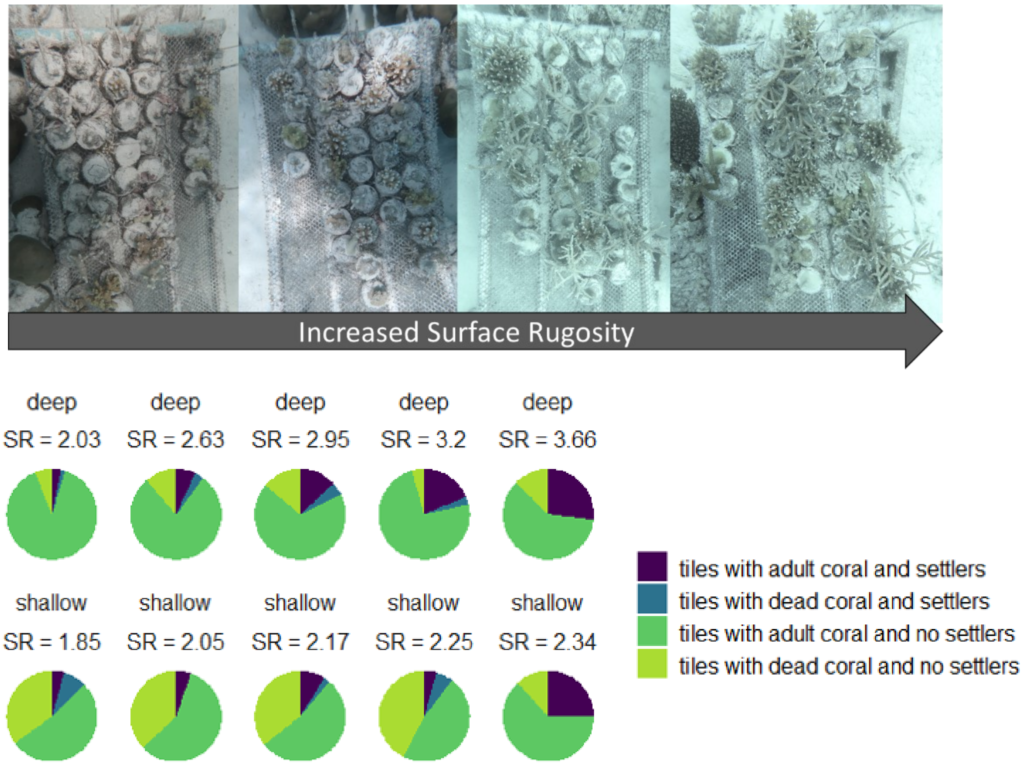


**Figure 4.2 – Example of increased rugosity and tile proportion in each rack.** On the top, four racks have been selected in order of increasing Surface Rugosity to show how complexity differences. On the bottom, pie charts show the proportion of tiles with live corals and settlers (dark blue), tiles live corals but without settlers (light green), tiles with dead coral and settlers (ocean blue) and tiles with dead corals and no settlers (lettuce green) Racks are arranged by increasing SR at each depth.

Settlers were found on 50 out of 339 tiles (Figure 4.2). I consistently detect an effect of SR, regardless depth or presence of live coral on the same tile (Table 4.1). Models that included rack SR had lower WAIC and LOOic (Table 4.1). Moreover, the model with SR as the only predictor variable (Figure 4.3a-b) had the best goodness of fit according to both criteria (Table 4.1). In this model, the estimated effect size of SR on settlement probability was 0,38, with credible intervals not overlapping zero (Figure 4.3b). This corresponds to an increase of 15,71 % of settler presence probability along the range of complexity considered. Together the results show that the probability of settlement increased with local structural complexity and highlight the importance of coral-generated structures for the beginning of benthic life stage of these organisms. Greater micro-scale complexity of the substratum enhances coral larval settlement (Hata *et al.*, 2017), this study provides evidence that larger scale coral-built habitat complexity has a positive effect on coral settlement as well, enhancing coral fitness.

**Table 4.1 Models results.** Effect sizes of the variables, Widely Applicable Information Criterion (WAIC) and leave-one-out cross validation information criteria (LOOic) for all the models. In grey, variables whose 95% Credible Interval (CrI) do not overlap with 0. Models are arranged by increasing WAIC and LOOic. All the models included rack ID as random factor.

| Model | Variable | Estimate | Lower 95% CrI | Upper 95% CrI | WAIC (se) | LOOic (se) |
|---|---|---|---|---|---|---|
| presence ~ SR | intercept | -1,84 | -2,26 | -1,47 | 283,38 (23,41) | 283,54 (23,50) |
| | SR | 0,38 | 0,02 | 0,78 | | |
| presence ~ SR + site | intercept | -2,13 | -2,94 | -1,43 | 284,47 (23,70) | 284,58 (23,72) |
| | SR | 0,57 | 0,02 | 1,19 | | |
| | site: shallow | 0,54 | -0,68 | 1,76 | | |
| presence ~ SR + status | intercept | -1,82 | -2,31 | -1,39 | 285,45 (23,72) | 285,43 (23,72) |
| | SR | 0,37 | 0,01 | 0,77 | | |
| | status: dead | -0,09 | -0,78 | 0,59 | | |
| presence ~ status + SR + site | intercept | -2,11 | -2,92 | -1,39 | 286,53 (23,98) | 286,55 (23,99) |
| | status: dead | -0,13 | -0,83 | 0,54 | | |
| | SR | 0,57 | 0,03 | 1,17 | | |
| | site: shallow | 0,57 | -0,63 | 1,85 | | |
| presence ~ site | intercept | -1,68 | -2,38 | -1,07 | 287,24 (23,56) | 287,46 (23,58) |
| | site: shallow | -0,34 | -1,31 | 0,58 | | |
| presence ~ status | intercept | -1,76 | -2,31 | -1,29 | 288,06 (23,63) | 288,15 (23,64) |
| | status: dead | -0,21 | -0,90 | 0,46 | | |
| presence ~ status + site | intercept | -1,65 | -2,30 | -1,05 | 289,30 (23,82) | 289,51 (23,90) |
| | status: dead | -0,13 | -0,85 | 0,56 | | |
| | site: shallow | -0,31 | -1,27 | 0,61 | | |

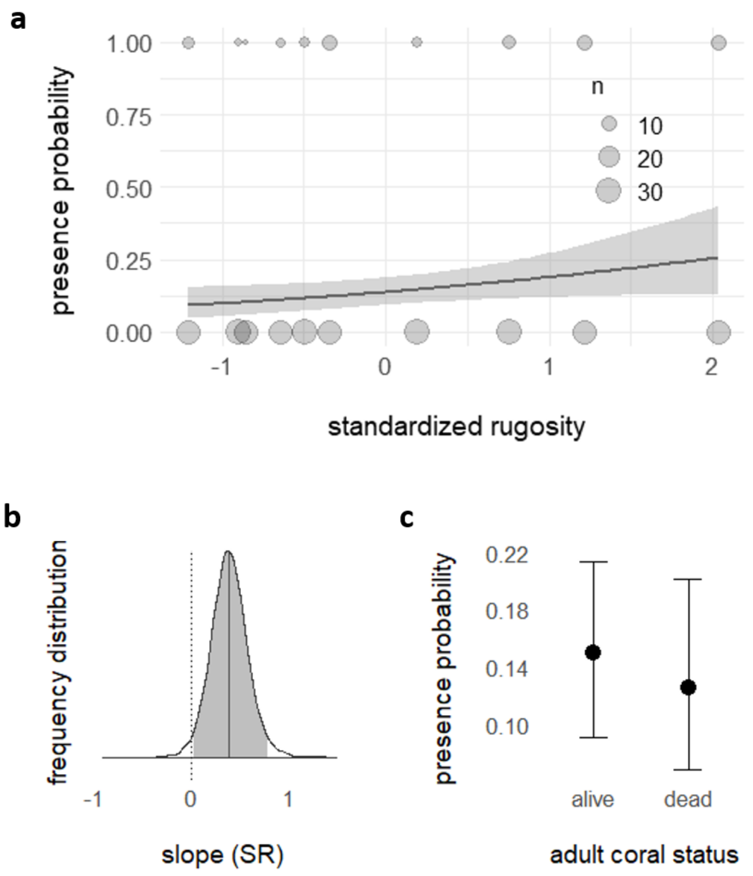


**Figure 4.3 – Relevant models results.** a) Marginal effect plot for the best fit model, which included only surface rugosity (SR) as fixed effect. Dots represent the number of tiles where settlers and juveniles were found or not. b) Posterior distribution of the slope of the best fit model with 95% credible intervals. c) marginal effect plot for the model which included the status of the adult coral attached to the tile as only explanatory variables, of which I did not detect an effect.

I failed to detect and effect of status of the coral attached to the tile on settling probability (Table 4.1, Figure 4.3c). This suggests that there was probably no biotic interaction between adults and settlers on sides and bottom surfaces of the tiles. As predicted, the presence of corals itself did not have an effect, but more importantly the complexity of their forms determined the positive ecological feedback found. Higher complexity has higher chances of diminishing water flow and creating eddies that lead the larvae towards the bottom (Zawada *et al.*, 2019). Skeleton structures from previous generations of corals can be considered as 'ecological inheritance' (Odling-Smee, Laland and Feldman, 2003) regardless of colony survival. An ecosystem engineer leaves ecological inheritance when the modification of the environment persists longer than the life-time of the ecosystem engineer

(Odling-Smee, Laland and Feldman, 2003). Here, this modification (i.e. structural complexity of the skeleton) potentiates coral fitness intergenerationally, and ecological inheritance contributes to the niche construction process.

Although light is a major factor affecting coral growth (Buddemeier and Kinzie, 1976; Hoogenboom and Connolly, 2009) and zonation (Wellington, 1982), I failed to detect an effect of light on settlement. Effects of light would likely have been more detectable when considering recruitment on tile topsides (Vermeij, 2006), which did not occur during this experiment. Furthermore, coral structures can also shadow the benthos, modulating the effect of light on the bottom surface (Brakel, 1979). Here, I measured fitness as settlement success (Hunt and Hodgson, 2010). Light may play a more important role in later coral ontogeny and certainly the effect of structural complexity on settler survivorship needs further investigation. Further experiments including non-coral-built structures and zero-complexity structures as controls could elucidate about the role of coral-built structures in enhancing coral fitness when compared to natural conditions. Nonetheless, these findings provide strong evidence that along a gradient of increasing structural complexity, settler presence increases as well.

As a metaphor, environmental filtering has been used to describe specific values of abiotic environmental variables that “filter out” certain species or traits, not allowing them to persist in specific areas (Keddy, 1992; Kraft *et al.*, 2015). In coral reefs, the environmental filtering concept can explain some aspects of reef zonation. For example flow conditions can filter out morphs not suited to face specific hydrodynamic forces and leave structurally clustered species coexisting under similar flow regimes (Madin and Connolly, 2006). The concept of environmental filtering (Keddy, 1992) has recently been criticized for being used incorrectly (Kraft *et al.*, 2015; Cadotte and Tucker, 2017; Thakur and Wright, 2017), especially when considering ecosystem engineers (Thakur and Wright, 2017). Problems arise when inferring the environmental filter from species or trait observational data, since environmental gradients can simultaneously affect other coexistence mechanisms, like competition for resources, or bioengineer activity (Kraft *et al.*, 2015; Cadotte and Tucker, 2017). Niche construction can sustain micro-modifications of the local environment at a small (individual) scale, affecting the local community interactively with the macro-environment (Cadotte and Tucker, 2017; Thakur and Wright, 2017). The latter seems to be the case for corals, since the differences in growth rates and forms of corals caused by environmental conditions promote heterogeneity in ecosystem functions (Zawada *et al.*, 2019). This results in an increase in the heterogeneity of community assemblages that in turn shape the overall environment in multitude ways. The environment cannot be considered independently, since reef habitats are literally built by their foundational organisms. The findings of the present experiment imply that different recruitment rates resulted from the dynamic construction of different microenvironments (as a consequence of the presence of different coral colonies) within the same macro-environment (two sites in the same lagoon). Since dependent on engineering activity, recruitment and new coral occurrence cannot be explained by biotic, abiotic or dispersal local conditions separately, but rather by a positive feedback interaction of all of the above. Focusing on environmental filtering overlooks this intricate network of reciprocal causation between corals and the environment.

Coral facilitation of settlement has also implications for recovery from disturbances. Human induced disturbances to coral reefs, such as temperature and acidification, are predicted to increase (Hughes *et al.*, 2017), together with the scale of the impacts on the reefs (Hughes *et al.*, 2003). Nonetheless, reef recovery from mass mortality is possible and coral larvae settlement is a necessary process for this recovery. These findings offer a mechanistic explanation for increased rates of recovery at sites with higher levels of structural complexity due to coral presence (Graham and Nash, 2013). Nevertheless, rigorous experimental tests and a better understanding of the mechanisms underlying coral niche construction is urgent and timely in order to promote ecosystem post-disturbance recovery. Indeed, by regulating habitats at a local scale, ecosystem engineering and niche construction can establish population and ecosystem feedbacks and maintain ecosystem health and resilience (Boogert, Paterson and Laland, 2006). The experimental system developed here, which can flexibly manipulate the composition, structure and species identity of coral pieces on racks, offers considerable potential to explore these issues further.

The ecological and evolutionary implications of the present findings deserve attention. In forest ecology, wildfires, which were considered a purely extrinsic factor, have been shown to be dependent on a set of niche-constructing flammability traits (e.g. branch-morphologies, self-pruning ability, leaf-size, oil content) (Schwilk, 2003; Schwilk and Caprio, 2011). This demonstrates how organism features can influence external environment in ways that modify selective feedback and eventually their evolution (Schwilk, 2003; Post and Palkovacs, 2009; Schwilk and Caprio, 2011). Coral shapes have an important role in shaping the evolutionary history of other taxa. For example, the emergence of coral branching morphologies are key for the diversification of small-size fish (Bellwood, Goatley and Bellwood, 2017). Yet, whether morphological coral traits affect the evolutionary history of coral groups remained undetermined. Given the three criteria for niche construction (Matthews *et al.*, 2014), I now show that corals meet criterion 2: they modify selection pressure upon themselves through modification of the environment. Defining traits that enhance population fitness enables to look at the evolutionary history of such traits, creating the ground for the test of criterion 3, i.e. studying the evolutionary history and phylogeny of such traits. Models that can predict a range of coral complexity traits from size and species are becoming available in the literature (House *et al.*, 2018; Zawada *et al.*, 2019; Zawada, Dornelas and Madin, 2019). This allows the use of geological datasets to investigate the evolution and prevalence of 3D traits of interest and the role of niche construction in coral evolution. Here, I make the first step forward in defining coral niche construction, presenting structural complexity as a niche-constructing trait in coral reef ecosystems.

# Chapter 5. Reef complexity mediates coral recruitment

Ecological niche construction mechanisms favouring the agent of construction can be different throughout an organism life span. Once settled and metamorphosized, corals need to grow and reach their reproductive stage. Here, I make a second test to assess whether corals meet the second criteria of niche construction, focusing on coral fitness measured as recruitment success, measured as juvenile recruit abundance. To achieve this aim, I performed an observational study to see whether the presence of adult corals and specific geometric reef traits influenced juvenile occurrence. After settlement, corals need habitats that provide enough protection from grazers and algae overgrowth, yet have reasonable light conditions and water flow. I found that juvenile abundance positively correlates with adult abundance, fractal dimension at the small local scale and surface rugosity at the larger reef patch scale. These results underline that post-settlement processes can also be mediated by corals and the habitat structures they build, and provides strong evidence for ecological niche construction.

## 5.1 Introduction

Corals are a natural class of putative niche constructors since the changes they make to their habitats affect macroevolutionary patterns and biodiversity (Jones, Lawton and Shachak, 1994b; Matthews *et al.*, 2014; Laland, Matthews and Feldman, 2016). Comprehensive tests of niche construction in corals are lacking, mainly because relationships between reef structure and coral population dynamics is poorly understood. Here, I aim at advancing the understanding of coral niche construction by testing whether structural reef features influence coral fitness via recruitment facilitation, measured as abundance of juvenile corals.

Corals have a planktonic life stage at the end of which they settle on suitable substratum, metamorphose and start their sessile life. To sustain their populations, corals, like many other marine organisms suffer high levels of early-life mortality, need a considerable larval supply. Once the survived larvae manage to settled, post-settlement survival increases as corals grow (Vermeij and Sandin, 2008). Among causes of death, there are competition, predation and disturbances such as bleaching and diseases (Ritson-Williams *et al.*, 2009). For example, algae prevalence may be detrimental to corals, since it reduces substratum available for coral settlement, and reduces light availability for the small colonies (Hughes and Tanner, 2000). While herbivory may help control algae prevalence, herbivorous fishes and invertebrates may kill small colonies while grazing, contributing to a decrease in coral recruitment (Doropoulos *et al.*, 2016). In this context, the habitat where corals settle plays an important role in modulating their survival. Non-exposed habitats are assumed to be with low productivity potential as they comprise typically low light environments, but because they protect coral recruits from stresses and disturbances, they can result in higher presence of juveniles (Babcock and Mundy, 1996). Observational studies found more juveniles in crevices (Doropoulos *et al.*, 2016) and even at the previous settling stage, corals rely on eddies created by small structural obstacles, such as sea urchin burrows in the field (Birkeland and Randall, 1981) or 1-cm blocks in the lab (Hata *et al.*, 2017), to be able to find suitable substratum and attach. As a result, a lot of post-settlement processes may be modulated by local habitat complexity. The fine topography of the reef, engineered by corals, may therefore affect coral fitness.

Reef structural complexity is a measure of how corals engineer the environment and is important for ecosystem function and maintenance when considering other taxa in their communities (Graham and Nash, 2013). Among reef features, surface rugosity and fractal dimension are widely used metrics to describe habitat structures, especially aquatic ones (Tokeshi and Arakaki, 2012). While similar values of surface rugosity can describe very different community scenarios (Tokeshi and Arakaki, 2012; Leon *et al.*, 2014; Duvall, Hench and Rosman, 2019), fractal dimension has been consistently found to be associated with coral prevalence and to be correlated to reef zonation and coral community composition (Zawada and Brock, 2009; Zawada, Piniak and Hearn, 2010; Leon *et al.*, 2014; Burns *et al.*, 2015b). When considering both parameters together with height range, Torres-Pulliza et al. (Torres-Pulliza *et al.*, 2020) found that reef complexity alone could explain more than 50% of the variation in reef coral species richness, diversity and abundance. This result is remarkable, since local biodiversity depends on several processes that are not directly linked to habitat complexity, such as environmental filtering, population dynamics, dispersal and species interactions (Torres-Pulliza *et al.*, 2020). From an ecological perspective, this type of association reflects the spatial reciprocity that links coral colonies as ecosystem engineers with the reef habitats they both build and simultaneously occupy. But to understand if this pattern has evolutionary consequences, the existence of preferential coral recruitment in highly coral engineered reef habitats must be detected.

To investigate the role of corals as niche constructors further, it is necessary to focus on intergenerational effects of reef structures, for example on the effects of habitat structure as built by adult corals on coral recruitment. The presence of coral structures - whether dead or alive- that systematically favours recruit occurrence is evidence of niche construction. In reefs, the presence of living corals is inversely related to substratum availability, and since unoccupied reef space is necessary for settlement, the presence of living adult colonies may disadvantage recruitment. In this chapter, the effects of both reef complexity and adult coral abundance on coral recruitment is investigated at different reef sites in Lizard Island (Great Barrier Reef) at a range of spatial scales. Juvenile recruits in this study are defined as newly acquired colonies that are visible upon scrutiny of the reef, i.e. I did not verify if recruits were sexually mature nor how old they were. Reef sites with higher larval supply were expected to have higher recruit abundance. High fractal dimension was expected to be positively correlated to recruit abundance due to the presence of micro-eddies that potentially increasing chances of larval settlement (Hata *et al.*, 2017). Surface rugosity was expected to be positively influencing coral recruitment because it quantifies surface availability per unit planar area. Because the two metrics are related to adult abundance, there could be a synergistic effect of adult abundance, which was also considered as a measure of (intra-generational) niche construction. I found that not only corals seem to settle in proximity of adults, but also that recruitment follows specific configurations of the reefs, highlighting functions of different aspects of complexity of the reef.

## 5.2 Methods

Data was collected in the same nine Lizard Island reef sites of Lizard Island of Chapter 2. As described there, in 2018 and 2019 circular digital elevation models (DEMs) and orthographic mosaics of each reef site were obtained following the spiral method described in Pizarro et al. (Pizarro et al., 2017) as further described in Torres-Pulliza et al. (2020). For this chapter, locations of adult coral colonies in 2018 and location of coral recruits (diameter < 5cm) in 2019 were annotated in the field on orthographic mosaics maps printed in underwater paper. Colonies with diameter <5cm that were previously annotated in 2018 were counted as adults. To make sure recruits were not small colonies or colony fragments, but rather new individuals, care was taken to make sure that there was a growing edge at the margin of the colonies. Thus, juvenile recruits in our analysis correspond to all the new colonies found. The geographic coordinates of each adult and recruit were subsequently obtained by entering the field annotations as shapefile over the reef mosaic rasters in QGIS (QGIS Development Team, 2019).

