Mapping benthic biodiversity variables of coral reefs using spatial interpolation of circular plot sampling

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Abstract

The spatialisation of essential biodiversity variables is a crucial step in assessing the health of coral reefs. However, few studies propose a comprehensive method for a large-scale assessment, such as coral reefs around Reunion Island. This requires a trade-off between the area, the study time, and the number of sampled stations needed to achieve spatial interpolations at an acceptable human and financial cost. We estimated nine sighting benthic biodiversity variables through visual assessments conducted in 2,599 circular plots per 100 m², distributed in two zones (reef flat, outer slope) and 14 habitats present across four sites (fringing reefs) on Reunion Island. A stratified sampling plan that is homogeneous within zones and differentiate between zones is appropriate, particularly for the study of a reef at several spatial scales (site, zone, habitat). We first demonstrated that the sampling effort enabled statistical discrimination and spatialisation of the nine benthic biodiversity variables within all the landscape units. Subsequently, we investigated the reliability limits of the spatial models by reducing the sampling effort of an increasing proportion of stations using bootstrap resampling. Results showed that station densities of 0.5 to 1.2 stations.ha^{-1} (outer slopes) and 1.5 to 4.3 stations.ha^{-1} (reef flats) provide very satisfactory to excellent spatialisation of the essential biodiversity variables. Depending on the objectives, the resolution and the available resources, our method allows an estimation of the trade-off between required information for mapping benthic biodiversity variables of coral reefs using spatial interpolation and sampling effort.

Introduction

Coral reefs provide over a billion people with food, commercial fisheries, and prevent coastal erosion, carbon sequestration and coastal protection against the storm surge (Eddy et al. 2021). These ecosystem services are essential for local populations and the balance of the earth's ecosystem (Hughes et al. 2017), while also providing habitats for a wide range of marine species, estimated between 550,000 and 1,330,000 species by Fisher et al. (2015). However, the global average cover of living hard coral has fluctuated globally over the past 40 years, punctuated by intermittent disturbances (Connell 1978; Souter et al. 2021). For instance, a global bleaching event in 1998 resulted in the loss of 8% of the world's corals, equivalent to the area of the Great Barrier Reef. Despite the inherent resilience mechanisms of coral reefs and an increase in live coral cover noted in 2009, 14% of corals disappeared between 2009 and 2018 (Souter et al. 2021). While climate change, particularly ocean acidification and extreme events like bleaching and storms, contributes to coral reefs decline, it alone does not account for the observed trends (Bellwood et al. 2004; Hoegh-Guldberg et al. 2007). Over 60% of the coral reefs worldwide are impacted by local human activities (Carlson et al. 2019), such as coastal amenagement, watershed pollution, and overfishing (Richmond et al. 2019). Thus, coral reefs are subjected to a complex array of pressures across multiple spatial and temporal scales (Hoegh-Guldberg et al. 2017; McFarland 2021).

The cumulative effect of pressures at multiple scales has compelled the scientific community to develop numerous methods to identify the different levers that can be used by authorities to limit pressures (Bellwood et al. 2019). Early pioneers in methodological development encountered challenges in standardizing these approaches, both technically and financially (English et al. 1997; Hill and Wilkinson 2004; Fennessy et al. 2007). Several methodological guides have been published, specifying for each method the objective, advantages and disadvantages, individual surface area of a station, level of precision of the information collected, required equipment, and the time per station including acquisition and processing (English et al. 1997; Hill and Wilkinson 2004). Given the diversity of existing field methods, the choice of approach should be guided by the study's objectives, the sampling plan, the associated statistical analyses and the available human and financial resources (Conand, 1997). Monitoring networks, such as the Global Coral Reef Monitoring Network, have focused on a limited number of stations and areas to ensure a high level of accuracy (Nadon and Stirling 2006). These choices have enabled the collection of a substantial high-quality temporal data on benthic communities and their linkages to climate change (Souter et al. 2021; Obura et al. 2022). However, the number of stations is often insufficient to interpolate data within a habitat or reef complex, thereby limiting the spatial representativeness of the information (Bajjouk et al. 2019; Monnier et al. 2021).

Spatialisation of benthic communities appears to be a useful tool for delineating reef habitats (Montaggioni and Faure 1980), providing index representative of reef conditions (Obura et al. 2019), determining species' spatial distribution (Corbel et al. 2024), and assessing pressures emanating from watersheds (Scopélitis et al. 2009; Allemande et al. 2011; Bajjouk et al. 2019; Carlson et al. 2019; Ford et al. 2020) as well as ecological losses following intermediate disturbances (Moran and De'ath 1992; English et al. 1997). The challenge of spatialisation lies in finding a trade-off between the study area's extent and the number of sampling stations, while maintaining data quality and minimizing operational time. Emerging technologies partially address this challenge by offering automated data collection tools (Obura et al. 2019). These include Autonomous Underwater Vehicles, Remotely Operated Vehicles (in the water), Autonomous Surface Vehicles (on the water), and high-resolution aerial and satellite remote sensing technologies by Small Unmanned Aerial Systems (in the air). Such new technologies, such as high-resolution remote sensing, can delineate coral reef geomorphology (Leon and Woodroffe 2007; Wang et al. 2022), predict live coral cover (Knudby et al. 2013), and forecast coral bleaching probabilities (Donner et al. 2017). Although these technologies are still under development and do not yet provide, to our knowledge, comprehensive information on the coral vitality, resilience (e.g., disease prevalence, juvenile coral density), community structure (e.g., colony diameter, structural complexity, Urbina-Barreto et al. 2021a), or proliferation of specific opportunistic benthic assemblages, such as corallimorphs and sponges (Work et al. 2008; Bell et al. 2013). Coupling rapid *in situ* assessment methods, capable of capturing essential biodiversity variables across many stations, with spatial interpolation analyses, represents another promising approach for enhancing spatialisation capacities (Bajjouk et al. 2019).

The difficulty in transforming a set of georeferenced points into a map of defined extent and accuracy lies in the degree of site heterogeneity, the area of the individual station and the sampling strategy (Cormack and Cressie 1992; Webster and Oliver 2007). The photoquadrat method was the first to combine *in situ* data and spatial interpolation analysis (Zarco-Perello and Simões 2017; Gómez-Andújar and Hernandez-Delgado 2020). However, this method uses a very small station area (< 1 m²) and requires considerable processing time to extract key information (Urbina-Barreto et al. 2021b), which has led to a reduction in total sampling area and interpolation quality (Li and Heap 2008).

Since 2016, the French Coral Reef Initiative has initiated research to assess the ecological status of coral reefs using a rapid assessment method based on a medium scale approach, using visual 100 m^2 circular plots (Pinault et al. 2017). This method, inspired by forest ecology, has been taken up and adapted by several studies in reef environments to meet very different objectives (Edwards et al. 2017; Pedersen et al. 2019; Corso et al. 2022). In this study, it enabled us to implement a consistent sampling plan, with a large sampling area, within an acceptable timeframe, and to access habitats exposed to intense environmental conditions (e.g., outer reef flat). The functional status of coral reefs was monitored using nine benthic biodiversity variables (BBVs), approaching the essential biodiversity variable's standards (Pereira et al. 2013). The BBVs were sampled on 2,599 circular plots on 4 fringing reefs on Reunion Island (Hermitage – La Saline, Saint-Leu, Etang-Salé, Saint-Pierre – Terre-Sainte), from the shore to 15 m depth.

The aims of the article are to test whether the sampling effort and the 100 m² station method (*i*) allow statistical discrimination and (*ii*) reliable spatialisation of the nine BBVs within the landscape units considered (site, zone and habitat). Then, we study (*iii*) the limits of the spatial model's reliability by sub-sampling the complete database. The final objective is (*iv*) to provide a method to identify the best trade-off between parsimony of sampling and robustness of interpolations for producing maps of the ecological status of coral reefs over time.

Materials and methods

Study area and coral reef sampling

Reunion Island is part of the Mascarene Archipelago, which also includes Mauritius and Rodrigues, located 800 km east of Malagasy (Fig. 1a). The island emerged 2.1 million years ago. The coral reefs, primarily found in the Western and Southern parts of the island, are about 10,000 years old, making them relatively young reefs (Montaggioni and Faure 1980). These reefs develop discontinuously along 25 km of coastline (Tessier et al. 2008). The four study sites (Fig. 1b) have a reef barrier where the waves break only a few hundred meters from the shore. Fringing reefs are mentioned: Hermitage – La Saline, Saint-Leu, Etang-Salé, and Saint-Pierre – Terre-Sainte (Fig. 1c-f).