To quantify the effect of spatial scale, sites were subdivided in into different sized patches (Figure 5.1a, Figure D.1a and D.2a). An 8 by 8 m square was centred in each of the reef DEMs and divided into grids with patch dimensions of 50x50cm, 1x1m, and 2 × 2 m. This process resulted 256, 64, and 16 contiguous reef patches of 0.25m$^2$, 1m$^2$ and 4m$^2$ respectively per site. DEMs for each site were cropped for each patch to calculate surface rugosity (R) and fractal dimension (D) (Figure D.3). Surface rugosity was obtained with the 'surfaceArea' function of the package 'sp' (Hijmans et al., 2020) and D was obtained according to Eq. 1 in

Torres-Pulliza et al. (2020). Recruit and adult counts for each patch were also extracted from the annotation layer.

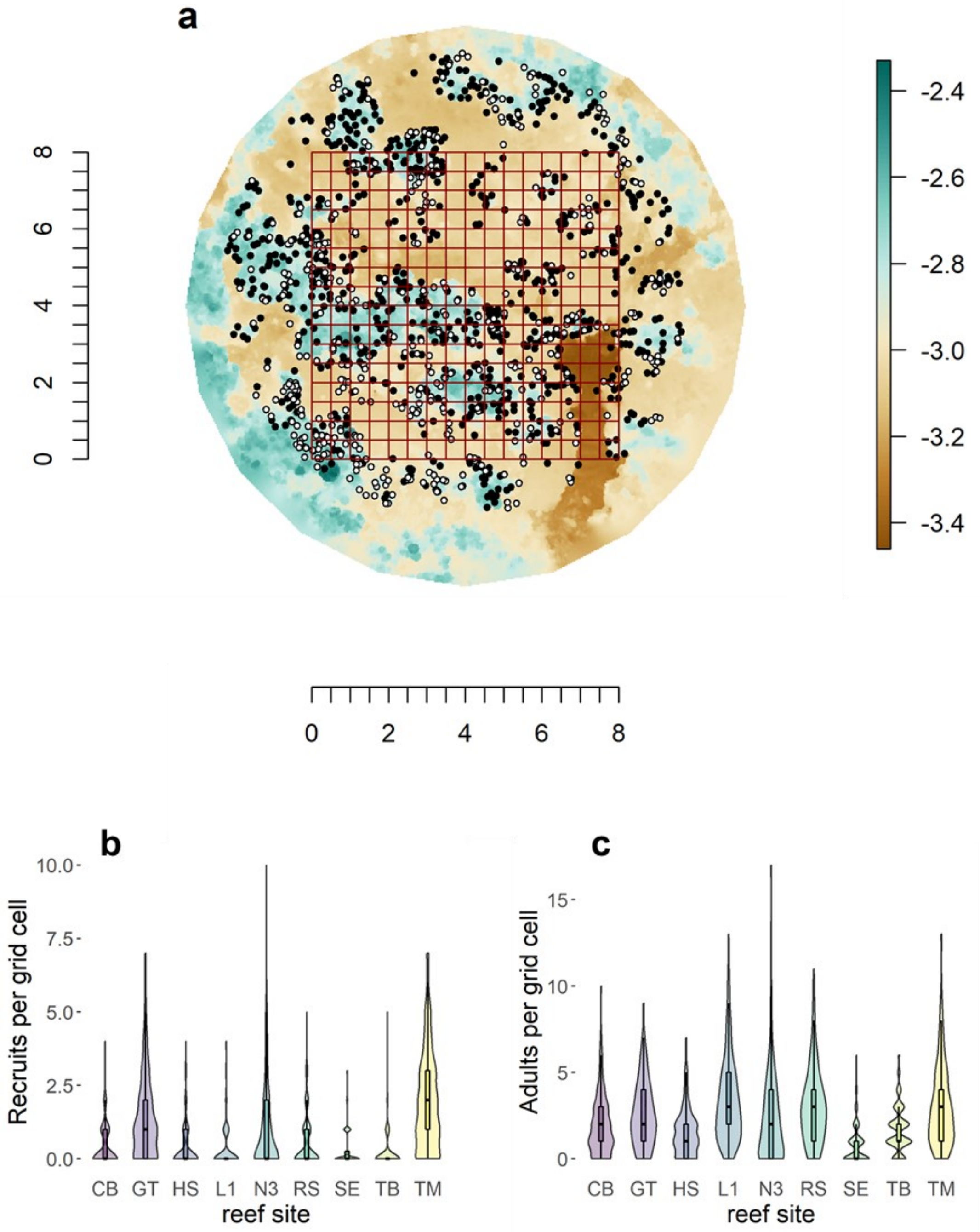


**Figure 5.1 - Digital elevation model example and recruit and adult counts for the 50x50cm grid**. a) Digital elevation model of the reef site at North Reef 3 (N3). Black dots represent the locations of adult colonies and white dots represent the locations of recruits. In dark red, the 50x50cm grid that divides the reef in 256 cells of area 0.25m$^2$. b) Recruit abundance divided by site represented with violin and boxplots. c) Adult abundance divided by site represented with violin and boxplots. For representation of bigger scale grids, refer to Figure D.1 and D.2.

To assess the brood stock available for settlement in 2018, the density of new coral settlers was measured on experimental substrates with settlement tiles (Mundy, 2000). At every site, six settlement tiles (11 cm × 11 cm, unglazed clay) were attached to the reef at least 3m apart from each other, 5 days before the predicted spawning date. Eight weeks after spawning (Hughes et al., 1999), tiles were retrieved (January 2019), soaked in bleach, and then left to dry. Each tile was carefully inspected under a stereo-dissecting microscope and all coral settlers found were counted. The average tile count of coral settlers per site was used as measure of coral settlement in 2018.

A Bayesian generalized additive model was fitted for each grid size to examine the effect of reef complexity on recruit counts in each grid cell of reef. Models were fitted with the probabilistic language RStan using the 'brms' package (Bürkner, 2017). Appropriate error distributions were chosen for each grid size: a zero-inflated Poisson distribution with a log link function for the finer grid (0.25m$^2$) and a Poisson distribution with a log link function for the other two grids (1 m$^2$ and 4m$^2$). When appropriate, predictors were transformed to improve their distribution and range (e.g., surface rugosity was log-transformed and coordinates were mean centred to zero and scaled to have a standard deviation of one). Because surface rugosity and fractal dimension have non-linear relationships with adult coral biodiversity and abundance (Torres-Pulliza et al., 2020a), the interaction between the two metrics was included as predictor term with a smoothing effect, leaving a default of 10 smooths (k=10). The adult abundance in each patch was included in the model as linear predictor as proxy for niche construction. In fact, while surface rugosity or fractal dimension can result from reef properties that are dependent from living coral presence, adult abundance can explain individual environmental effects beyond the impact of the coral structure within the reef space. To account for differences in larval settlement across sites, the mean count of settlers in the tile from 2018 was also included as linear predictor. To account for spatial autocorrelation, I included latitude and longitude as predictors in the models by including coordinates of the centre of each square with a Gaussian process smoothing basis and allowing latitude and longitude to interact (implemented by specifying 'bs = "gp", m=2' in the smooth function). To check robustness of the results with respect to spatial autocorrelation, the models were re-fitted with site as random effect instead of coordinates. All the priors for model fitting were left as default values, and for each model four chains for 20000 iterations were run, with a warm-up period of 4000 iterations and a thinning rate of

10 iterations. I ensured that Rhat values were ~ 1 and goodness of fit was assessed by visual inspection of the chains. All analyses were performed in R version 3.3.2 (R Core Team, 2018).

## 5.3 Results

A total of 1642 coral recruits in 2019 and 5230 adult colonies in 2018 were found in the grid area. At the finest grid, most of the cell reef patches did not have any recruits and mean recruits per patch was 0.71 (Figure 5.1b), while the other grids showed at least one recruit in most cases (1x1m grid: mean recruits per patch = 2.85, 2x2m grid: mean recruits per patch = 11.40, Figure D.1b and D.2b).

For the smaller scale considered, fractal dimension values ranged from 1.913 and 2.466, while surface rugosity ranged between 1.019 and 5.597 (Figure 5.2). With increasing grid size (Figure D.4), fractal dimension increased in values to a range of 2.129 - 2.499 (1x1m grid) and 2.264 - 2.592 (2x2m grid). Surface rugosity, conversely, decreased range width to 1.078 - 3.500 (1x1m, grid) and 1.196 - 3.483 (2x2m, grid), but maintaining similar mean values (Figure D.4).

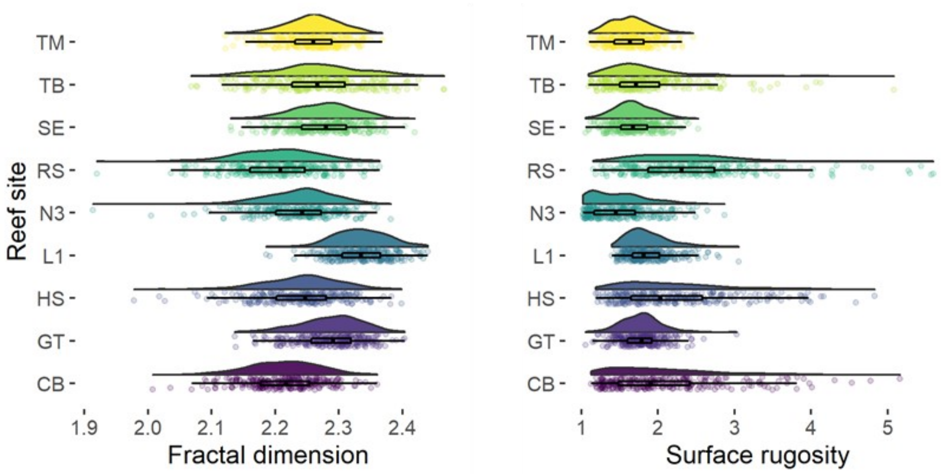


**Figure 5.2 - Raincloud plots of reef patch fractal dimension and surface rugosity for the 50x50cm grid cells divided by site.** For comparison with bigger scale grids, refer to Figure Figure D.4.

All the models converged, although some predictor incidences have very wide confidence intervals (Table 5.1). All the models showed that recruit abundance is affected similarly by the predictors. Adult abundance had a positive effect on recruit presence across all scales, while there was no effect of tile settler abundance at any scale (Table 5.1). Smoothed effects of fractal dimension at the finer grid and for surface rugosity at the bigger grid were detected. When considering the interaction between the two, incidence variation ("sds") was high across scales, so a visual inspection of the interaction was necessary. Figure 5.3 shows the effect of the non-linear interaction between fractal dimension and surface rugosity for the smaller and for the bigger grid. At small scales, high recruitment was found in areas of low rugosity and high fractal dimension. At large scales, high recruitment was found in areas of intermediate rugosity and relatively low fractal dimension. Coordinate pairs (interaction between longitude and latitude) effects were also strongly detected, showing that recruitment is spatially autocorrelated. Qualitatively results were the same for models fitted with site as random effect instead of coordinates (Table D.1).

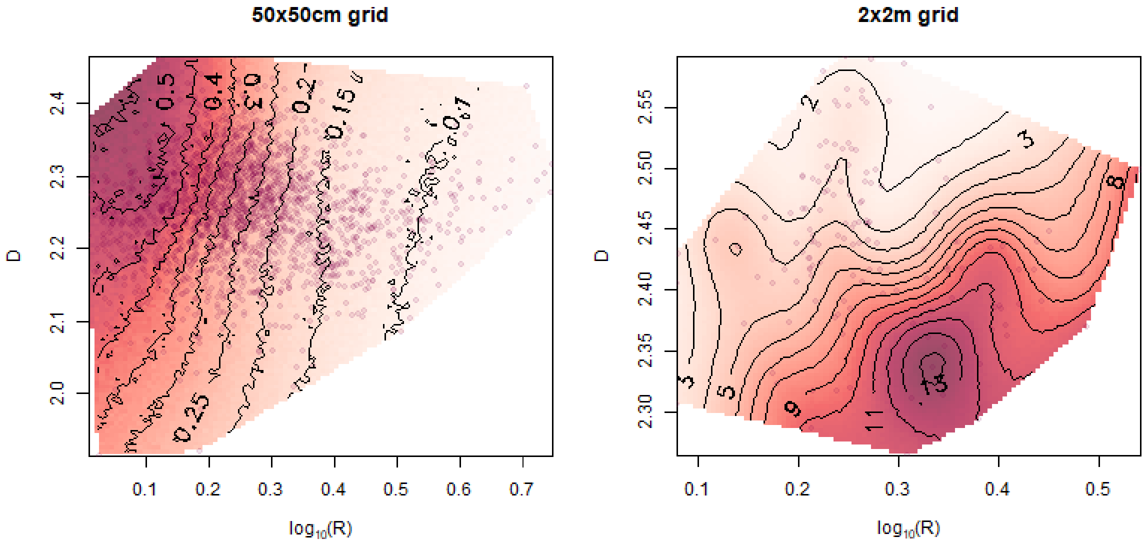


**Figure 5.3 - Predicted coral recruitment (recruit count for 0.25m$^2$ and 4m$^2$ reef areas) when plotted on the surface complexity plane given by rugosity and fractal dimension.** Notice that rugosity has been log$_{10}$-transformed. Dots represent data pairs used to fit the model at each scale and contours represent predicted increments in counts of 0.05 for the finer grid and 1 for the bigger grid. For comparison with prediction for the intermediate scale, refer to Figure D.5.

**Table 5.1– Model estimates for recruitment abundance for each of the grid considered**. The incidence of the parameters and the confidence intervals are shown as recruit counts. Because of the log link function, effects are detected when the confidence interval (CI) does not overlap 1 (shaded in the table). For smoothed variables, incidence of the smooths ("s", row 4 to 7) and standard deviation of the smoothed interaction ("sds", row 8-9) is reported.

| | **50x50cm grid** | | **1x1m grid** | | **2x2m grid** | |
|---|---|---|---|---|---|---|
| *Predictors* | *Incidence* | *CI (95%)* | *Incidence* | *CI (95%)* | *Incidence* | *CI (95%)* |
| intercept | 0.35 | 0.00 – exp(13.05) | 2.02 | 0.00 – exp(12.93) | 9.52 | 0.00 – exp(12.55) |
| adult abundance | 1.17 | 1.15 – 1.20 | 1.04 | 1.03 – 1.05 | 1.01 | 1.00 – 1.02 |
| mean settler abundance | 1.03 | 0.01 – 95.71 | 0.89 | 0.02 – 48.42 | 0.86 | 0.03 – 20.85 |
| s($\log_{10}$(Rugosity)) | 0.30 | 0.02 – 3.02 | 3.86 | 0.08 – exp(5.49) | 896.37 | 15.64 – exp(10.87) |
| s(Fractal dimension) | 101.77 | 5.03 – exp(8.95) | 0.01 | 0.00 – 1.33 | 0.02 | 0.00 – 1.50 |
| s(longitude) | 0.23 | 0.00 – exp(99.00) | 0.71 | 0.00 – exp(101.96) | 9.51 | 0.00 – exp(70.02) |
| s(latitude) | 220.24 | 0.00 – exp(116.94) | 0.39 | 0.00 – exp(79.79) | 0.80 | 0.00 – exp(103.95) |
| sds($\log_{10}$(R),D) | 1.80 | 1.10 – 3.97 | 2.73 | 1.51 – 7.08 | 7.80 | 3.07 – 26.16 |
| sds(lat,lon) | exp(13.50) | exp(8.98) – exp(19.92) | exp(11.98) | exp(7.50) – exp(18.06) | exp(10.99) | exp(6.16) – exp(17.78) |
| *Observations* | 2303 | | 574 | | 144 | |
| *$R^2$ Bayes* | 0.427 | | 0.598 | | 0.792 | |

## 5.4 Discussion

This study shows that coral recruitment benefits from presence of adult corals when measured at a range of scales, indicating that corals may engage and succeed in collective niche construction. Furthermore, I find that reef rugosity is important for recruitment at larger patch scales, and that fractal dimension is important at small patch scales. The most parsimonious explanation for these results is that settling coral larvae collect in regions of the reef where rugosity is high, but they tend to settle and survive to juveniles in patches with higher fractal dimension within these larger patches. These results altogether suggest that corals improve their own fitness by facilitating larval settlement and their survival. Such a feedback loop is the signature of ecological niche construction.

It may be argued that as high complexities correspond to high surface availability at any given planar area, results are due to a higher availability of reef space for recruitment. But this interpretation relies on a uniform larval supply across sites, which was not the case in this analysis. Here, while I did find that specific intermediate combinations of the two complexity metrics corresponded to higher recruitment, there was also a synergistic effect of adult abundance, indicating that corals may have environmental effects beyond their impact on reef structure.

According to Torres-Pulliza et al. (2000), the area of the surface complexity plane where I find more recruitment at smaller scales corresponds to reef patches with low height ranges. At this local scale, this condition may be beneficial to recruits, since they need an open and relatively irradiated environment, where big protuberances in the proximity casting shadow would not benefit the newly settled corals (see chapter 2). Fractal convoluted surfaces within these small patches though, while not affecting overall light patterns, may increase chances for the larvae to settle in that area, by breaking flow and allowing the larvae to come across the substratum capturing larvae in micro eddies (Hata *et al.*, 2017). Fractal dimension may also mediate other post-settlement local processes, such us predation (Richardson, Graham and Hoey, 2017) or other biotic interactions. Additionally, higher fractal dimension is usually associated to coral presence in reefs (Leon *et al.*, 2014; Burns *et al.*, 2015b), which again has been found to be beneficial for recruitment, so this result may enforce the positive effects that adults already have.

At the larger patch scale, the detail of spatial association between recruit and surrounding is less precise (recruits can be at any location within the 4m$^2$ area), but nonetheless, patches with higher height range represent reef patches with higher recruitment. This makes sense, since high surface rugosity corresponds to reef with more surface available for colonization, increasing the chances of recruit presence. By a visual inspection of the DEMs (for example in Figure 5.1), we see that recruitment happens at the edges of the structures, which is likely the aspect of recruitment that the model at this scale captures.

Contrary to expectation, we do not detect an effect of larval supply on the reef, measured through coral settlers count on settlement tiles, on number of recruits present in the reef. This finding is particularly unexpected since settlement estimates obtained with this method are used to infer recovery ability of reefs around the world (Hughes *et al.*, 2019). This result may be due to: i) settlers on tile surface behave differently than on reef substratum, and/or ii) coral juveniles detected only became visible after more than one year (as found in *Siderastrea radians* in Vermeij and Sandin, 2008). As a result, we should interpret settlement data from settlement tile analysis carefully, since by eliminating structure interaction, they may not be very informative on future of the reef. Nonetheless, the present results show that post-settlement processes play a major role in coral survival, with respect to what previously through (Vermeij, 2006).

The study sites were reefs that underwent severe disturbance (Madin *et al.*, 2018) and were given low recovery probability due to the lack of larval supply found after the 2 years of consecutive mass bleaching. Seeing that corals settle and successfully survive to the recruit stage is reassuring, especially in light of the fact that corals will likely facilitate new recruitment. Once coral grows, they will also increase local fractal dimension, hopefully reinforcing the demographic feedback loop. It looks like the site found to have the highest recruit abundance in this analysis (Trimodal reef, TM) corresponds to reefs known to have high coral diversity and coverage before disturbances (Madin *et al.*, 2018). This may be happening because coral skeleton residual still has a role in recruitment retention regardless of whether the coral is alive or dead. Of course it may also depend on deeper coral population availability at each site (Baird *et al.*, 2018) or other dispersal variable.

Fractal dimension and rugosity at the 50x50cm scale were qualitatively consistent with the results the random sampling gave in chapter 2. The ranking of their mean value among sites remained practically the same. Here, three fractal dimension values were smaller than 2, which is technically impossible for surfaces, but the data was retained regardless since values are likely to rank similarly.

Not only the presence and abundance of corals had an effect, but also the complexity of their forms determined the positive ecological feedback that I found. In particular, it looks like not only live corals, but also skeleton structures from previous generations of corals that were making up the reef shape enhanced recruitment. This is a sign of ‘ecological inheritance’, i.e. a modification of the local environment that persists longer than the life span of the ecosystem engineer (Odling-Smee *et al*. 2003). The modification (i.e. structural complexity of the skeletons) potentiates coral fitness intergenerationally, and ecological inheritance contributes here to the ecological niche construction process. Follow-up studies following development of the recruits (i.e. measuring growth, reproductive and survival variance) may elucidate other mechanisms involved in the process.

The recruitment and new coral colonies on reefs cannot be explained by biotic, abiotic or dispersal local conditions separately, but rather by a positive feedback interaction of these factors. Focusing on environmental and biotic filtering barriers on dispersal overlooks this intricate network of reciprocal causation between corals and the environment and the present findings underlay the significance of using a niche construction approach.