The study sites are composed of two geomorphological zones: the outer slope (-2 to -15 meters) and the reef flat (0 to -2 meters, Montaggioni and Faure 1980), which are themselves divided into 14 habitats: four on the outer slope and 10 on the reef flat (Nicet and Andres, *in press*). Since the precision of spatialisation analyses depends on the number of stations (Webster and Oliver 2007), and reef topography is positively related to benthic spatial complexity (Chabanet et al. 1997; Graham and Nash 2013; Duvall et al. 2019), we proposed a differential sampling plan between the outer slope and the reef flat. The habitat map, coupled with a preliminary study (Broudic and Pinault 2022) and the assumption that habitats represent relatively homogeneous ecological units at a mesoscale (Andréfouët and Guzman 2005; Scopélitis et al. 2009; Bajjouk et al. 2019), led us to consider that the sampling plan should be proportional to the number and heterogeneity of habitats. A larger sampling effort involves a higher risk (e.g., surf zone, rocky coast) and a higher cost for a gain in information that seemed negligible in view of the composition of the benthic populations in the areas studied.

Reef flats, inherently more sensitive to physico-chemical variations (Naïm 1993), were sampled during the shoulder seasons of 2021 and 2022 (September to December) to avoid thermal stress and seasonal algal blooms. They were gridded into sectors of 3,600 m^2 (60 x 60 m), within which three stations were randomly sampled (i.e. 8.4 $stations.ha^{-1}$). The outer slopes, requiring the most favorable meteorological conditions (low swell) and being less sensitive to physico-chemical variations and watershed influence (Bell 1992; Tedetti et al. 2020), were sampled during the calm season, from February to May 2023.

For both logistical (more difficult access) and ecological reasons (more homogeneous benthic communities with only four habitats), they were gridded into sectors of 3,025 m^2 (55 x 55 m) within which a single station was sampled at their center (i.e., 3.3 $stations.ha^{-1}$). However, due to intermittent unfavorable weather conditions during sampling, certain sectors located closest to the reef crest (except at the Hermitage – La Saline) or nearest to the coastal basaltic rock (e.g., Etang-Salé), could not be sampled (Fig. 1e). This reduced the mean sampling density to 7.6 $stations.ha^{-1}$ on the reef flat and to 1.6 $stations.ha^{-1}$ on the outer slope (Table 1). The two field campaigns were not combined for analysis to avoid any seasonal bias.

Sampling was carried out in 100 m^2 circular plots, each plot being a station with the center marked by a weighted rope and the 5.6 m radius by a fiberglass tape measure, in accordance with Ortiz and Tissot (2008) and Edwards et al. (2017). The coordinates of the center of each circular plot were recorded using a Garmin 76© GPS. At each station, nine BBVs were visually estimated during a short time, no longer than 5 to 7 minutes. Three of these are from the International Coral Reef Initiative's "Five A's" of the Coral Reef Indicators: (1) Live Coral Cover, (2) Fleshy Algae Cover, and (3) Opportunistic Species Cover (i.e. Corallimorphs, Sponges, Anemones, soft corals, etc.) estimated in percentages according to Dahl's method (1981). To obtain more details on the ecological structure of coral populations, the following BBVs were added: (4) Structural Complexity, estimated between 1 and 5 according to Gratwicke and Speight's method (2004), which is strongly determined by the diversity of growth forms of coral colonies, (5) Percentage of *Acropora* genus within the coral population and (6) Mean Diameter of coral colonies estimated in centimeters (Obura and Grimsditch 2009). Finally, to provide additional information on the resilience and demographic dynamics of coral populations, we added : (7) Juvenile Corals Density (number of colonies from 1 to 5 cm in diameter observed in four quadrats of 50 cm side, randomly positioned in the sampling station, according to Penin and Adjeroud (2013), (8) Coral State of Health (prevalence and importance of recent coral necrosis and mortality, estimated between 0 - completely dead and 3 - excellent health) according to Obura and Grimsditch (2009) and Séré et al. (2015) and (9) Sea Urchins Density, according to Dang et al. (2020).

Representativeness of sampling according to study sites, zones, and habitats

The representativeness of the sampling effort was tested by analyzing the variability of each BBV across zones (outer slope and reef flat) and reef habitat within each study site. A polynomial function was applied to each BBVs to follow a Gaussian distribution, allowing for continuous quantitative response variables. The variance of each BBVs was compared using ANOVA analyses, with sites, zones, and habitats as explanatory variables. Variables were tested for normality and homoscedasticity using the Shapiro-Wilk (Shapiro and Wilk 1965) and Bartlett (Bartlett 1992) tests, respectively. Choropleth maps were produced by averaging each BBV within each polygon of the habitat map (bounds have been defined according to a normal distribution of the data).

Generalized Linear Models (GLM, Nelder et al. 1972) were used to relate a linear function of each BBV (response variable) to sites and habitats (explanatory variables). The nature of the variables (quantitative for BBVs and qualitative for sites and habitats), the data distributions (Gaussian or Poisson) and the linear relationship between the response variables and the explanatory variables led us to use GLM rather than GAM (Generalized Additive Model). GLM allows us to test the hypothesis that sites and habitats, as well as interactions between sites and habitats, significantly explain the variation in each BBV.

Semi-variogram and spatial interpolation

Before selecting the spatial interpolation analyses, Moran's I index (Moran 1950) was calculated, highlighting significant spatial autocorrelation for each BBV in each geomorphological unit. The spatial interpolation method was chosen using the dichotomous tree of Li and Heap (2008). Maps were produced by spatial interpolation using ordinary kriging (Matheron 1963). Semi-variogram parameters were defined manually using the “variogram” function (gstat library). For each BBV, the number of even-numbered neighbors and the parameters were defined (i.e., sill, exponential model or spherical model when exponential was not suitable, range, and nugget) based on the complete dataset. From the model defined by the semi-variogram, ordinary kriging was generated with the “gstat” function (gstat library) on the outer slope, on one hand, and reef flat on the other, of each study site. Each interpolation produces a prediction and variance map. A cross-validation analysis was used to calculate the mean and the standard error of the residuals. The effect of anisotropy was examined according to the four cardinal points. Each of the predictions was compared by ANCOVA analysis with the interpolation generated in an isotropic context.

The spatial resolution was calculated according to the station density of each site and zone (Hengl 2006) and compared with the recommendations of Bajjouk et al. (2019). Their analysis on the Hermitage – La Saline reef flat suggests that the resolution suitable for capturing coral spatial heterogeneity must be around 8 to 10 m at the worst. On the reef flat, the values were between 12 m and 14 m, and between 45 m and 65 m on the outer slope. These latter were compared with the 10 m recommended by ANCOVA. As there was no significant difference, the resolution was set at 10 m for each zone. Analysis were produced using RStudio (Posit team 2023), and the layout was created using QGIS 3.34.0 (QGIS Development Team 2023).

Trade-off between sampling parsimony and spatial interpolation reliability at each study site, zone, and habitat

The effect of reducing station density on the quality of spatial interpolation maps was tested for each BBV at each site and in each zone. These tests were carried out in three successive stages: (*i*) ordinary kriging was performed with the complete dataset, (*ii*) Ordinary kriging was conducted on a sub-sample (station density ranging from 0.3 to 1.6 with a step of 0.1 for the outer slope and from 1 to 7.5 with a step of 0.5 for the reef flat) and (*ii*) spatial correlations between the map generated with the complete dataset and each map generated with the reduced datasets were calculated. The diagnosis of collinearity between the maps was studied using the absolute value of correlation coefficients.

For each BBV in each site and zone, 30 semi-variograms were calculated using 30 sub-sampling datasets obtained by random permutation without replacement. The semi-variogram parameters defined on the basis of the complete dataset were used to perform interpolations on the sub-sampling dataset. If the sub-sampling changed the distribution of the data to such an extent that the fixed parameters of the semi-variogram no longer fitted the data, then a new sub-sampling was carried out. Ordinary kriging was generated for each semi-variogram, producing 30 sub-sampling dataset prediction maps. For each, the spatial correlation with the prediction map of the complete dataset was analyzed using a 5x5 pixel “focal” analysis (“raster” library). Finally, each prediction map was cut according to reef habitat map. A database containing information on the reef habitat and absolute value of correlation coefficients for each pixel of each map was produced in order to determine the evolution of the absolute value of correlation coefficients as a function of the station density (station.ha^{-1}). However, the outer slope of Etang-Salé could not be studied because the number of stations with reduced densities was too low (4 stations for a density of 0.3 station.ha^{-1}).