# Chapter 6. General Discussion

## 6.1 Novel contributions and summary of findings

Quantifying and understanding ecosystem engineering activities and the feedback they can establish for their own population performance may provide further insights on the mechanisms of niche construction. By focusing on a well-established class of ecosystem engineers, hard corals, and their relationships within coral reef systems, this thesis contributes to a better understanding of the mechanisms involved in ecological niche construction. The analyses performed included observational and experimental approaches, I used novel methods to quantify complexity traits and focus on different ecological scales in which niche constructing patterns could be found. Moreover, this thesis highlights that using niche construction as a framework to connect ecology and evolution can stimulate novel research in coral reef ecology, which hopefully will be informative for the understanding of coral and reef evolution.

To the best of my knowledge, this investigation is the first attempt to organically approach coral ecological niche construction. First, I have demonstrated that reef quantitative surface descriptors that measure coral engineering, particularly surface rugosity, affect patterns of light availability among reef habitats. While meteorological and tidal-phase-linked variables also had an effect, structure-mediated environmental variation is not temporally and stochastically variable and can systematically bias local environments, affecting habitats in ways that are likely to accumulate and eventually interfere with ecological processes of the reef. Second, I have shown that the different macro environmental conditions may consistently induce differently varied habitat structures in reef ecosystems. For this, I performed a reciprocal transplant experiment which also showed less plasticity in niche-constructing traits in certain taxonomic groups, which provide less diverse habitats across environments. Additionally, I found little effect of site of origin of the fragments used in the experiment, indicating that prime the role of plasticity rather than environmental filtering in shaping the spatial distribution of different coral shapes. Third, I have explored fitness consequences of coral structures on the coral niche constructing populations, focusing on two different recruitment success metrics: coral larval settlement and juvenile abundance. I showed an increase in settler presence on artificial tiles deployed in the field along a gradient of coral-built structural complexity measured as surface rugosity. Structural complexity had a positive effect on settlement, with an increase of 15,7% of settler presence probability along the range of rugosity considered. I also showed an increase of juvenile abundance across reefs characterized by small-scale high fractal dimension and big-scale high surface rugosity. Juvenile abundance was also affected by adult abundance, showing that the effects of the adult structure may be counteracting the competition for space posed by adult colonies. Nonetheless, both fitness analysis provide evidence that coral-built structural complexity creates conditions that facilitate coral settlement and survival to the juvenile stage.

Altogether, my findings suggest that corals can bias selection pressures regardless from their genetic identity through their plastic forms and structures. At ecological time scales, corals ameliorate their environment enhancing their fitness, which in turn increases coral engineering rates. These ecological feedbacks can have had repercussion in the evolutionary history of Scleractinia, as they pose the basis for niche construction evolutionary processes to take place. They also have practical implications for reef restoration and conservation and suggest some other research opportunities to advance our understanding of coral ecological niche construction.

## 6.2 Evolution through niche construction

This thesis used Niche Construction Theory as a framework to explore the dual relationship between corals and their environment in a merely ecological setting. As such, it enables detecting ecological processes that may influence coral evolution (see Criterion 3 in Figure 1.1).

Disentangling the portion of the environment modified by corals allowed me to identify environmental variables that intrinsically change with changing coral composition and extended (reef) phenotype. So far, it became clear that local structural complexity metrics (Torres-Pullitza et al. 2020, and Chapter 3 and 5) and light patterns (Chapter 2) can change orthogonally with respect to the external environment. I also found that recruitment mechanisms depend on these local complexity metrics and on coral presence (Chapter 4 and 5). This means that recruitment not only relies on the reef structure (ecological inheritance) built by corals, but also on the presence of living colonies. With this information, eco-evolutionary models could explore the evolutionary ramification of this organismal sustained environmental alteration and explore patterns of evolution through niche construction.

I also described coral traits that engage in reef ecosystem engineering focusing on their effects on ecological mechanisms and coral fitness. This could allow us to compare the rate of evolutionary change in traits of recipient populations (measured in Haldane) along gradients of ecological engineering, as suggested by Matthews et al. (2014). This would be done in reef ecosystem by comparing corals between reefs with different coral-built complexity. As a result, we would recognize the role of niche construction in trait change and we would detect a coral-dependent rate of change in natural selection.

One of the main challenges in coral reefs could be dealing with the cumulative effect that corals have on recipient populations. In the dataset used in chapter 5 for example, it was not possible to identify juveniles at the species level, since it takes some time before they develop their species-specific features. For this reason, repercussions on the different taxonomic groups cannot be studied individually with the datasets used for this dissertation. But following the development of those recruits through reef monitoring will enable back identification of each colony and provide a taxa explicit dataset for further analysis, which could be valuable to investigate cumulative niche construction further.

## 6.3 Highlight for coral restoration

Extremely diverse tropical ecosystems, including coral reefs, are highly threatened by the current climate crisis (Hoegh-Guldberg, 1999b; Hughes *et al.*, 2003; Barlow *et al.*, 2018; Terry P Hughes *et al.*, 2019). Anthropogenic effects on ocean acidification, water temperature increase and increase in frequency of extreme weather events (i.e. typhoon and cyclones) can have huge impacts on the reef ecosystems (Kleypas *et al.*, 1999; Bellwood *et al.*, 2004; Madin *et al.*, 2018). In the last five years, for example, the Great Barrier Reef underwent two unprecedented back-to-back bleaching events that left two-thirds of its 2,300km-long reef communities highly affected (Terry P. Hughes *et al.*, 2019). And in the last decade, there have been five cyclones hitting those same reefs from different directions (Madin *et al.*, 2018; Terry

P. Hughes *et al.*, 2019). Concerns about the future of the reefs are rising and the call for action increasing. While priority should be given to cut our carbon emission, some short-term positive results in reef restoration (Chamberland *et al.*, 2017; Ashfaq *et al.*, 2018) and reef management (Cinner *et al.*, 2016) are encouraging.

In this scenario, ecosystem engineering have potential in conservation biology and it became clear soon after the ecosystem engineering concept definition itself (Jones, Lawton and Shachak, 1997). In fact, by modulating ecosystem feedbacks they may increase its resilience (Jones, Lawton and Shachak, 1997; Boogert, Paterson and Laland, 2006). By focusing on mechanisms of feedback facilitation within coral communities, some findings of this thesis may be of interest for reef conservation and restoration.

For example, while exploring patterns of light and temperature variability within reef patches (chapter 2), I found that while light was modulated by the reef structure and varying within reefs, water temperature was spatially constant. This may suggest that reef processes that display patchiness, such us bleaching and mortality (Brown, 1997), may be linked primarily to light patterns and its interaction with temperature, rather than temperature *per se*. In particular, my results suggest that in shallow reefs, more patchiness could be expected in relatively flat reefs (low surface rugosity) and especially when characterized by a range of fractal dimensions. This information may be advantageous for prioritizing protection of certain types of reefs, which may be more vulnerable, since it is often the cumulative stress that restrict reef recovery (Ortiz *et al.*, 2018).

I also showed that corals could improve their own recovery by facilitating larval settlement and their survival through the structure they built in the reef. But while it seemed as if adult presence was increasing juvenile abundance, I detected an effect of the reef structure on the pattern of the settlers as well. Ensuring high reef rugosity at the large scale with high fractal dimension patches interspersed, may help sustain coral recruitment post-disturbances. In fact, I found that coral larvae may be gathering in regions of the reef where rugosity is high, and then tend to settle and survive to juveniles in patches with higher local fractal dimension. This could inform restoration programs in different practical ways. For example, based on my local scale results, I showed that designing nursery recruitment structures (seeds) with fractal dimension ranging from 2.3 to 2.5 may enhance survival after transplantation back in the reefs. Furthermore, nursery with higher surface rugosity may help increasing settlement on the seeds. Additionally, based on my reef scale results, artificial reefs and/or seeding transplant locations that ensure a reef surface rugosity ranging between 3-4 may increase recruitment survival as well.

Another relevant result could be that niche constructing traits are plastic, and their plasticity varies according to taxonomic group (chapter 3). Information about coral plasticity can be used to foresee future directions of shape composition of reefs. For example, less plastic poritids can be used expecting the same behaviour in different environment, with respect to more diverse reaction norms that may be expected in acroporids. This, combined to the fact that branching morphologies have higher fractal dimension (Zawada, Dornelas and Madin, 2019), may be informative to prioritize the fragmentation of certain taxa.

Overall, using these findings to inform protected area design or reef restoration plans could increase chances of long-term success by benefitting from the establishment of niche constructing processes (Boogert, Paterson and Laland, 2006).

## 6.4 Coral diversity and ecological niche construction

The findings of this thesis add evidence of increased facilitation in more diverse coral assemblages. One of the novelties is the use of structural metrics to describe diverse coral assemblages, instead of taxonomical composition. Traditionally, diversity is measured taxonomically, for example using coral species richness. High taxonomic diversity increases reef recovery (Kayal *et al.*, 2018), enhances coral growth (McWilliam *et al.*, 2018), and decreases partial mortality and local macroalgal growth (Clements and Hay, 2019), all of which show an increase of performance in corals. The studies that yielded at those discoveries speculated about the indirect effects of diverse surfaces on flow in the interpretation of their results (Kayal *et al.*, 2018; McWilliam *et al.*, 2018; Clements and Hay, 2019). In particular, McWilliam et al. (2018) found evidence of facilitation in coral growth with diverse neighbours under high flow conditions, mostly in morphologically simple corals. He concluded that species that tend to have more complex shapes would provide modifications to flow that could be beneficial to the whole assemblage net growth (McWilliam, Chase and Hoogenboom, 2018). But using taxonomic diversity oversees coral intra-specific variability.

Results from chapter 4 and 5 suggest that facilitation through engineering may be the mechanism behind the increased recruitment since structures can affect flow (Hench and Rosman, 2013). By using structure rather than species composition, the link between the organism and flow is mechanistically tighter and tackles ecosystem functions though measurable quantitative traits rather than by using taxonomic diversity as proxy. In the same study sites I used in my analysis, habitat complexity could explain over 50% of the variance in richness and diversity (Torres-Pulliza *et al.*, 2020), which is impressive, given the number of processes that drive species coexistence. So while there is clearly a link between reef complexity and coral composition, some of the unexplained variance could reflect that since corals are plastic, even assemblages with the same species compositions could result in different complexity, since the individual species may display varied forms across sites through plasticity. A focus on coral structure can describe mechanisms that depend on that organismal trait better.

In this thesis, the effect of complexity on recruitment was analysed at two different stages and with 2 different approaches. While experiments with settlement tiles showed an effect of increased surface rugosity on settlers, juveniles patterns observed on unmanipulated reefs peaked at specific combinations of surface rugosity and fractal dimension, depending on the scale of focus. This suggests that the effects of structure on post-settlement processes may be as dramatic as its effect on settlement, since the pattern in recruitment abundance found in the reef changes. Holbrook *et al.* (2018) followed reefs in Moorea after disturbances and found that coral cover returned more rapidly at sites where the least amount of live coral persisted after the disturbances. Whether the skeletal structures were left on the sites contributing to local reef complexity is unknown and using coral cover as predictor for complexity overlooks ecological inheritance of complex skeletal structures. For example, the status of the corals (alive or dead) on the settlement tiles used in chapter 4 did not affect settlement probability, but still contributed to local complexity. Long-term reef recovery in Holbrook *et al.* (2018) was nonetheless driven by juvenile abundance in the early years of monitoring, rather than their survival or growth. So even if the models are not directly comparable to mine, evidence for the primary role of recruitment in reef recovery highlights the benefits that may come from a deeper understanding of coral ecological niche construction.

## 6.5 The importance of flow

The thesis findings, together with the body of research described in the previous section 6.4, suggest that the effect of structure on flow may be of primary relevance to detect consequences on coral fitness and performance.

While this thesis focused on light and temperature as environmental variables of interest, a focus in flow variability of habitats at the reef scale would be fundamental to understand the extent to which the local environment depends on corals. Ideally, applying the methods used in chapter 2 to describe flow niches would allow to have a better picture of environmental niches variation across the reef structural descriptor plane (Torres-Pulliza *et al.*, 2020). As a matter of fact, I initially planned to measure flow patterns among reef sites as well. To achieve that, flow had to be measured simultaneously and continuously in different locations within the same reef site and with sensors that only minimally disrupted the flow. Finding the right sensor to achieve this kind of measurements was challenging, and because of the lack of ready-to-use dataloggers, I designed a couple of different loggers to be deployed in the reef, broadly based on the principles used in Figurski et al. (Figurski *et al.*, 2011). Unfortunately, equipment failure in the field rendered the data unusable. Still, in situ data about flow variability would provide useful insights on the degree of habitat provision provided by corals in natural settings.

## 6.6 Analysis limitations and comments

There are two main limitations in the analyses presented in this thesis.

In Chapter 2, differences in local temperature have not been detected. Because the precision of the loggers used was of 0.5°C, it is unknown whether there are not differences in temperature niches or whether there are, but they are smaller than half degree C. If the latter is the case, it is worth mentioning that these small sustained differences could lead to temperature environmental niche differences that can result in diverse selective pressures on corals and other organisms within the reef (as discussed in Gorospe and Karl, 2011). This finding was surprising because differences in temperature regimes among reefs have been described at both larger and smaller scales (Bainbridge, 2017; Ong *et al.*, 2017). Further investigation using more precise thermometers may achieve finding structural geometry effects on temperature niches.

In Chapter 3, 2D proxy for the 3D trait categories of shape traits were used instead of 3D metrics. Using those proxy made sense from a theoretical standpoint, but the use of structure-from-motion could allow a direct measure of the 3D shape traits. While I intended to use that methods, unfortunately most 3D models of the nubbins at the beginning of the experiment did not converge. While calibrating the structure from motion algorithm (House *et al.*, 2018), it became clear that 3D features of corals, namely surface area and volume obtained with photogrammetry, scale linearly with the two-dimensional planar area measured from pictures (House *et al.*, 2018), and this is why I settled with using 2D proxies. Nonetheless, a comparison between 2D proxies and 3D counterparts (e.g. shape traits measured in chapter 3 vs. 3D shape traits in Zawada, Dornelas and Madin, 2019) could inform about the goodness of the use of 2D metrics as proxies. Furthermore, this could allow to use archive pictures of corals, traditionally used to measure planar area, to infer 3D metrics and back trace how these traits developed.

## 6.7 Conclusion

In this thesis, I investigated the role of coral in niche construction from a purely ecological perspective. The methodology developed here is applicable to other systems as well, with rainforests being the immediate terrestrial counterpart system. The measurements of different environmental variables and novel three-dimensional coral traits allowed me to define relevant traits to study corals as bioengineers under a niche construction perspective and identify to what extent local environmental filters can be biased by bioengineering activity. Conclusions drawn over the repercussion for rehabilitation of reefs may be important for reef conservation and finding enable future research on coral evolution through niche construction.

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** I acknowledge Fisher's contribution to the genetical theory of natural selection, but I want to disclose that I do not endorse his personal views on eugenics nor his political and racist pursues*

# Appendix A. Temperature logger calibration

To check whether loggers were subject to overheating under sunlight while submerged in the water providing wrong estimates of water temperature, loggers were deployed simultaneously in a flow chamber and set to record temperature from 12.15 to 14.15 every 30 second for 6 days. The flow chamber used was exposed to the sun and had a portion of the tunnel covered, having shadow on some of the water body. The flow chamber pumped water from the sea and because of the flowing water, the temperature is assumed constant at every point of the channel and regardless of the sun exposure. Loggers were deployed both in the shaded portion of the chamber and the portion exposed to the sunlight. To test whether an aluminium foil wrapping was an efficient method in case of overheating, dataloggers wrapped in in aluminium foil were deployed in the flow chamber both under sunlight exposure and on the shaded portion of the chamber. Temperature recorded by the loggers with aluminium foil consistently gave readings comparable with the logger deployed with no wrap. When sunny, the logger exposed to the sunlight was consistently recorded temperature above water temperature.

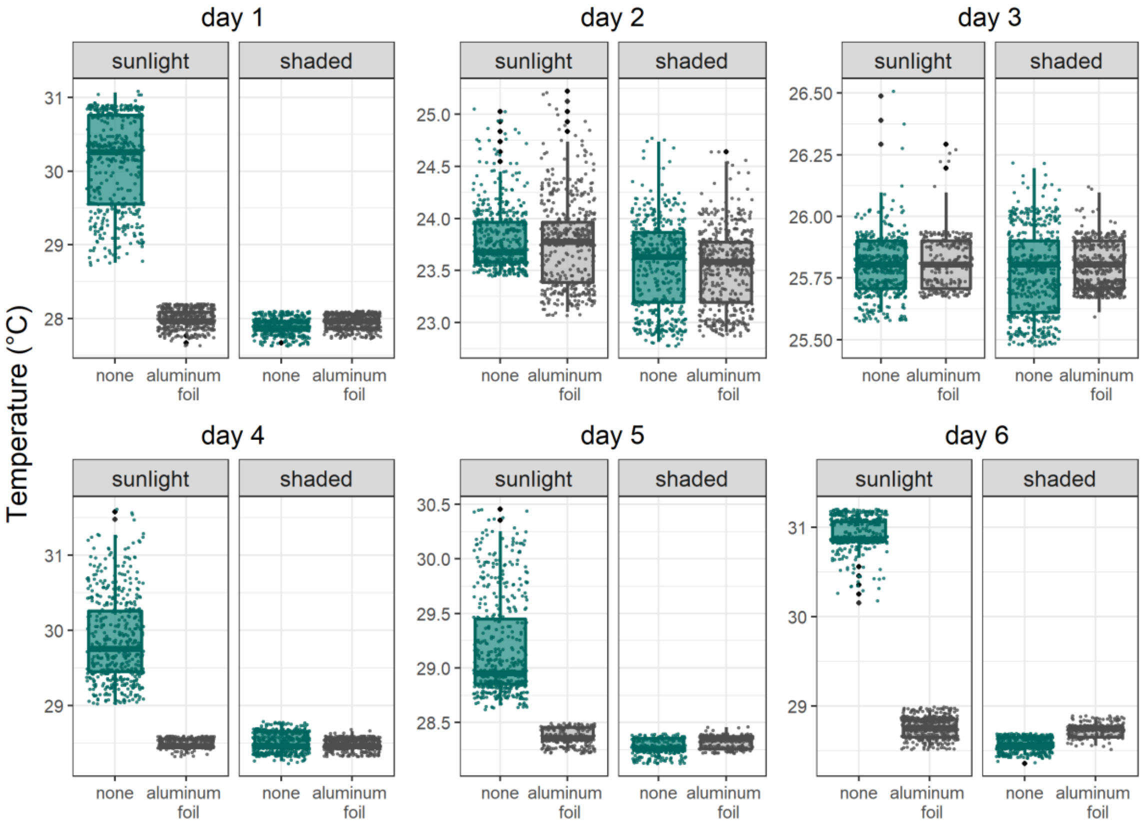


**Figure A.1 – Temperature readings under different treatment.** Temperature readings from loggers exposed to sunlight and shaded in the flow chamber for the whole cross-validation period. Loggers were wrapper in aluminium foil Day 2 and Day 3 had low sunlight due to storms.

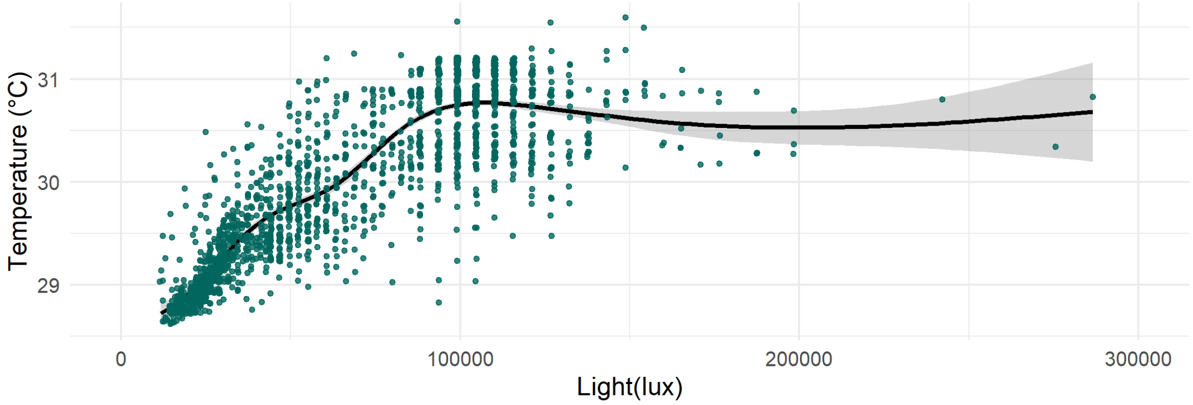


**Figure A.2 – Increase of temperature accordingly to increase of light.** Temperature readings against light readings made from the loggers without wrapping exposed to the sunlight when sunlight was detectable. Dots represent simultaneous readings of light and temperature. In black, a smoother with confidence interval shows how temperature increases from the actual water temperature (~28°C) for more than 5 times the precision of the instrument (>2.5°C of total difference).

# Appendix B. Supplementary material for chapter 2

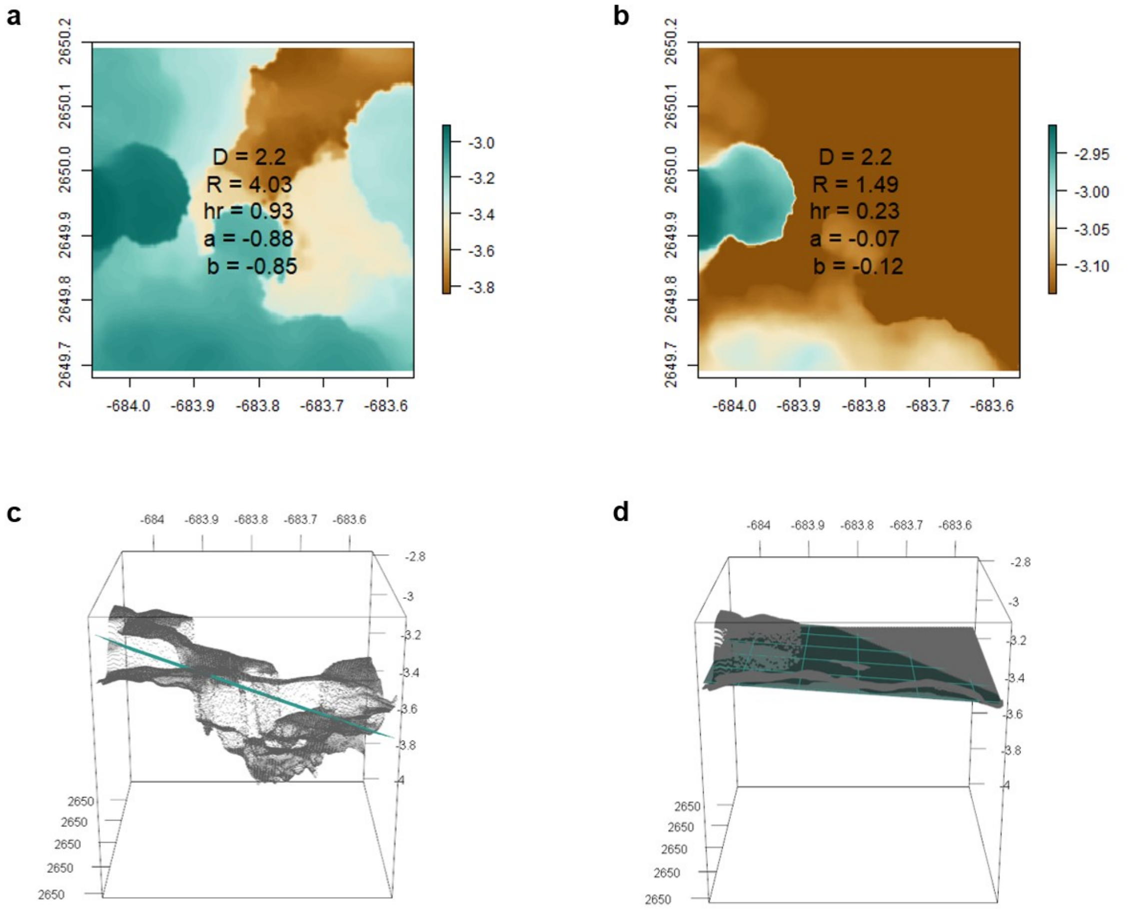


**Figure B.1 – Geometric variables representation.** Example of surface descriptors of the 50cm-side square corresponding to the location of U18 in Corner Beach in 2018 (see Figure 2.1 for position within the reef site). On the top, a) shows the digital elevation model (DEMs) of the area, while b) shows the correspondent DEM used to compute variables to predict light (i.e. when maximum depth is flattened to unit location depth). In the centre of the DEM, values of fractal dimension (D), surface rugosity (R), height range (hr), sloping (a) and northing (b) of the areas are shown. On the bottom, the 3D representation of the DEMs, where every dot represents the elevation of each pixel of the corresponding DEM. In gridded green the best fit plane used to estimate sloping (a) and northing (b). Notice that the coordinates are in metres, that the legend scales differs in a) and b), and that D is invariant between the surfaces, because only computed for the surface as is.

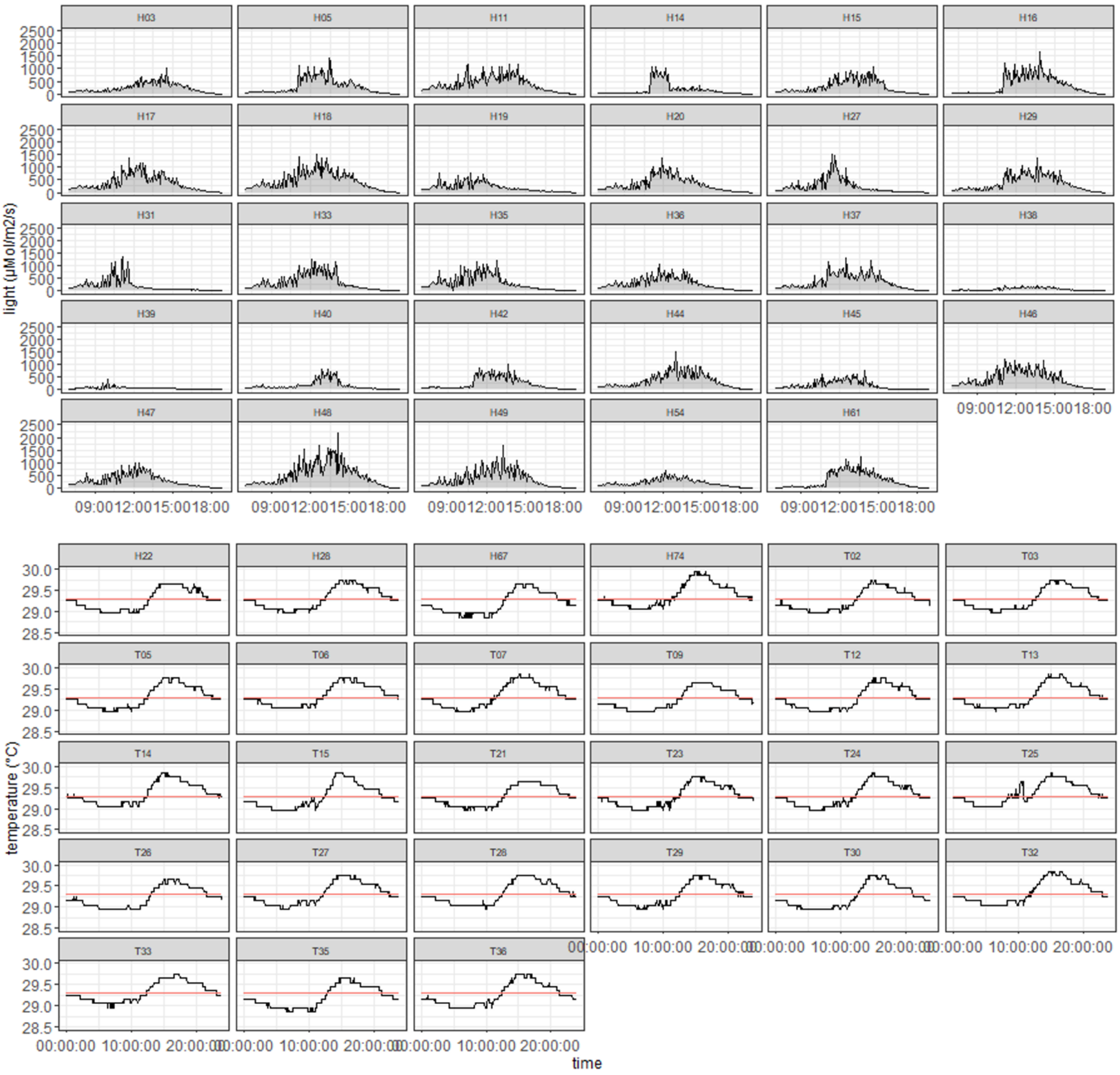


**Figure B.2 – Raw data example.** Example of light (top) and temperature (bottom) recorded with dataloggers from the units deployed simultaneously in Corner Beach reef in 2018. In black, light and temperature readings. In grey, the area that corresponds to the light daily integral. In red, mean daily temperature. Notice that while light is plotted only for 12h, temperature is plotted for 24h.

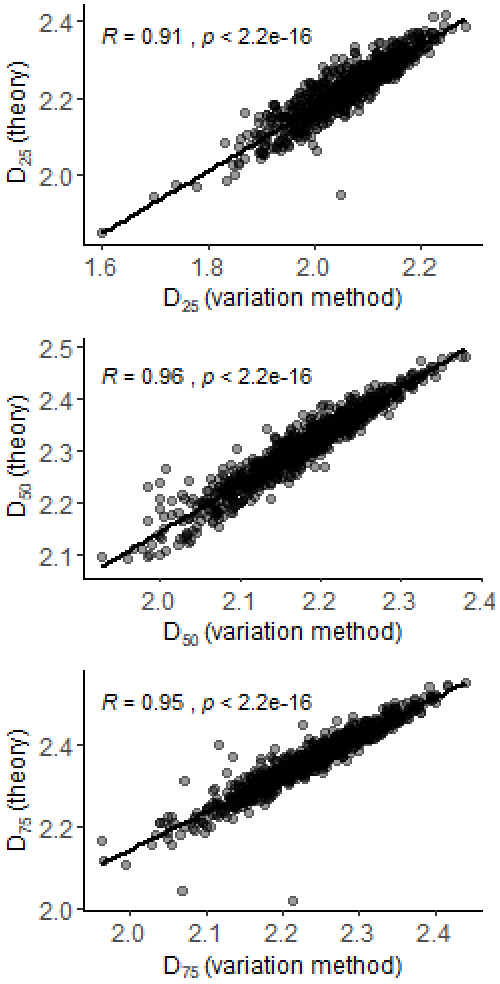


**Figure B.3 – Fractal dimension value from the theory compared to the empirical values.** Correlation between empirical fractal dimension obtained through the variation method and fractal dimension as obtained from theory when considering 25cm (a), 50cm (b), 75cm (c) squares of area around the dataloggers. R = Pearson's coefficient.

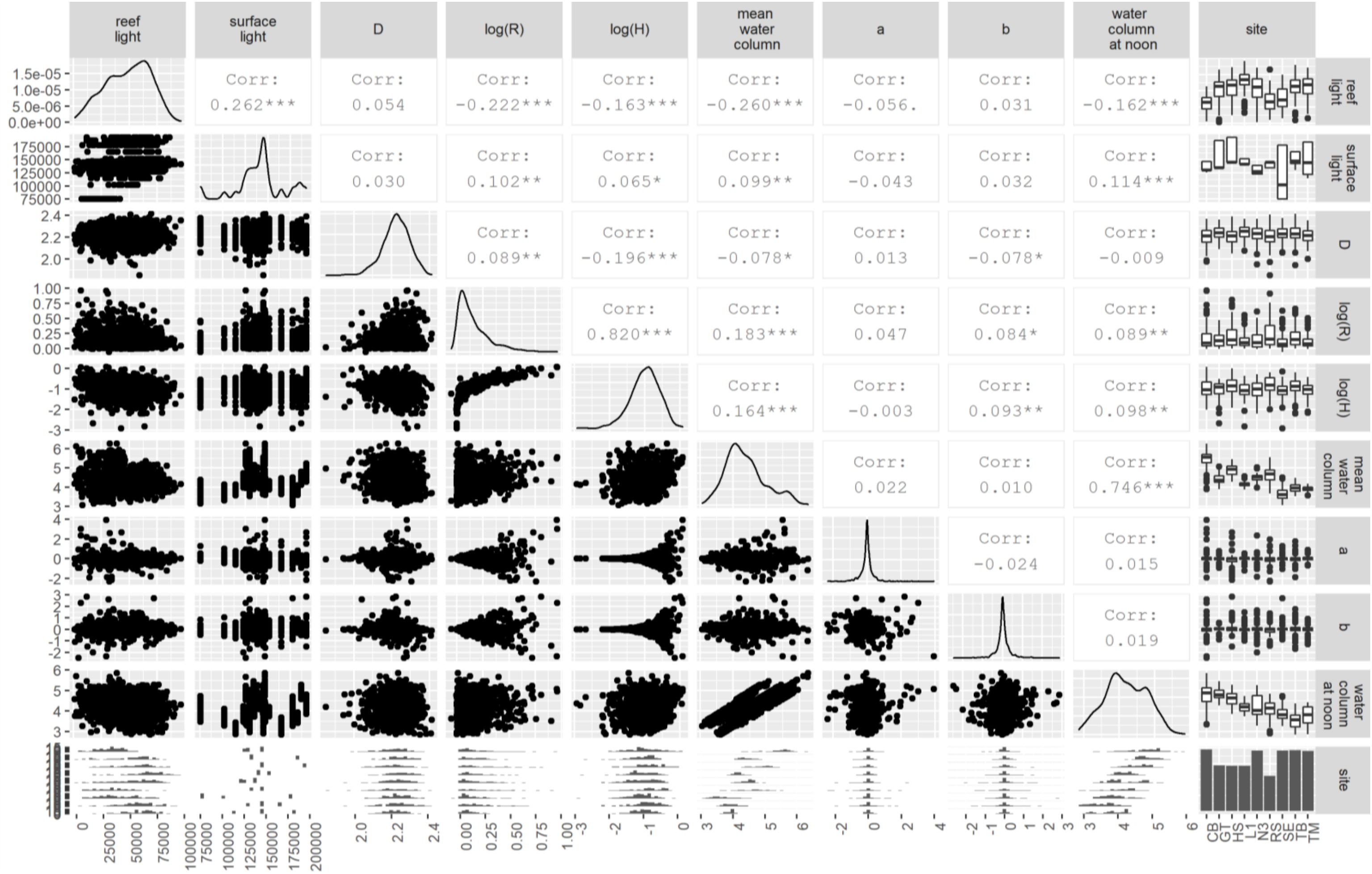


**Figure B.4a – Pair plots for variables computed with 25cm-side areas.**

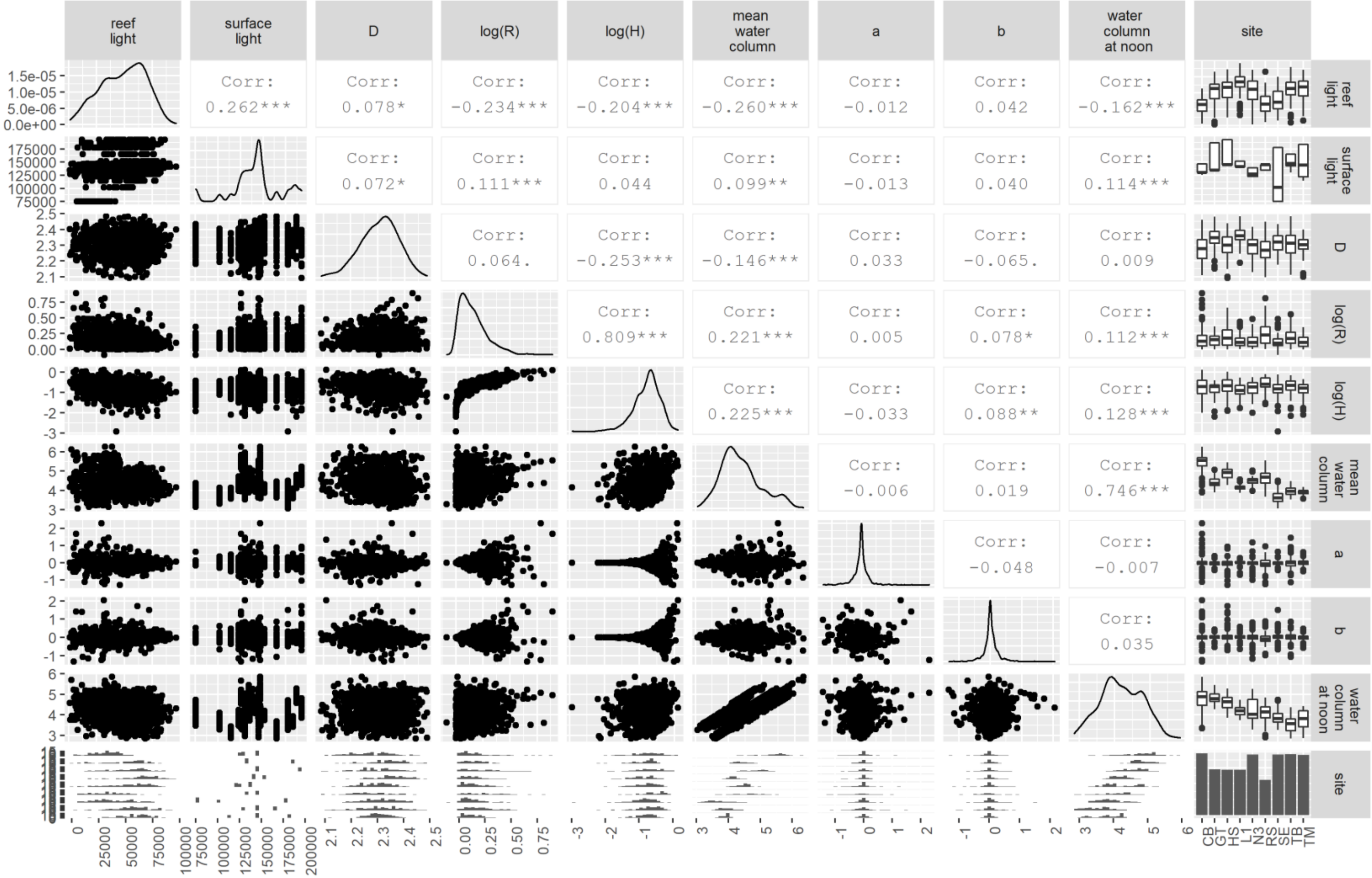


Figure B.4b – Pair plots for variables computed with 50cm-side areas.

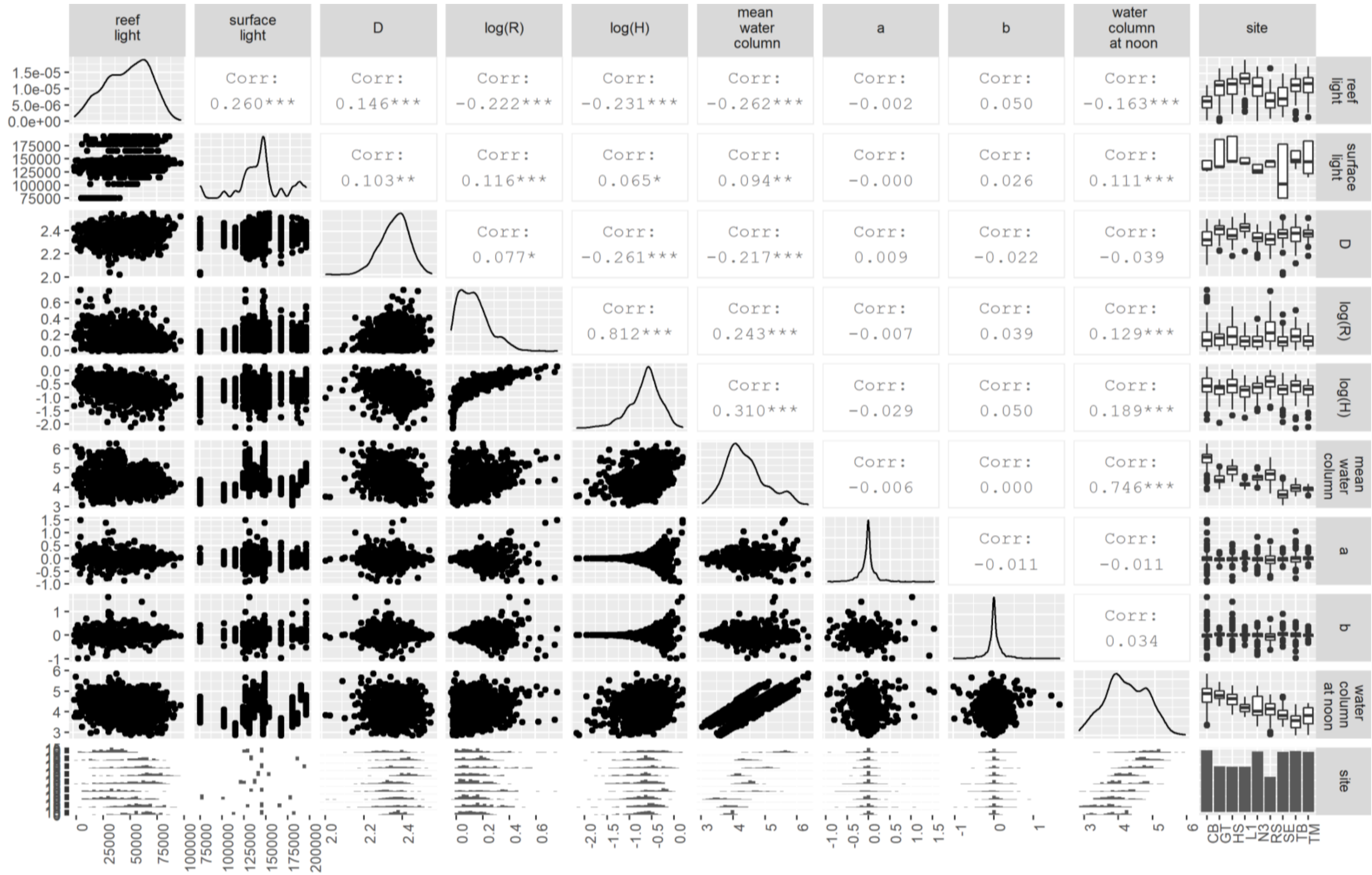


Figure B.4c – Pair plots for variables computed with 75cm-side areas.