Once all results had been obtained, a boxplot was generated for each sub-sampling dataset, expressed in stations.ha^{-1} on the x-axis, and the absolute values of correlation coefficients with complete dataset on the y-axis for each BBV in all zones (outer slope and reef flat) and by habitat. Dormann and al. (2013) point out that the absolute value of spatial correlation coefficient above 0.5 provides an acceptable correlation, and above 0.7 is very satisfactory correlation. For the present study, we have added the threshold of 0.9 to testify to an excellent correlation. Boxplots show all the BBVs by zones and by habitats to represent the variability of station densities sufficient to exceed the 0.5, 0.7 and 0.9 threshold, with information on outer slope and reef flat. It was not possible to study the basaltic fore reef and the pass, which are too rare in the study area. Nevertheless, these two boxplots give an indication of the balance between sampling effort and spatial precision.

Results

Representativeness of sampling according to sites, zones and habitats

The outer slope (0–15 m), covering an area of 401 ha, was sampled with 709 stations, equivalent to 7.1 ha (Table 1). The number of stations.ha^{-1} within the outer slope varied from 1.0 for Etang-Salé to 1.9 for Saint-Pierre. Low-relief and high-relief spurs and grooves were the most densely sampled with an effort of 1.1 and 1.2 $station.ha^{-1}$ respectively (Fig. 2). The basaltic fore reef, mainly present at the end of Etang-Salé reef and at Terre-Sainte, was difficult to sample, as was the reef crest, located in the wave breaking zone. These environmental constraints limited the sampling effort on these habitats to 0.2 and 0.3 $station.ha^{-1}$ respectively.

Table 1

Sampling effort by site and zone, with the number of stations (Nb station), the area (ha), the sampling density ($station.ha^{-1}$), the sampled area (ha) and the number of field trips.

	Outer slope					**Reef flat**				
Site	Nb station	Area (ha)	$Station.ha^{-1}$	Sampled area (ha)	Nb fieldtrip	Nb station	Area (ha)	$Station.ha^{-1}$	Sampled area (ha)	Nb fieldtrip
Hermitage – La Saline	359	194	1.8	3.6	9	1 223	163	7.5	12.2	22
Saint-Leu	100	55	1.8	1.0	4	221	29	7.6	2.21	4
Etang-Salé	40	173	1.0	0.4	1	175	22	7.9	1.7	2
Saint-Pierre – Terre-Sainte	212	111	1.9	2.1	4	271	35	7.7	2.7	5
Total	709	401	1.6	7.1	18	1 890	250	7.6	18.9	33

The reef flat, covering an area of 249 ha, was sampled using 1,888 stations, equating to 18.9 ha. The station densities ranged from 7.5 $station.ha^{-1}$ at Hermitage – La Saline to 7.8 $station.ha^{-1}$ at Etang-Salé. Although smaller than the outer slope, the reef flat was more extensively sampled due to its very high heterogeneity. 10 habitats make up the reef flat, with five dominant habitats (coral-rubble ridges, outer reef flat, reef flat with transverse stripes, reef flat with scattered patches and inner reef flat with branching coral). Station densities in the main habitats were between 6.4 $station.ha^{-1}$ for the outer reef flat and 9.0 $station.ha^{-1}$ for the inner reef flat with branched coral. Smaller habitats or those located at the end of the reef (basalt boulders, slabs, cobbles and outcrops, pass and channels) had lower mean station densities (0.3, 2.1, and 3.6 $station.ha^{-1}$ respectively, Fig. 2).