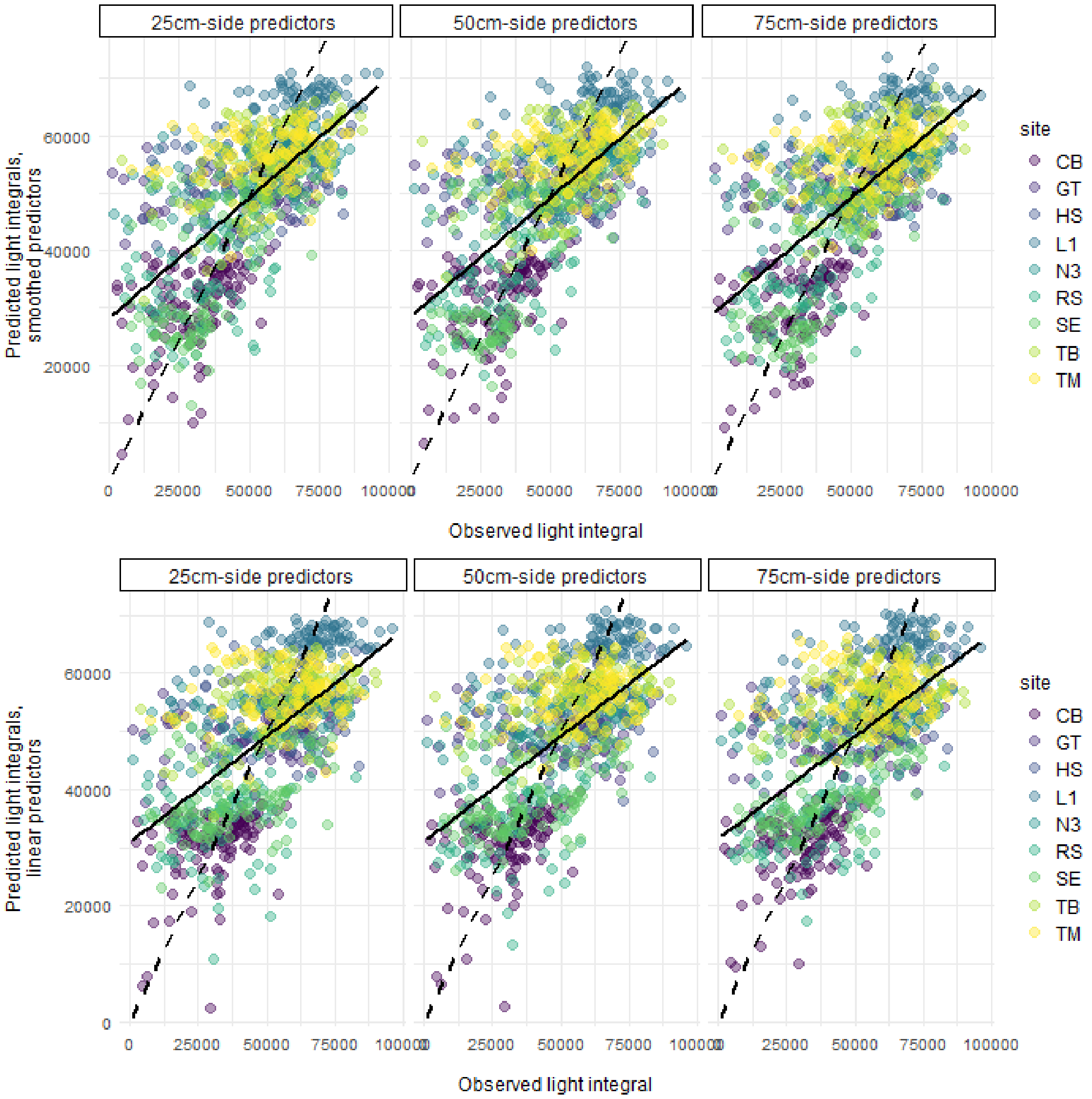


**Figure B.5 – Model accuracy.** Light predictions as function of the observed values for the primary models fitted. On the top, predictions of models with smoothed predictors. On the bottom, predictions of models with linear predictors. The black solid line shows the best fit linear regression. The dotted line shows the identity (i.e. where predicted values would be the same as the observed). Dots are color-coded by site.

**Table B.1a – Smoothed predictors and site as random effect (sr) model coefficients**. Model coefficients, adjusted $R^2$ and deviance explained for the GAM model fitted with a smooth term for latitude and longitude for each of the area considered to compute surface descriptors. Statistic shows the T statistic for the linear predictors and the F statistic for the smoothed terms.

| | **25-cm side predictors** | | | | **50-cm side predictors** | | | | **75-cm side predictors** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *coefficients* | *estimates* | *statistic* | *p-value* | *edf* | *estimates* | *statistic* | *p-value* | *edf* | *estimates* | *statistic* | *p-value* | *edf* |
| intercept | **48409.35** | **13.84** | **<0.001** | **874.28** | **48423.47** | **13.40** | **<0.001** | **874.32** | **48426.92** | **13.01** | **<0.001** | **873.06** |
| s(fractal dimension) | **1.54** | **3.17** | **0.036** | **6.17** | 1.00 | 0.34 | 0.559 | 5.88 | 1.00 | 1.06 | 0.304 | 5.85 |
| s(surface rugosity) | **2.16** | **9.02** | **<0.001** | **1.01** | 3.21 | **3.18** | **0.011** | **1.00** | **3.71** | **2.78** | **0.017** | **1.01** |
| s(height range) | **1.01** | **4.95** | **0.027** | **2.68** | 1.00 | 0.26 | 0.608 | 2.49 | 1.00 | 2.54 | 0.111 | 2.18 |
| s(northing) | 1.00 | 3.09 | 0.079 | 2.77 | 1.00 | 3.33 | 0.068 | 4.08 | 1.00 | 2.96 | 0.086 | 4.66 |
| s(sloping) | 1.01 | 0.12 | 0.736 | 1.94 | 1.00 | 1.24 | 0.266 | 1.00 | 1.03 | 0.51 | 0.495 | 1.00 |
| s(mean water column) | 4.97 | 1.83 | 0.092 | 1.01 | 4.71 | 1.72 | 0.129 | 1.01 | 4.68 | 1.85 | 0.100 | 1.05 |
| s(water column at noon) | **2.10** | **3.55** | **0.020** | **8.00** | **1.96** | **2.90** | **0.042** | **8.00** | **1.73** | **3.10** | **0.040** | **8.00** |
| s(surface PAR integral) | **6.46** | **11.18** | **<0.001** | **1.02** | **6.28** | **10.96** | **<0.001** | **1.00** | **6.27** | **11.45** | **<0.001** | **1.00** |
| s(rec) | **7.48** | **15.75** | **<0.001** | **7.51** | **7.50** | **15.43** | **<0.001** | **7.35** | **7.52** | **15.48** | **<0.001** | **7.34** |
| Observations | 903 | | | | 903 | | | | 902 | | | |
| Adjusted R2 | 0.412 | | | | 0.407 | | | | 0.401 | | | |
| Deviance explained | 43.0% | | | | 42.6% | | | | 42.0% | | | |

**Table B.1b– Linear predictors and site as random effect (lr) model coefficients**. Model coefficients, adjusted $R^2$ and deviance explained for the GAM model fitted with a smooth term for latitude and longitude for each of the area considered to compute surface descriptors. Statistic shows the T statistic for the linear predictors and the F statistic for the smoothed terms.

| | **25-cm side predictors** | | | **50-cm side predictors** | | | **75-cm side predictors** | | |
|---|---|---|---|---|---|---|---|---|---|
| *coefficients* | *estimates (SE)* | *statistic* | *p-value* | *estimates (SE)* | *statistic* | *p-value* | *estimates (SE)* | *statistic* | *p-value* |
| intercept | 50705.95<br>(19517.08) | 2.60 | **0.010** | 85581.36<br>(22138.09) | 3.87 | **<0.001** | 67706.84<br>(23932.86) | 2.83 | **0.005** |
| fractal dimension | 12433.86<br>(8821.30) | 1.41 | 0.159 | -8605.21<br>(9856.09) | -0.87 | 0.383 | -2219.23<br>(10294.10) | -0.22 | 0.829 |
| surface rugosity | -39564.15<br>(8243.40) | -4.80 | **<0.001** | -27781.04<br>(9422.89) | -2.95 | **0.003** | -26894.64<br>(10678.02) | -2.52 | **0.012** |
| height range | 5028.42<br>(2590.52) | 1.94 | 0.053 | -187.50<br>(2978.83) | -0.06 | 0.950 | -1468.07<br>(3395.68) | -0.43 | 0.666 |
| northing | 1864.06<br>(1276.37) | 1.46 | 0.145 | 3202.67<br>(1960.28) | 1.63 | 0.103 | 4524.72<br>(2684.49) | 1.69 | 0.092 |
| sloping | -61.25<br>(2119.39) | -0.03 | 0.977 | -3715.12<br>(3421.58) | -1.09 | 0.278 | -2981.28<br>(4778.52) | -0.62 | 0.533 |
| mean water column | -4158.59<br>(2672.28) | -1.56 | 0.120 | -2995.76<br>(2724.18) | -1.10 | 0.272 | -2629.80<br>(2799.67) | -0.94 | 0.348 |
| water column at noon | -38.76<br>(1954.70) | -0.02 | 0.984 | 222.07<br>(1959.73) | 0.11 | 0.910 | 311.34<br>(1974.60) | 0.16 | 0.875 |
| surface PAR integral | 3485.81<br>(624.60) | 5.58 | **<0.001** | 3473.96<br>(626.41) | 5.55 | **<0.001** | 3452.36<br>(630.01) | 5.48 | **<0.001** |
| s(rec) | 7.64 | 28.14 | **<0.001** | 7.64 | 27.69 | **<0.001** | 7.62 | 26.11 | **<0.001** |
| Observations | 903 | | | 903 | | | 902 | | |
| Adjusted R2 | 0.357 | | | 0.354 | | | 0.344 | | |
| Deviance explained | 38.8% | | | 36.5% | | | 35.6% | | |

**Table B.1c – Linear mixed model with site as random effect (lm) coefficients**. Model fixed effect coefficients, marginal $R^2$ and conditional $R^2$. Results are for each of the area considered to compute surface descriptors. Statistic shows the T statistic for the linear predictors and the F statistic for the smothed terms

| | **25-cm side predictors** | | | **50-cm side predictors** | | | **75-cm side predictors** | | |
|---|---|---|---|---|---|---|---|---|---|
| *coefficients* | *estimates (SE)* | *statistic* | *p-value* | *estimates (SE)* | *statistic* | *p-value* | *estimates (SE)* | *statistic* | *p-value* |
| intercept | 50705.95<br>(19517.08) | 2.60 | **0.009** | 85581.36<br>(22138.09) | 3.87 | **<0.001** | 67706.84<br>(23932.86) | 2.83 | **0.005** |
| fractal dimension | 12433.86<br>(8821.30) | 1.41 | 0.159 | -8605.21<br>(9856.09) | -0.87 | 0.383 | -2219.23<br>(10294.10) | -0.22 | 0.829 |
| surface rugosity | -39564.15<br>(8243.40) | -4.80 | **<0.001** | -27781.04<br>(9422.89) | -2.95 | **0.003** | -26894.65<br>(10678.02) | -2.52 | **0.012** |
| height range | 5028.42<br>(2590.52) | 1.94 | 0.052 | -187.50<br>(2978.83) | -0.06 | 0.950 | -1468.07<br>(3395.68) | -0.43 | 0.665 |
| northing | 1864.06<br>(1276.37) | 1.46 | 0.144 | 3202.67<br>(1960.28) | 1.63 | 0.102 | 4524.72<br>(2684.49) | 1.69 | 0.092 |
| sloping | -61.25<br>(2119.39) | -0.03 | 0.977 | -3715.12<br>(3421.58) | -1.09 | 0.278 | -2981.28<br>(4778.52) | -0.62 | 0.533 |
| mean water column | -4158.59<br>(2672.28) | -1.56 | 0.120 | -2995.75<br>(2724.18) | -1.10 | 0.271 | -2629.80<br>(2799.67) | -0.94 | 0.348 |
| water column at noon | -38.76<br>(1954.70) | -0.02 | 0.984 | 222.07<br>(1959.73) | 0.11 | 0.910 | 311.34<br>(1974.60) | 0.16 | 0.875 |
| surface PAR integral | 3485.81<br>(624.60) | 5.58 | **<0.001** | 3473.96<br>(626.41) | 5.55 | **<0.001** | 3452.36<br>(630.01) | 5.48 | **<0.001** |
| Observations | 903 | | | 903 | | | 902 | | |
| Marginal R2 | 0.099 | | | 0.086 | | | 0.078 | | |
| Conditional R2 | 0.333 | | | 0.331 | | | 0.319 | | |

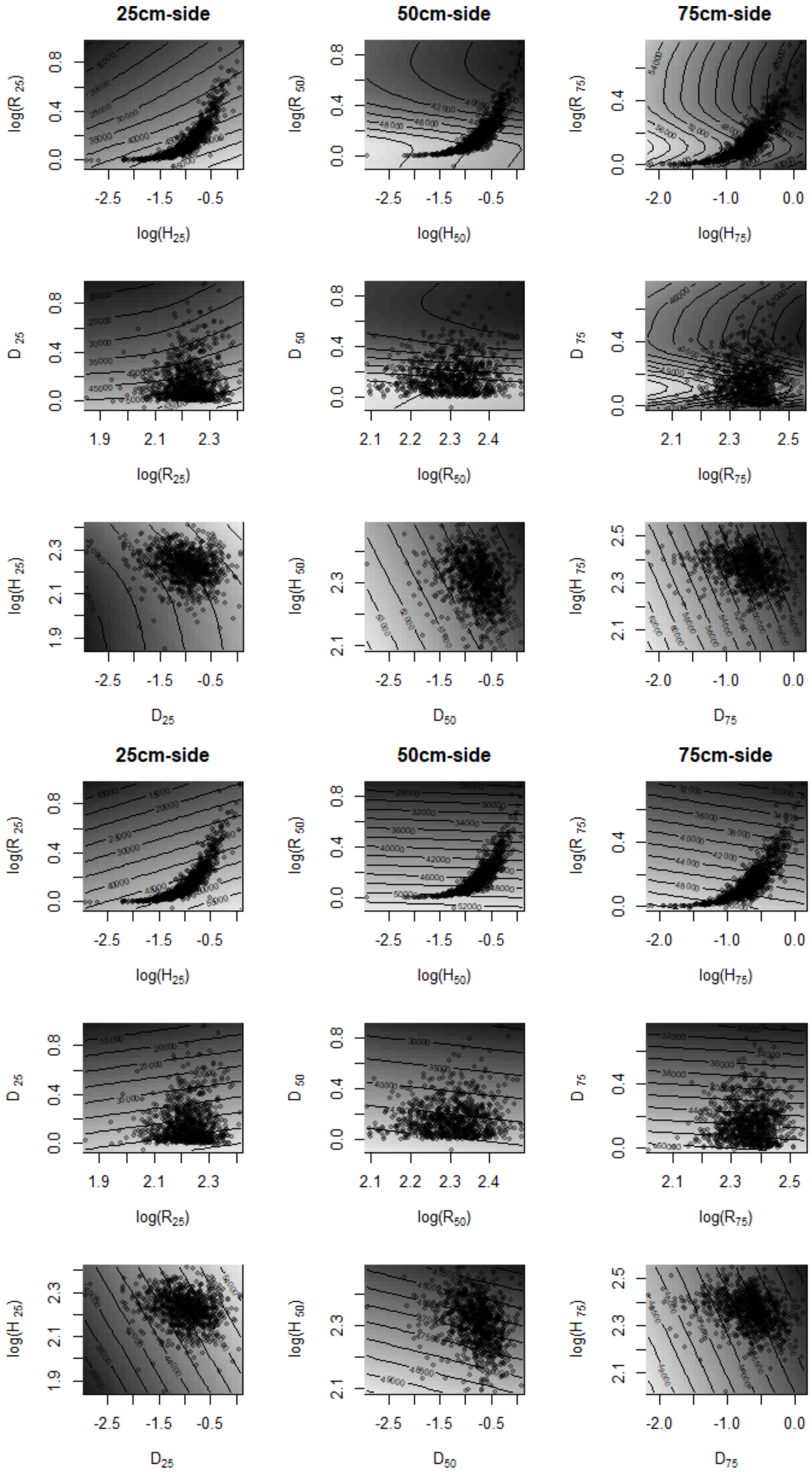
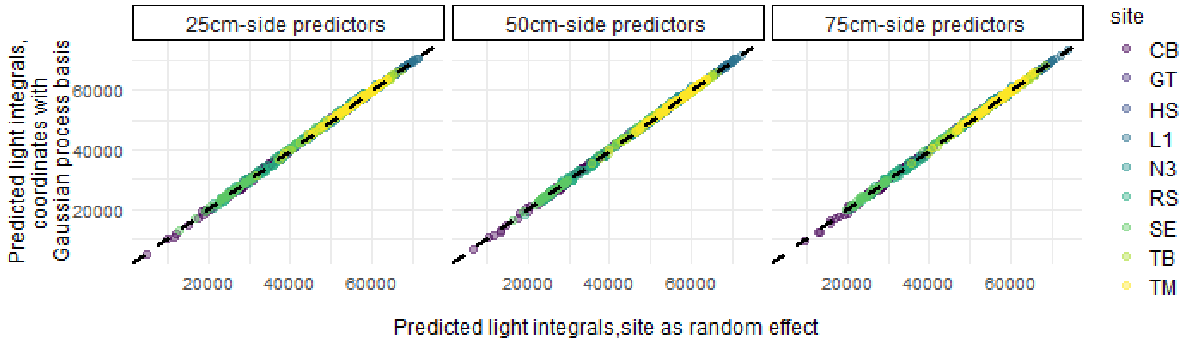
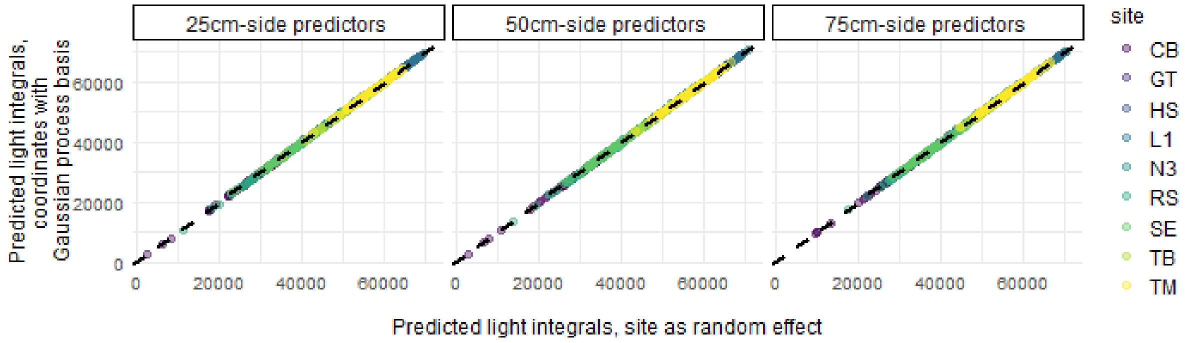


**Figure B.6 – Light prediction on the habitat complexity plane.** Predictions of light among the space of the surface descriptors that describe the habitat complexity plane. Variables (D – fractal dimension, R – surface rugosity, H – height range) are plotted in pairs for each areal used to compute surface descriptors. On the top, linear predictors fit. On the bottom, smoothed predictors fit. Dots are observed data.