Whether on the outer slope or on the reef flat, Saint-Pierre – Terre-Sainte and Saint-Leu had the highest mean live coral cover (outer slope: 35.6% ± 19.5% and 37.6% ± 16.0%, reef flat: 16.3% ± 17.5% and 12.3% ± 23.4%). In contrast, Hermitage – La Saline and Etang-Salé, had the lowest mean live coral cover (outer slope: 20.6% ± 15.3% and 21.5% ± 17.8%, reef flat: 8.2% ± 13.4%, and 10.0% ± 9.6%, Fig. 3). At all sites, mean live coral cover was higher on the outer slope than on the reef flat. Saint-Pierre – Terre-Sainte was the site with the most structured coral communities, including the percentage of *Acropora*, structural complexity and diameter of coral colonies (on the outer slope: 29.9% ± 20.0%, 5.8 ± 1.5 shape numbers, and 42 ± 12 cm respectively, reef flat: 23.9% ± 20.1%, 5.8 ± 0.8 shape numbers, and 39 ± 28 cm respectively). Mean opportunistic species cover and juvenile coral density were higher on the outer slope than on reef flat (except at Saint-Pierre - Terre-Sainte, where they did not vary). Mean fleshy algae cover varied very little between reef zones (except for Etang-Salé) and sites (between 1.0% ± 10.6% at Saint-Leu to 3.5% ± 21.0% at Saint-Pierre – Terre-Sainte on the outer slope and 1.1% ± 14.2% at Saint-Leu to 3.3% ± 9.8% at Saint-Pierre – Terre-Sainte on the reef flat). Sea urchin abundance was highest in Saint-Leu, both on the outer slope and on the reef flat (5.4 ± 2.8 $ind.m^{-2}$ and 3.5 ± 2.3 $ind.m^{-2}$ respectively).

Site and habitat has a significant influence on all the ecological variables measured (Table 2). The deviance explained by the BBV ranged from 29.2% for opportunistic species cover to 93.0% for sea urchins density.

Table 2
GLM analysis with the p-value of the site and habitat effects (*: $p < 0.01$, **: $p < 0.001$ and ***: $p < 0.0001$) and the deviance explained by the interaction between site and habitats (%) according to the nine BBVs.

BBV	Function	Site	Habitats	Deviance explained (%)
Sea urchins density	quasipoisson	***	***	93.0
Juvenile corals density	quasipoisson	***	***	88.7
Percentage of Acropora genus within the coral population	quasipoisson	***	***	68.4
Diameter of coral colonies	gaussien	***	***	50.0
Coral state of health	gaussien	***	***	44.8
Structural complexity	gaussien	***	***	44.2
Fleshy algae cover	quasipoisson	***	***	39.7
Live coral cover	gaussien	***	***	39.1
Opportunistic species cover	quasipoisson	***	***	29.2

Semi-variogram and spatial interpolation

A total of 72 spatial interpolation analyses were carried out (following box a procedure, Fig. 4.). The spatial distribution of the estimated value of a given variable at each circular plot provides an initial cartographic representation (Fig. 4 – a1). The 36 semi-variograms of data from the outer slope and the 36 from the reef flat have mean nuggets of 0.07 ± 0.11 and 0.21 ± 0.14 respectively. All semi-variograms of outer slope data reach the sill, the value where the variogram function flattens off at increasing distance (spatial autocorrelation zone). This sill is 0.37 ± 0.19 and was located at a mean distance (range) of 229 ± 149 m (i.e. the Fig. 4 – a2). For the reef flat semi-variograms, the mean values of the sill and range were 0.79 ± 0.35 and 314 ± 200 respectively. Four variables in Etang-Salé reef flat (*Acropora* percentage, structural complexity, juvenile corals and sea urchin's density) and two variables in Saint-Leu reef flat (structural complexity and diameter of coral colonies) do not reach the threshold. The interpolations appear to be consistent with the field data. Figure 4 – a3 shows the prediction and variance of coral cover after ordinary kriging. The variance is around 1% in the center of the right of way and around 2% at the periphery (i.e. either near the waves or at the maximum depth of 15 m). The residual analysis gives a mean of 7^{e-04} ± 0.432. All prediction and variance results and cross-validation results are available in the supplementary information (Fig. S1, S2 and Table S1).

Trade-off between sampling effort and spatialisation quality on reef zones and habitats

In order to achieve a mean correlation coefficient of 0.9 between the model produced from the complete dataset and those derived from the partial datasets (Fig. 4–1b, 2b, 3b, c and d), the mean station densities on the outer slope and reef flat habitats were 1.0 ± 0.2 stations.ha^{-1} and 3.7 ± 0.8 stations.ha^{-1} respectively (Fig. 5). These means vary according to zone and model parameter, from 0.9 ± 0.2 stations.ha^{-1} for the *Acropora* percentage to 1.3 ± 0.2 stations.ha^{-1} for fleshy algae cover on the outer slope and from 2.8 ± 0.8 stations.ha^{-1} for sea urchins density to 4.0 ± 1.0 stations.ha^{-1} for fleshy algae cover on the reef flat. To reach the correlation threshold of 0.7, station densities for all habitats on the outer slope and reef flat need to be 0.3 ± 0.0 stations.ha^{-1} and 1.0 ± 0.0 stations.ha^{-1} respectively. Still targeting a mean correlation coefficient of 0.9, mean station densities for all the BBVs measured in the outer slope and reef flat habitats were 1.2 ± 0.2 stations.ha^{-1} and 4.2 ± 1.1 stations.ha^{-1} respectively (Fig. 6). The outer slope shows very little variations between habitats (0.2 stations.ha^{-1}), ranging from 1.0 ± 0.3 stations.ha^{-1} for low-relief spurs and grooves to 1.2 ± 0.2 stations.ha^{-1} for high-relief spurs and grooves. In comparison, the reef flat shows greater variations between habitats (1.1 stations.ha^{-1}), ranging from limestone platform (3.5 ± 0.8 stations.ha^{-1}) to emergent reef flat (4.6 ± 1.0 stations.ha^{-1}). To reach the correlation threshold of 0.7, station densities for all BBVs measured on the outer slope and reef flat habitats must be 0.5 ± 0.2 stations.ha^{-1} and 1.5 ± 0.7 stations.ha^{-1} respectively. The evolution of the mean correlation coefficient value as a function of station density for each BBVs (such as Fig. 4d) and habitats at all sites is provided in supplementary information (Fig. S3, S4).

Discussion

The circular plot method and sampling effort reflect the spatial heterogeneity of each scale (site, zone and habitat).

The 100 m² circular plot sampling method was fast, inexpensive and easy to implement while free diving. A total of 2,599 circular plots were assessed over two field campaigns on four fringing reefs, from the reef flat to the outer slope (15 m depth), covering 14 habitats. As shown by Zarco-Perello and Simões (2017), the photoquadrat method can also be used to sample a large number of 0.8 m² stations. The circular plot and photoquadrat methods are preferred due to their high reproducibility. However, the size of the photoquadrat stations is too small to detect mesoscale benthic variations (Clua et al. 2006) and post-processing time is high (Urbina-Barreto et al. 2021b).

Based on the 100 m² circular plot sampling method and although the sampling effort differed between the outer slope and the reef flat, our results showed a relatively homogeneous station density across each site, zone and habitat. This difference in sampling effort between zones can be justified by the fact that the number of habitats was lower and more homogeneous on the outer slope than on the reef flat (Andréfouët and Guzman 2005; Wismer et al. 2009; Duvall et al. 2019). Only in the outer slope of Etang-Salé and the reef end habitats (basalt fore reef and boulder, slab, cobble and outcrop), which are very small (pass) or risky (reef crest), were there lower station densities. Although the reef crest were weakly represented, Faure (1982) described this habitat within the Mascarene archipelago as homogeneous and mainly colonized by *Alcyonaria* and a few Chlorophyceae. For the basaltic fore-reef and basaltic blocks, slabs, cobbles and outcrops, under-sampling should not affect the following results due to their very low representativeness (1.1% of the study area).

A comparison of each BBV value between sites and zones showed that they were characterized by specific benthic communities. Indeed, Reunion's coral reefs, discontinuously distributed along the island's West and Southwest coasts, are exposed to different hydrodynamic, temperature and watershed pressure conditions (Montaggioni 1974; Montaggioni and Faure 1980). In addition, the reef flats are exposed to the influence of tides and highly variable physico-chemical water parameters, such as higher temperatures than on the outer slopes (Reid et al. 2020). For example, results showed that the southern reefs (Saint-Pierre - Terre-Sainte) had a higher mean coral cover than the northern reefs. Montaggioni and Faure (1980) point out that southern reefs are more exposed to trade winds. This exposure could promote the renewal of reef waters and allow better oxygenation of corals, particularly during the warm season (Taddei et al. 2008; Nelson and Altieri 2019). It could also help maintain sea surface temperature, which is around one degree lower on southern reefs than on western reefs, thus limiting the intensity of bleaching episodes. In 2016, the global bleaching episode relatively spared the reefs of Saint-Pierre and Terre-Sainte (Bigot et al. 2019).