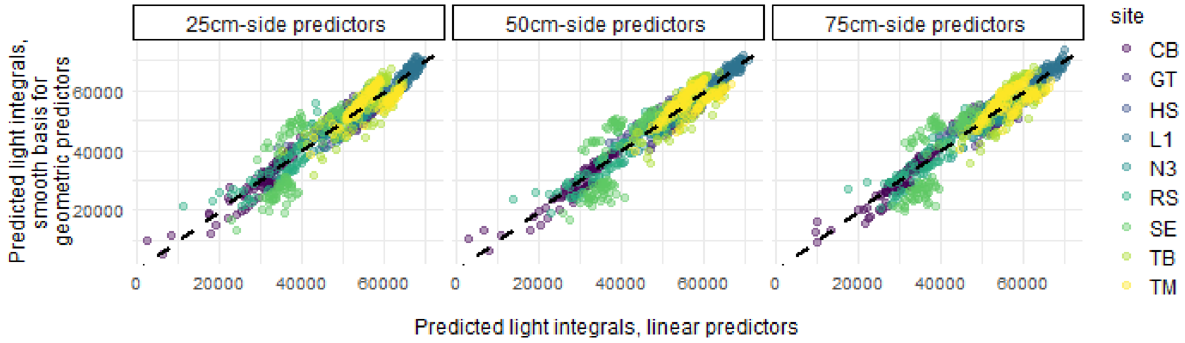
**a. Models with smooth basis for geometric predictors**



**b. Models with linear geometric predictors**



**c. Models with site as random effect**



**d. Models with coordinates with Gaussian process basis**

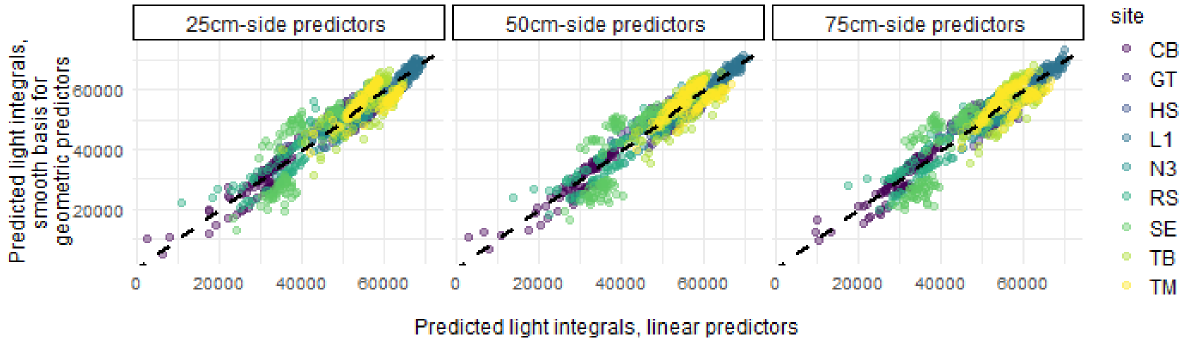
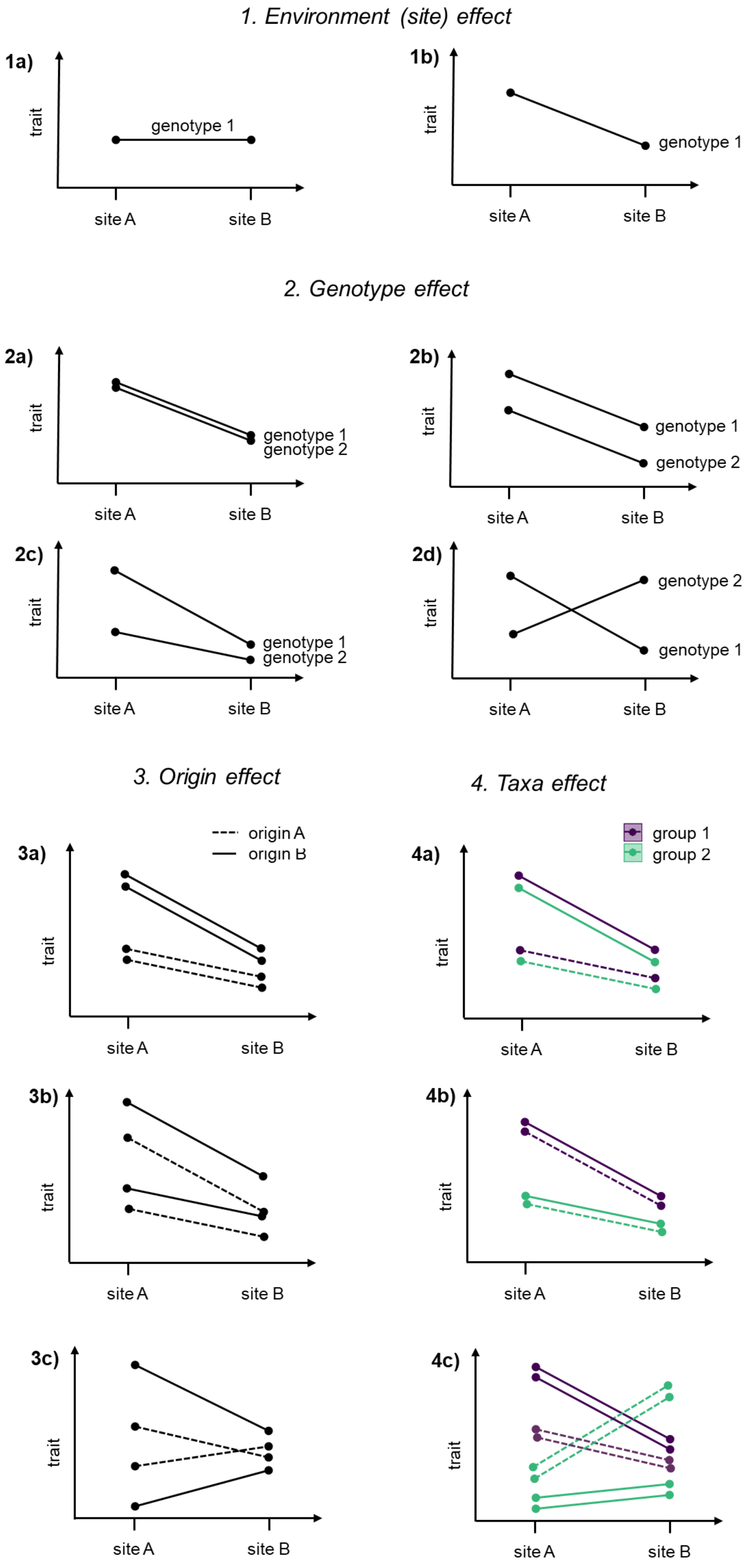


**Figure B.7 – Models' sensitivity analysis.** Pair-wise comparison of light daily integral predictions generated with the different models fitted. The dotted line shows the identity (i.e. where predicted from a model would be the same as the predictions from the other model). Dots are color-coded by site.

# Appendix C. Supplementary material for chapter 3

**Figure C.1 (next page) – Reaction norms in reciprocal transplant experiments.** These plots represent how reaction norms are usually represented and offer keys of interpretations specifically for reciprocal transplant experiments (when the site of origin of the genotype can also influence the norm). In the first panel, figure 1a and 1b represent the reaction of one individual genotype. 1a shows a genotype that display the same trait value among sites (canalized norm), while 1b represent a plastic trait, which display different values according to the environment. In the second panel, 2 genotypes per plot are present. In the second panel, different genotypic effects are displayed. The genotypes of figure 2a) and 2b) are influenced in the same fashion by the environment (i.e. the difference in the trait between sites is the same), but while in 1a) the norms are identical, in 2b) they are parallel. In figure 2c) and 2d) there are genotype by environment interactions. In 2c) the norms of the genotypes differ for magnitude, while in 2d) they differ in direction of response. In the third panel, effects of the origin site, represented by different line type, are introduced. Norms in 3a) show an effect of the interaction between site of origin and environment, since norms of individuals with the same origin have the same reaction norms when exposed to the same environments. Norms in 3b) show when differences in the magnitude are not affected by origin. Norms in 3c) show the null effect of origin on the direction of the norms. In the fourth panel, taxonomic groups are included as different colours. In 4a) norms show an effect of origin, rather than taxonomic groups. In 4b) there is an effect of the taxonomic group, rather than origin. In 4c) there is an interaction between origin, taxonomic group and environment.


1. Environment (site) effect
1a)
trait
genotype 1
site A
site B
1b)
trait
genotype 1
site A
site B
2. Genotype effect
2a)
trait
genotype 1
genotype 2
site A
site B
2b)
trait
genotype 1
genotype 2
site A
site B
2c)
trait
genotype 1
genotype 2
site A
site B
2d)
trait
genotype 2
genotype 1
site A
site B
3. Origin effect
origin A
origin B
3a)
trait
site A
site B
3b)
trait
site A
site B
3c)
trait
site A
site B
4. Taxa effect
group 1
group 2
4a)
trait
site A
site B
4b)
trait
site A
site B
4c)
trait
site A
site B

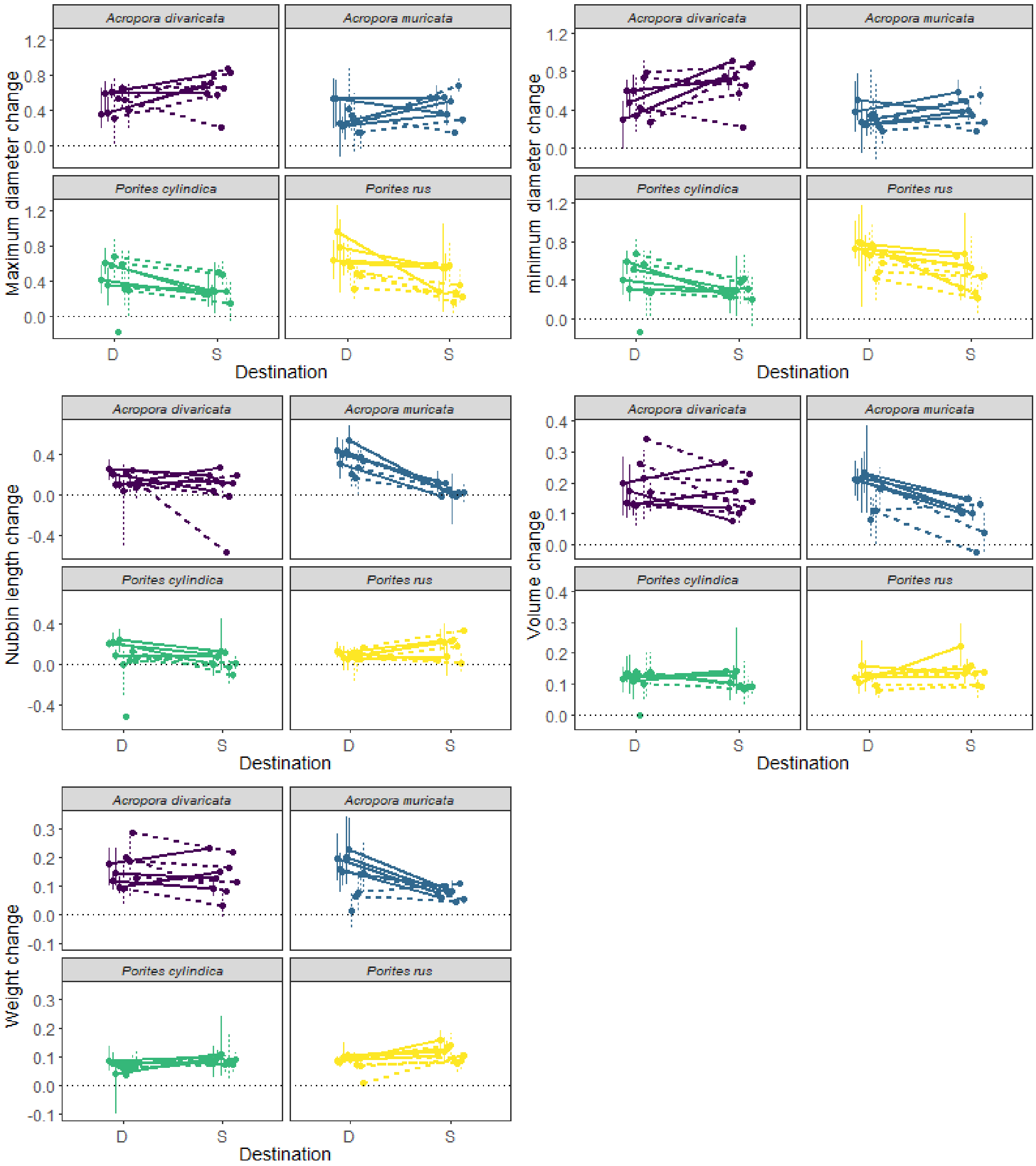


**Figure C.2 – Species reaction norms for the change in traits (log ratio) measured in situ** (for interpretation, refer to Figure C.1)**.** Vertical lines represent the range of the trait values of each genotype at each Destination. Dots represent mean value of traits per each genotype at each Destination site. Mean values corresponding to the same genotype are connected by a line. Line type changes according to Origin site (dotted for shallow Origin and dotted for deep Origin). Data is color-coded by species.

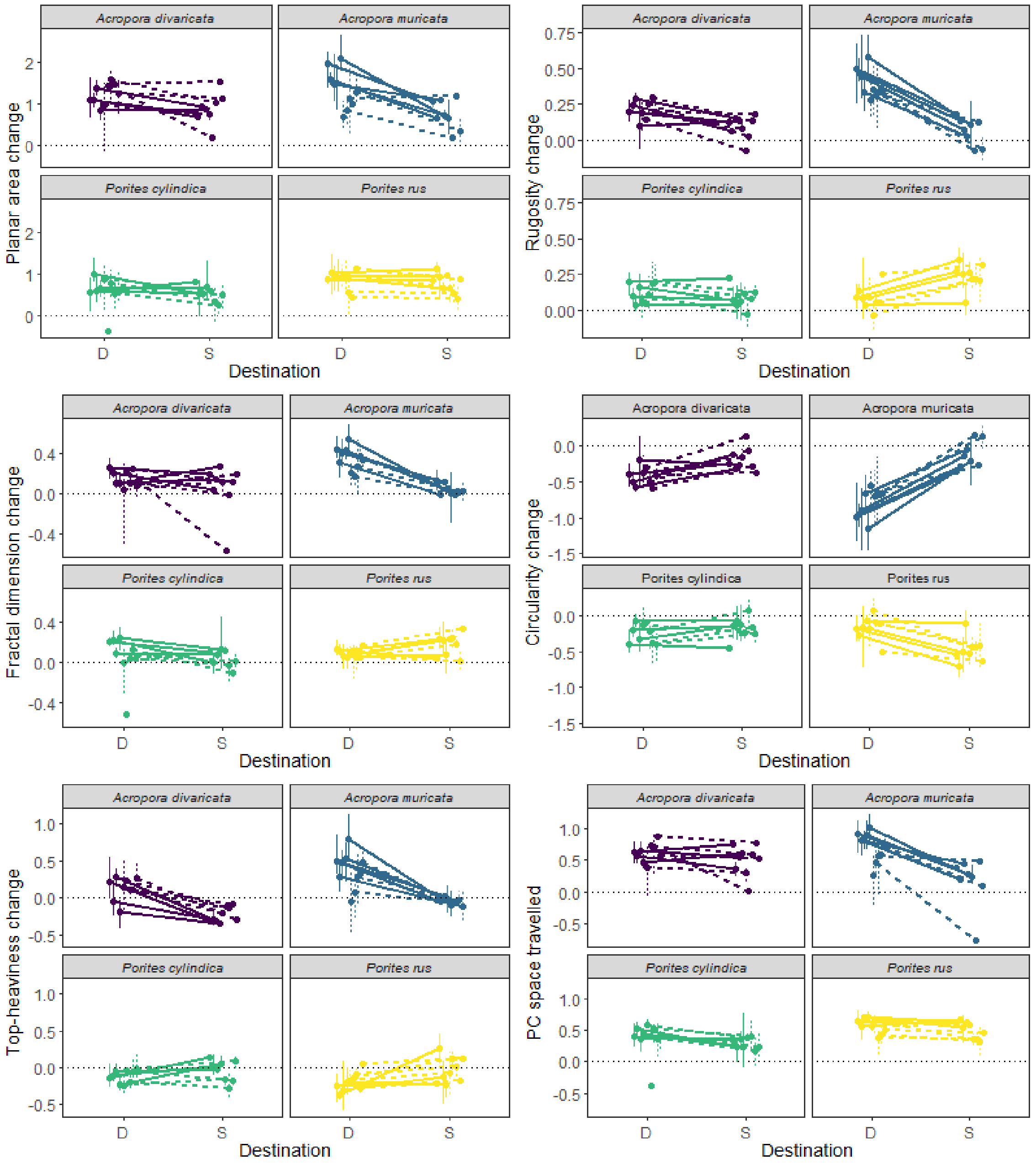


**Figure C.2 – Species reaction norms for the change in traits (log ratio) derived from nubbin outlines** (for interpretation, refer to Figure C.1)**.** Vertical lines represent the range of the trait values of each genotype at each Destination. Dots represent mean value of traits per each genotype at each Destination site. Mean values corresponding to the same genotype are connected by a line. Line type changes according to Origin site (dotted for shallow Origin and dotted for deep Origin). Data is color-coded by species.

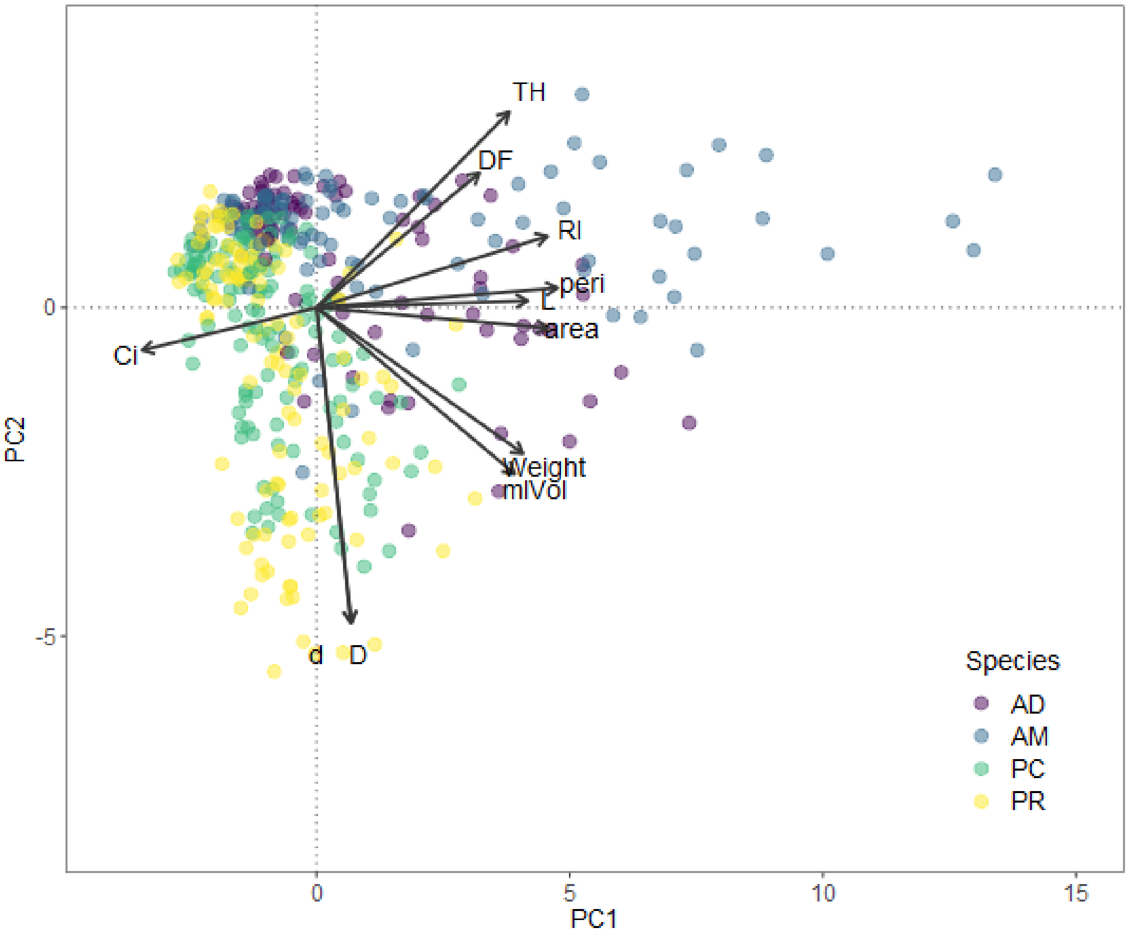


**Figure C.3 – Biplot of the morphospace.** The multidimensional space was built with all the observed trait combinations in the nubbins at the beginning and at the end of the experiment. Dots are color-coded by species (AD = *Acropora divaricata*, AM = *Acropora muricata*, PC = *Porites cylindrica*, PR = *Porites rus*). Arrow lengths show how much each trait influence the two principal components of the morphospace (scaled by a factor of 5).

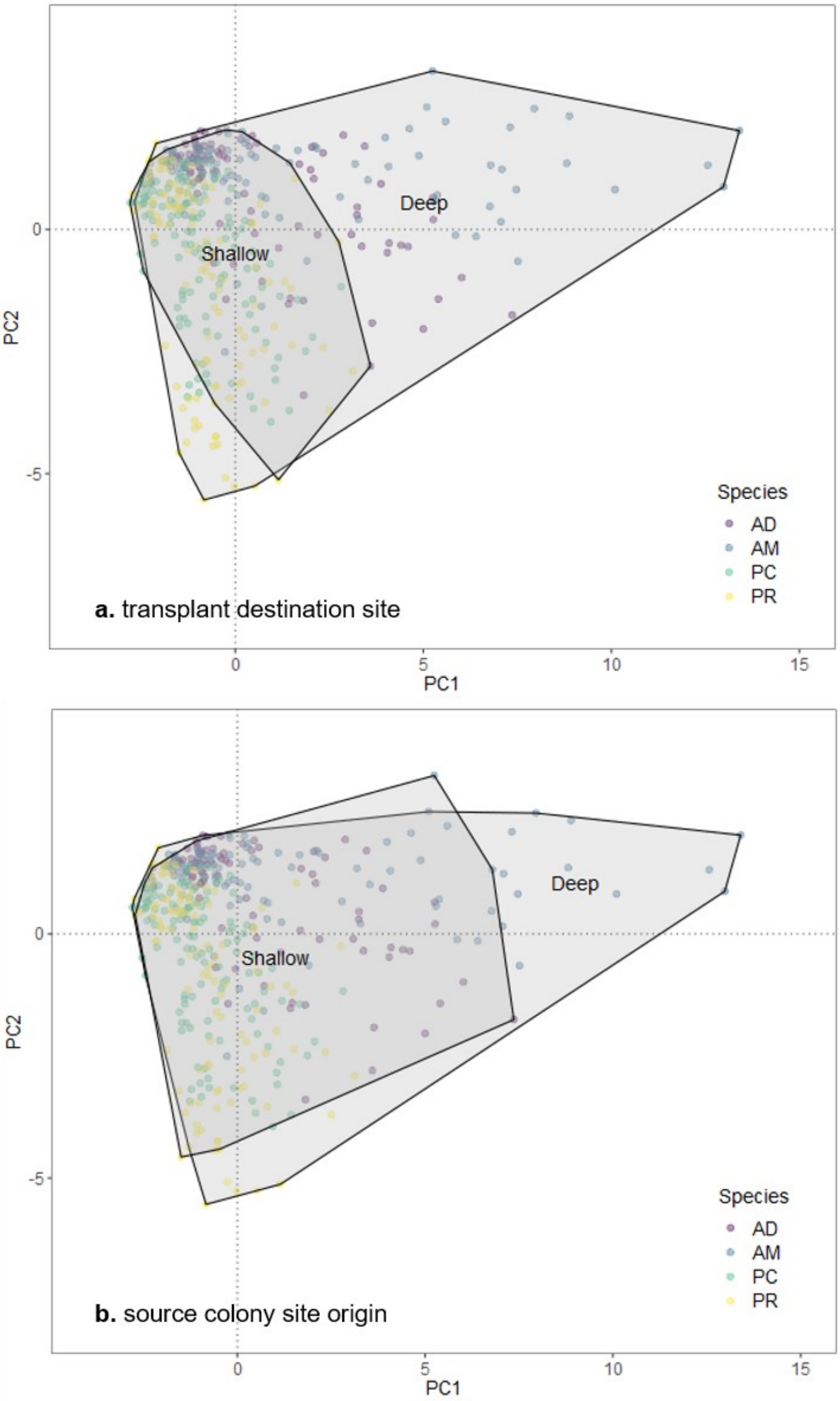


**Figure C.4 – Morphological traits space occupied by different site of Origin and Destination**. Dots are color-coded by species (AD = *Acropora divaricata*, AM = *Acropora muricata*, PC = *Porites cylindrica,* PR = *Porites rus*). In a) the 2 polygons represent the space occupied by the nubbins that were transplanted on the shallow or the deep site. In b) the 2 polygons represent the space occupied by the nubbins that were originally from the shallow and the deep site.

**Table C.1 Model selection table.** Aikake Information Criterion (AIC) for each fitted model. In bold, the lowest AIC corresponding to the best model selected.

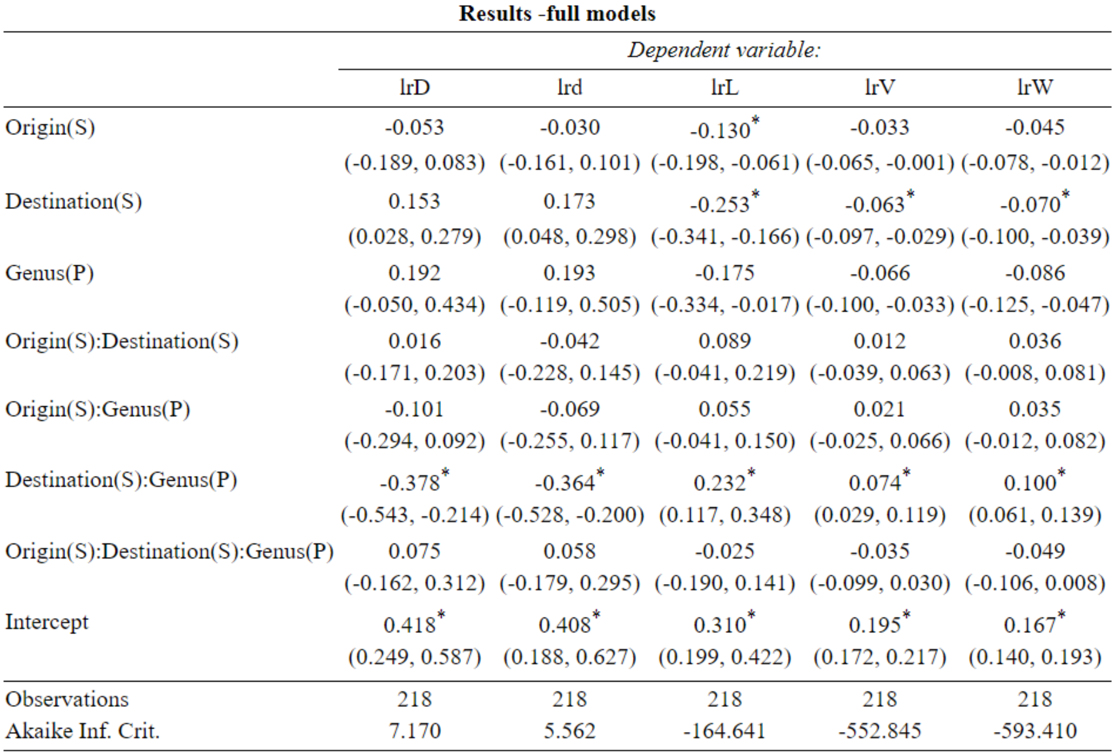
**Model selection - AICs table**

| | *Dependent variable:* | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Fixed terms structure* | lrD | lrd | lrL | lrV | lrW | lrPA | lrC | lrR | lrF | lrT | deltaPCA |
| Origin*Destination*Genus | 5.17 | 3.56 | -166.64 | -556.82 | -597.04 | 236.06 | 48.29 | -241.45 | -848.58 | -25.40 | 11.95 |
| Origin*Destination + Origin*Genus + Genus*Destination | 1.17 | -0.60 | -171.66 | -562.69 | -601.44 | 236.09 | 44.68 | -246.45 | -855.71 | -24.32 | 8.29 |
| Origin*Destination+ Origin*Genus | 25.06 | 22.44 | -152.23 | -559.22 | -584.65 | 246.04 | 97.96 | -194.55 | -847.07 | 43.25 | 17.29 |
| Origin*Destination+ Genus*Destination | -3.08 | -5.33 | -176.91 | -570.43 | -608.54 | 232.50 | 42.22 | -250.29 | -865.02 | -28.17 | 4.13 |
| Origin*Genus + Genus*Destination | -3.52 | -6.43 | -175.00 | -570.79 | -609.91 | 232.06 | 39.60 | -252.90 | -863.09 | -30.28 | 2.89 |
| Origin*Destination+ Genus | 20.71 | 17.66 | -157.57 | -566.97 | -591.70 | 242.41 | 95.69 | -198.20 | -856.44 | 39.33 | 13.17 |
| Genus*Destination +Origin | -7.95 | -11.16 | **-179.45** | -578.59 | -616.95 | **228.51** | 37.42 | -256.47 | -872.35 | -34.11 | **-1.17** |
| Origin*Genus + Destination | 19.70 | 16.99 | -154.54 | -567.50 | -592.50 | 242.57 | 93.89 | -200.00 | -853.62 | 38.18 | 12.37 |
| Origin*Destination | 16.10 | 13.67 | -161.92 | -564.85 | -587.98 | 255.88 | 94.00 | -201.29 | -836.55 | 37.96 | 9.01 |
| Genus*Destination | **-10.87** | **-15.11** | -175.01 | **-582.35** | **-621.80** | 228.58 | **32.37** | **-262.91** | -880.63 | **-40.30** | 0.66 |
| Origin*Genus | 14.96 | 12.90 | -151.15 | -569.51 | -601.95 | 265.35 | 98.91 | -196.37 | -863.57 | 39.52 | 42.47 |
| Origin + Genus + Destination | 15.25 | 12.27 | -159.05 | -575.30 | -599.39 | 239.02 | 92.21 | -203.07 | -862.92 | 34.47 | 8.45 |
| Origin + Genus | 10.50 | 8.17 | -155.66 | -577.29 | -608.84 | 261.77 | 97.12 | -199.54 | -872.88 | 35.81 | 38.71 |
| Genus + Destination | 12.17 | 8.19 | -155.15 | -578.76 | -603.81 | 239.23 | 86.93 | -209.74 | -871.05 | 28.20 | 10.48 |
| Origin + Destination | 10.64 | 8.28 | -163.38 | -573.16 | -595.78 | 252.38 | 90.52 | -206.15 | -843.06 | 33.11 | 4.29 |
| Origin | 5.84 | 4.12 | -159.70 | -573.31 | -604.71 | 279.40 | 95.72 | -202.33 | -851.89 | 34.67 | 35.16 |
| Genus | 7.43 | 4.09 | -152.11 | -580.67 | -613.23 | 262.33 | 91.88 | -206.17 | **-880.97** | 29.53 | 41.14 |
| Destination | 7.50 | 4.16 | -159.38 | -577.47 | -600.81 | 251.62 | 85.26 | -212.80 | -851.52 | 26.84 | 6.50 |

**Table C.2 Coefficient estimates (and p.values) for the best models for each of the response variables.**

| | *Dependent variable:* | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | response | | | | | | | | | | |
| | lrD | lrd | lrL | lrV | lrW | lrPA | lrC | lrR | lrF | lrT | deltaPCA |
| GenusP | 0.135 | 0.155 | -0.151 | -0.058$^*$ | -0.070$^*$ | -0.553$^*$ | 0.422 | -0.211 | -0.037$^*$ | -0.418 | -0.163 |
| | (0.113) | (0.151) | (0.078) | (0.013) | (0.013) | (0.092) | (0.137) | (0.068) | (0.005) | (0.117) | (0.099) |
| DestinationS | 0.161$^*$ | 0.154$^*$ | -0.213$^*$ | -0.058$^*$ | -0.054$^*$ | -0.559$^*$ | 0.486$^*$ | -0.243$^*$ | | -0.435$^*$ | -0.352$^*$ |
| | (0.048) | (0.047) | (0.033) | (0.013) | (0.011) | (0.083) | (0.053) | (0.027) | | (0.044) | (0.048) |
| OriginS | | | -0.072$^*$ | | | -0.198$^*$ | | | | | -0.138$^*$ |
| | | | (0.020) | | | (0.085) | | | | | (0.046) |
| GenusP:DestinationS | -0.337$^*$ | -0.336$^*$ | 0.226$^*$ | 0.057$^*$ | 0.078$^*$ | 0.419$^*$ | -0.575$^*$ | 0.287$^*$ | | 0.542$^*$ | 0.245$^*$ |
| | (0.060) | (0.060) | (0.042) | (0.016) | (0.014) | (0.105) | (0.068) | (0.034) | | (0.056) | (0.061) |
| Constant | 0.393$^*$ | 0.393$^*$ | 0.285$^*$ | 0.179$^*$ | 0.145$^*$ | 1.412$^*$ | -0.623$^*$ | 0.312$^*$ | 0.028$^*$ | 0.263$^*$ | 0.728$^*$ |
| | (0.080) | (0.106) | (0.056) | (0.009) | (0.009) | (0.077) | (0.097) | (0.048) | (0.004) | (0.083) | (0.073) |
| Observations | 218 | 218 | 218 | 218 | 218 | 217 | 217 | 217 | 217 | 217 | 217 |
| Akaike Inf. Crit. | -10.875 | -15.114 | -179.455 | -582.350 | -621.799 | 228.513 | 32.370 | -262.911 | -880.967 | -40.295 | -1.166 |

**Table C.3 - Coefficient estimates (and confidence intervals) for full models.** Significance levels (*) are Bonferroni-adjusted (n = 8) to account for multiple comparisons.



**Results -full models**

| | *Dependent variable:* | | | | |
|---|---|---|---|---|---|
| | lrD | lrd | lrL | lrV | lrW |
| Origin(S) | -0.053 | -0.030 | -0.130$^{*}$ | -0.033 | -0.045 |
| | (-0.189, 0.083) | (-0.161, 0.101) | (-0.198, -0.061) | (-0.065, -0.001) | (-0.078, -0.012) |
| Destination(S) | 0.153 | 0.173 | -0.253$^{*}$ | -0.063$^{*}$ | -0.070$^{*}$ |
| | (0.028, 0.279) | (0.048, 0.298) | (-0.341, -0.166) | (-0.097, -0.029) | (-0.100, -0.039) |
| Genus(P) | 0.192 | 0.193 | -0.175 | -0.066 | -0.086 |
| | (-0.050, 0.434) | (-0.119, 0.505) | (-0.334, -0.017) | (-0.100, -0.033) | (-0.125, -0.047) |
| Origin(S):Destination(S) | 0.016 | -0.042 | 0.089 | 0.012 | 0.036 |
| | (-0.171, 0.203) | (-0.228, 0.145) | (-0.041, 0.219) | (-0.039, 0.063) | (-0.008, 0.081) |
| Origin(S):Genus(P) | -0.101 | -0.069 | 0.055 | 0.021 | 0.035 |
| | (-0.294, 0.092) | (-0.255, 0.117) | (-0.041, 0.150) | (-0.025, 0.066) | (-0.012, 0.082) |
| Destination(S):Genus(P) | -0.378$^{*}$ | -0.364$^{*}$ | 0.232$^{*}$ | 0.074$^{*}$ | 0.100$^{*}$ |
| | (-0.543, -0.214) | (-0.528, -0.200) | (0.117, 0.348) | (0.029, 0.119) | (0.061, 0.139) |
| Origin(S):Destination(S):Genus(P) | 0.075 | 0.058 | -0.025 | -0.035 | -0.049 |
| | (-0.162, 0.312) | (-0.179, 0.295) | (-0.190, 0.141) | (-0.099, 0.030) | (-0.106, 0.008) |
| Intercept | 0.418$^{*}$ | 0.408$^{*}$ | 0.310$^{*}$ | 0.195$^{*}$ | 0.167$^{*}$ |
| | (0.249, 0.587) | (0.188, 0.627) | (0.199, 0.422) | (0.172, 0.217) | (0.140, 0.193) |
| Observations | 218 | 218 | 218 | 218 | 218 |
| Akaike Inf. Crit. | 7.170 | 5.562 | -164.641 | -552.845 | -593.410 |

**Table C.3 (continuation)- Coefficient estimates (and confidence intervals) for full models.** Significance levels (*) are Bonferroni-adjusted (n = 8) to account for multiple comparisons.

**Results -full models**

| | *Dependent variable:* | | | | | |
|---|---|---|---|---|---|---|
| | lrA | lrC | lrR | lrF | lrTl | deltaPCAl |
| Origin(S) | -0.316 | 0.160 | -0.080 | -0.016 | -0.115 | $-0.209^{*}$ |
| | (-0.563, -0.069) | (0.021, 0.298) | (-0.149, -0.011) | (-0.032, 0.0003) | (-0.247, 0.018) | (-0.346, -0.071) |
| Destination(S) | $-0.703^{*}$ | $0.535^{*}$ | $-0.267^{*}$ | $-0.038^{*}$ | $-0.512^{*}$ | $-0.397^{*}$ |
| | (-0.920, -0.486) | (0.394, 0.676) | (-0.338, -0.197) | (-0.055, -0.021) | (-0.627, -0.397) | (-0.525, -0.270) |
| Genus(P) | -0.635 | 0.507 | -0.253 | -0.050 | -0.507 | -0.219 |
| | (-0.957, -0.314) | (0.227, 0.786) | (-0.393, -0.114) | (-0.067, -0.033) | (-0.755, -0.259) | (-0.435, -0.002) |
| Origin(S):Destination(S) | 0.325 | -0.109 | 0.055 | 0.024 | 0.171 | 0.101 |
| | (0.001, 0.650) | (-0.319, 0.100) | (-0.050, 0.160) | (-0.001, 0.049) | (-0.001, 0.343) | (-0.089, 0.291) |
| Origin(S):Genus(P) | 0.180 | -0.177 | 0.088 | 0.007 | 0.182 | 0.115 |
| | (-0.172, 0.532) | (-0.373, 0.020) | (-0.010, 0.187) | (-0.016, 0.029) | (-0.006, 0.371) | (-0.081, 0.311) |
| Destination(S):Genus(P) | $0.597^{*}$ | $-0.617^{*}$ | $0.309^{*}$ | $0.045^{*}$ | $0.668^{*}$ | $0.291^{*}$ |
| | (0.312, 0.882) | (-0.802, -0.432) | (0.216, 0.401) | (0.023, 0.067) | (0.517, 0.819) | (0.123, 0.458) |
| Origin(S):Destination(S):Genus(P) | -0.393 | 0.100 | -0.050 | -0.019 | -0.266 | -0.103 |
| | (-0.805, 0.019) | (-0.167, 0.367) | (-0.183, 0.084) | (-0.050, 0.013) | (-0.485, -0.047) | (-0.344, 0.139) |
| Intercept | $1.463^{*}$ | $-0.698^{*}$ | $0.349^{*}$ | $0.042^{*}$ | $0.316^{*}$ | $0.761^{*}$ |
| | (1.240, 1.687) | (-0.894, -0.502) | (0.251, 0.447) | (0.030, 0.054) | (0.143, 0.490) | (0.610, 0.912) |
| Observations | 217 | 217 | 217 | 217 | 217 | 217 |
| Akaike Inf. Crit. | 238.932 | 50.290 | -239.446 | -844.667 | -23.402 | 13.951 |

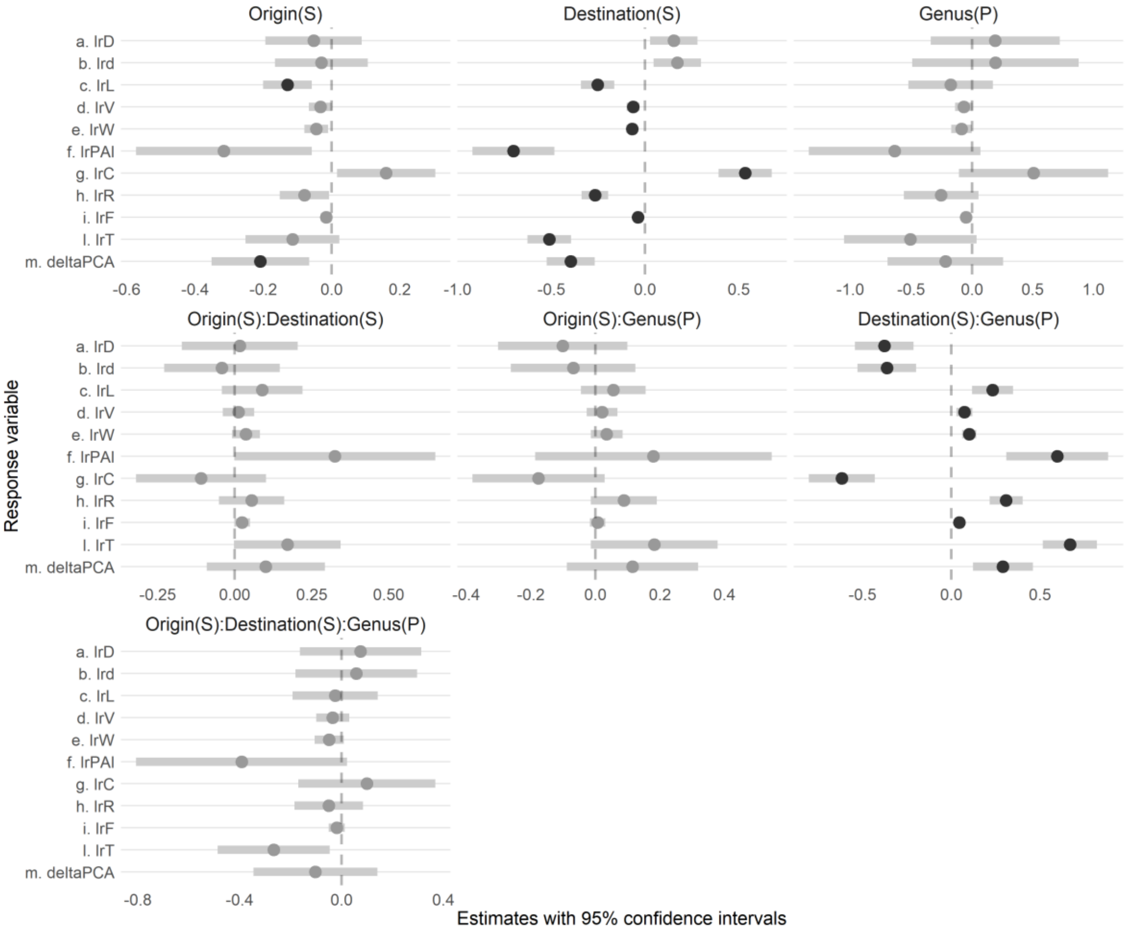


**Figure C.5 - Effect size estimates for fixed factors and interaction terms included in the full models.** Dots represent the estimated effect size of each fixed term in each model and grey bars represent the 95% confidence intervals. Black dots are significant values and significance levels are Bonferroni-adjusted to account for multiple comparisons (n = 8).

# Appendix D. Supplementary material for chapter 5

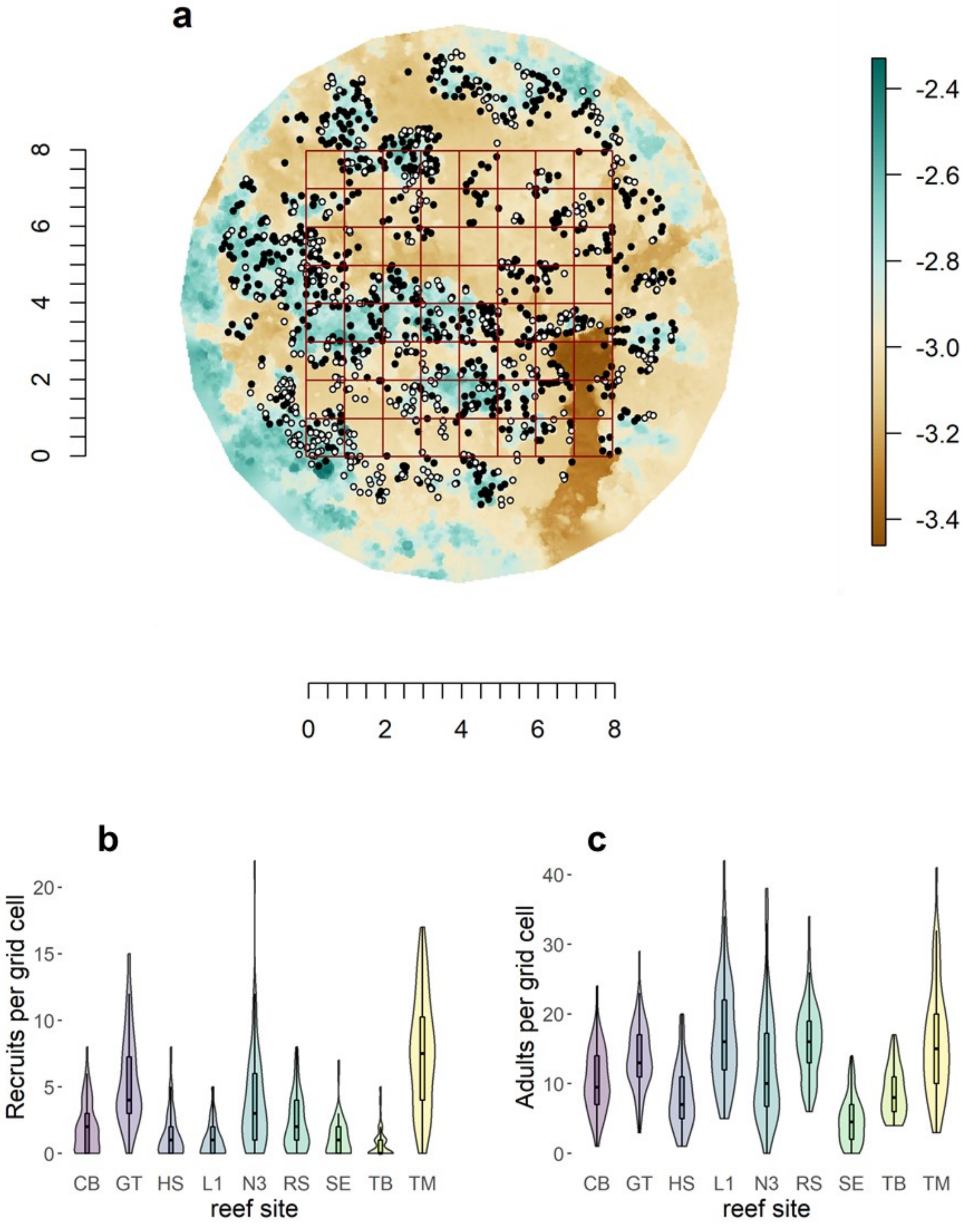


**Figure D.1 – Digital elevation model example and recruit and adult counts for the 1x1m grid**. a) Digital elevation model of the reef site at North Reef 3 (N3). Black dots represent the locations of adult colonies and white dots represent the locations of recruits. In dark red, the 1x1mcm grid that divides the reef in 64 cells of area 1m$^2$. b) Recruit abundance divided by site represented with violin and boxplots. c) Adult abundance divided by site represented with violin and boxplots.

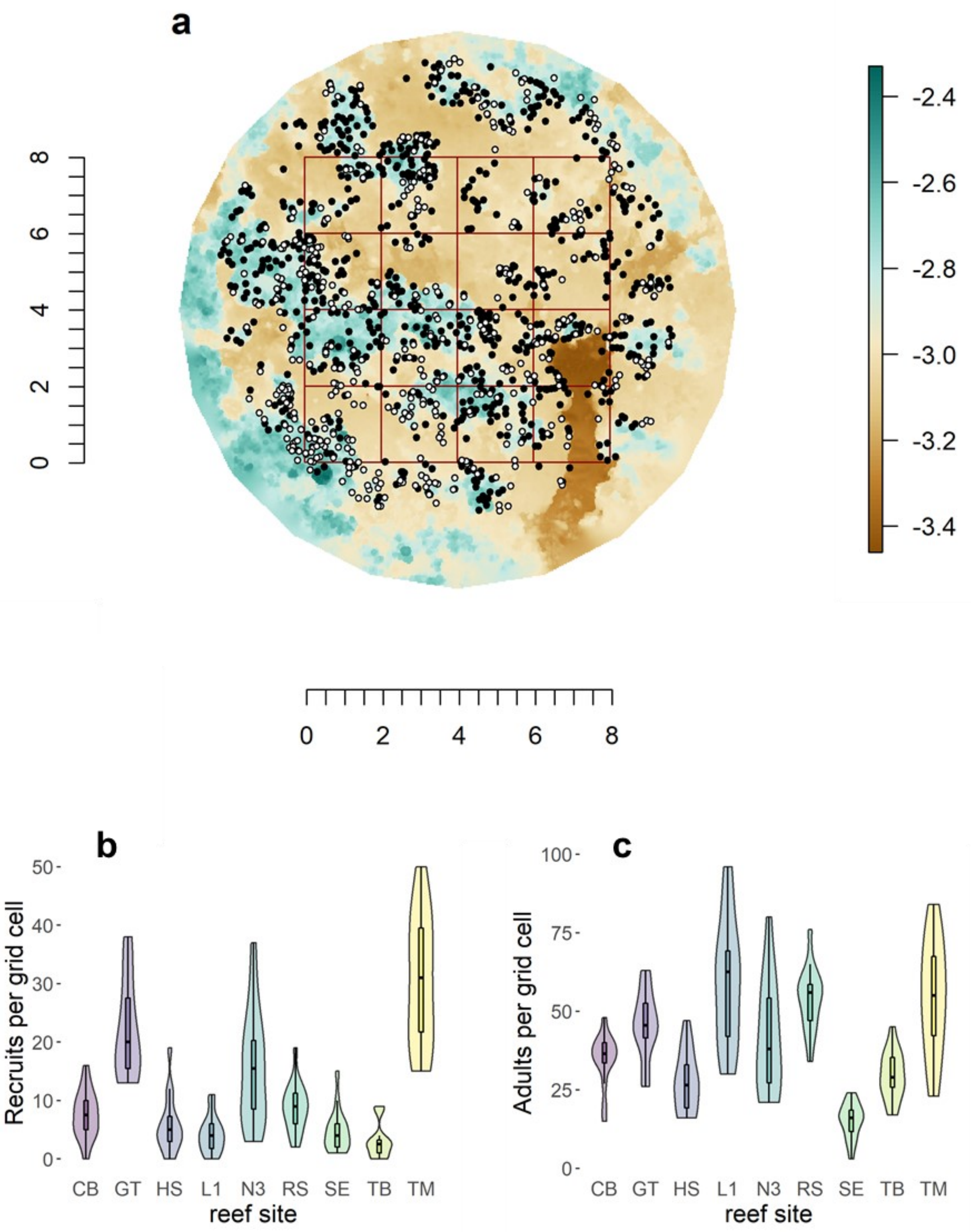


**Figure D.2 – Digital elevation model example and recruit and adult counts for the 2x2m grid**. a) Digital elevation model of the reef site at North Reef 3 (N3). Black dots represent the locations of adult colonies and white dots represent the locations of recruits. In dark red, the 1x1mcm grid that divides the reef in 16 cells of area $4m^2$. b) Recruit abundance divided by site represented with violin and boxplots. c) Adult abundance divided by site represented with violin and boxplots.

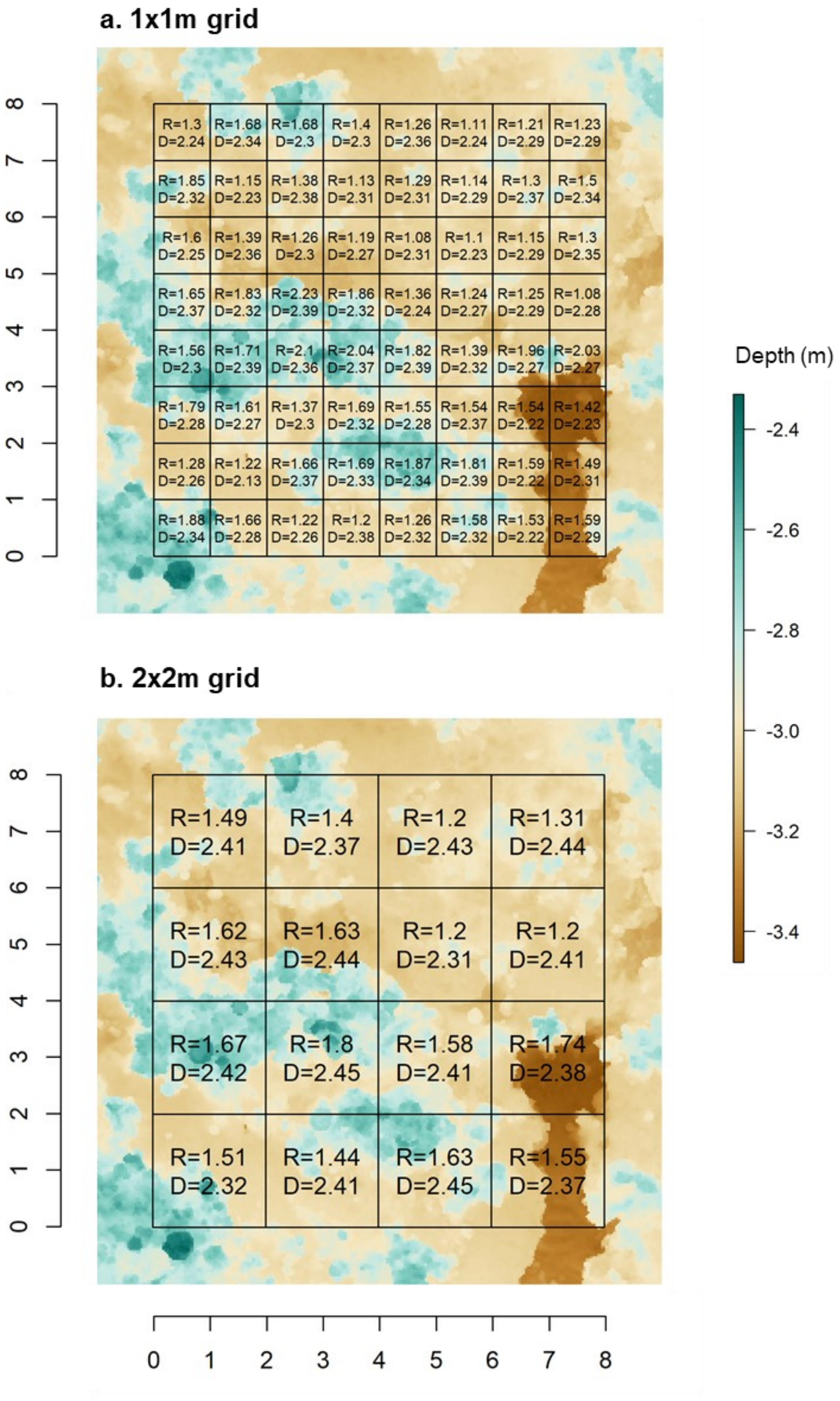
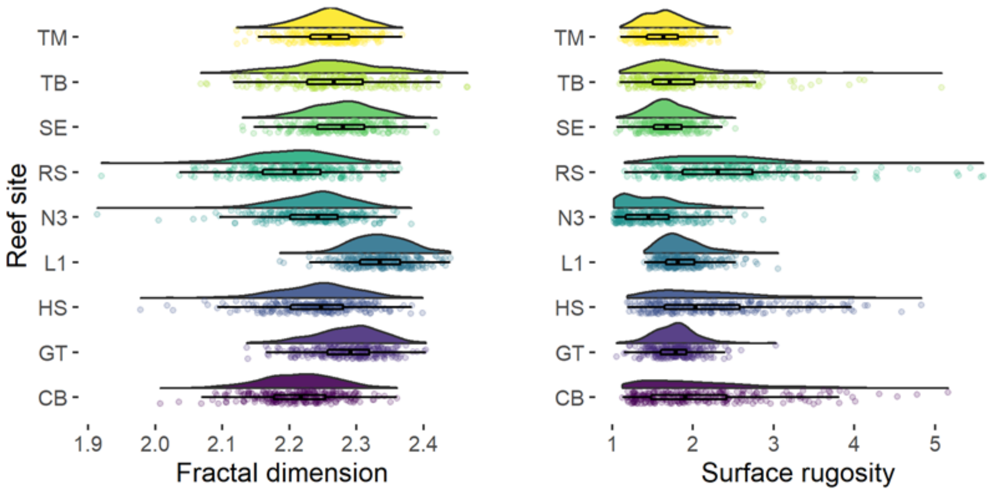


**Figure D.3 – Example of complexity metrics as measured in North Reef 3 (N3) among 1x1m cells** (a) and 2x2m cells (b). R = Surface rugosity. D = Fractal dimension. Notice how the combination of low R and D values corresponds to flat and smooth areas.

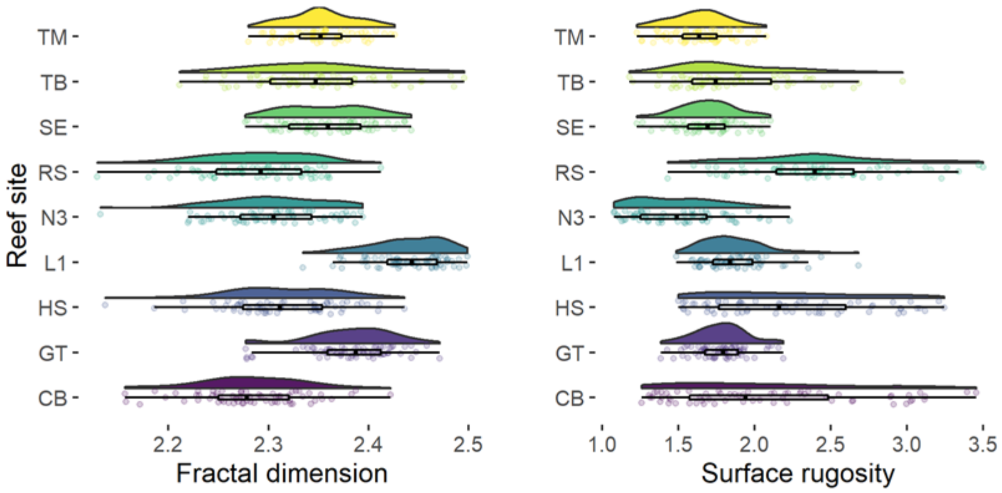
**Table D.1 – Model estimates for recruitment abundance for each of the grid considered whem using site as random effect**. The incidence of the parameters and the confidence intervals are shown as recruit counts. Because of the log link function, effects are detected when the confidence interval (CI) does not overlap 1 (shaded in the table). For smoothed variables, incidence of the smooths ("s", row 4 and 5) and standard deviation of the smoothed interaction ("sds", row 6) is reported. For the random effect (site), the standard deviation among groups ("sd", row 7) is reported.

| | **50x50cm grid** | | **1x1m grid** | | **2x2m grid** | |
|---|---|---|---|---|---|---|
| *Predictors* | *Incidence* | *CI (95%)* | *Incidence* | *CI (95%)* | *Incidence* | *CI (95%)* |
| intercept | 0.45 | 0.00 – exp(13.05) | 1.68 | 0.48 – 5.85 | 10.52 | 2.44 – 44.35 |
| adult abundance | 1.14 | 1.15 – 1.20 | 1.03 | 1.02 – 1.03 | 1.00 | 1.00 – 1.01 |
| mean settler abundance | 0.98 | 0.01 – 95.71 | 0.96 | 0.69 – 1.34 | 0.90 | 0.62 – 1.31 |
| s($\log_{10}$(Rugosity)) | 0.26 | 0.02 – 3.02 | 4.02 | 0.07 – 558.99 | exp(8.32) | 104.23 – exp(12.05) |
| s(Fractal dimension) | 484.53 | 5.03 – exp(8.95) | 0.00 | 0.00 – 0.18 | 0.01 | 0.00 – 0.89 |
| sds($\log_{10}$(R),D) | 2.38 | 0.27 – 3.97 | 3.63 | 1.84 – 11.18 | 9.69 | 3.97 – 30.76 |
| sd(site) | 2.64 | 1.73-6.05 | 2.69 | 1.77 – 6.17 | 3.25 | 1.94 – 8.25 |
| *Observations* | 2303 | | 574 | | 144 | |
| *$R^2$ Bayes* | 0.419 | | 0.598 | | 0.753 | |

a. 50x50cm grid



b. 1x1m grid



c. 2x2m grid

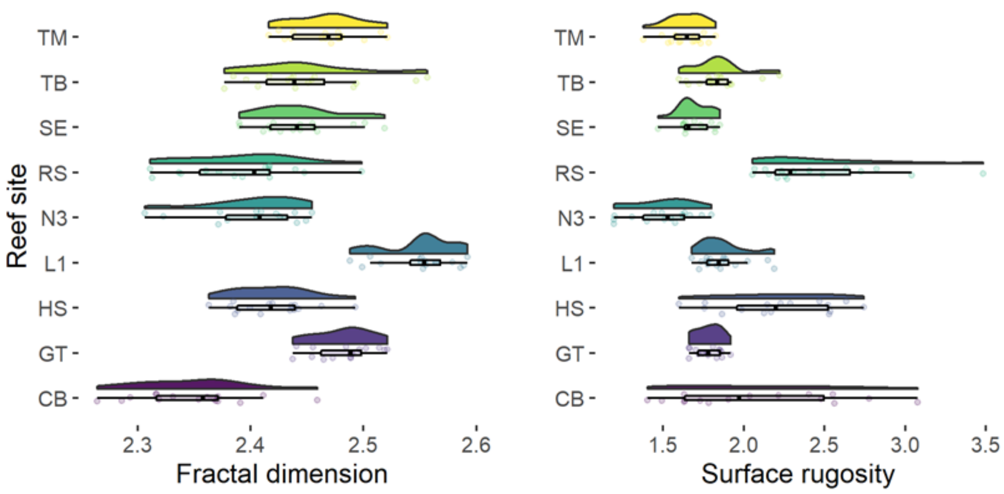


**Figure D.4 (previous page) – Raincloud plots of reef patch fractal dimension and surface rugosity for the 3 different grids used in the analysis divided by site.** Notice changes in the horizontal axis when increasing grid size.

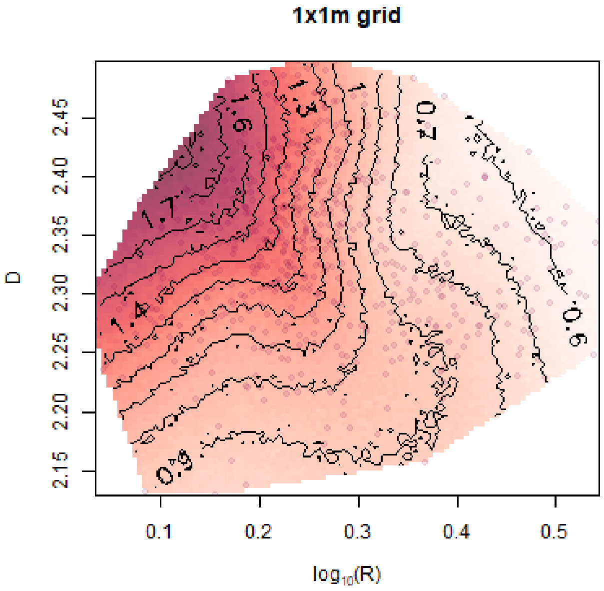


**Figure D.5 – Predicted coral recruitment (recruit counts for 1 m$^2$ reef areas) when plotted on the surface complexity plane given by rugosity and fractal dimension**. Notice that rugosity has been log$_{10}$-transformed. Dots represent data pairs used to fit the model at this scale and contours represent predicted increments in counts of 0.1.