In terms of differences between zones, mean coral cover is higher on the outer slope (31.8% ± 18.4%) than on the reef flat (15.8% ± 17.1%). This result is consistent with previous observations made on Reunion Island by Bouchon (1981), Faure (1982), Bigot et al. (2000, 2019), Zhao et al. (2012) and IFRECOR (2016). Similarly, the mean diameter of coral colonies is greater on outer slope (around 40 cm) than on reef flat (around 15 cm). Several reef flat habitats are sub-emergent and therefore limited in their growth (shapes and diameters) by water height. These habitats regularly emerge during extreme low tide events, causing significant coral mortality (Cordier et al. 2013). For example, the 2015 episode in the Southwest Indian Ocean caused 45.5% coral mortality on the reef flats of Reunion Island (Hoarau et al. 2023).

Logically, all BBVs have distributions significantly influenced by site and habitat. For example, the distributions of sea urchins and juvenile corals density or *Acropora* percentage are more than 65% explained by site and habitat interactions. These are taxa with aggregative traits that are characteristic of specific habitats – e.g. sea urchins on the outer reef flat (Peyrot-Clausade et al. 2000; Nishihira et al. 2020). These results support the use of 100 m² circular plots for spatialisation purposes.

Spatial interpolation of BBVs

Parameterization of the semi-variograms resulted in a nugget effect close to zero for the majority of the models. This means that stations located close to each other have a much higher probability of having similar values than distant stations (Goovaerts 1997). A difference is observed between generally lower nuggets and sills on the outer slope than on the reef flat. This confirms ecological observations that indicate greater homogeneity on the outer slope than on the reef flat. Six out of 72 semi-variograms showed the absence of a threshold where the semi-variance stabilizes (Saint-Leu and Etang-Salé reef flat). The search for parsimony required models adapted to sub-sampling. The parameters of the model were defined so that the semi-variogram could follow the distribution of the data both completely and after each sub-sampling. However, for the minimum density (1 station.ha^{-1}), the number of stations was 29 for Saint-Leu and 22 for Etang-Salé. Indeed, according to Chang et al. (1998), at least 28 stations are needed to stabilize the semi-variogram, and according to Webster and Oliver (1992) and Burrough and McDonnell (1998), the limit is 50 stations.

Thus, given that we complied with the application conditions and ordinary kriging is one of the best interpolation tool (Li et al. 2011), we were able to perform ordinary kriging whereas other studies often use the inverse of the distance weighting (IDW). The few studies in reef ecology that interpolate benthic community data either use the IDW directly (D'Antonio et al. 2016) or compare the two approaches (Zarco-Perello and Simões 2017; Gómez-Andújar and Hernandez-Delgado 2020). IDW is a non-geostatistical analysis, i.e. the spatial structure is not studied and error assessment can't be calculated (Li and Heap 2008). Finally, in addition to the variance map, interpolation quality can be studied using the results of the cross-validation. All these verifications lead us to affirm that the interpolations produced are of good quality. Even areas difficult to access and therefore less sampled have a low variance (e.g. 2% for live coral cover) and a benthic community that is homogeneous and not very complex (Faure 1982).

Although reef crest and outer reef flat are difficult areas to access and require calm weather for sampling, the data collected are unprecedented for Reunion Island (IFRECOR 2020) because aerial images are blurred by wave scum (Bajjouk et al. 2019). Future development of aerial imagery analyses will provide diachronic data, allowing to identify major changes on benthic population - changes in habitat edges, coral patches, bleaching, etc. (Andréfouët et al. 2002; Scopélitis et al. 2009; Ziskin 2011; Bajjouk et al. 2019). The location of these changes could allow *in situ* spatialisation to better target the areas to be sampled. In addition, the *in situ* data, assessing more biotic compartments, could serve as a database for searching further proxies using aerial images.

Although ordinary kriging is an optimal and unbiased spatial interpolation method (Oyana 2013), its conditions of application remain restrictive and highly dependent on sampling effort. The definition of the sampling plan associated with the field method is therefore an essential step in the application of ordinary kriging. To ensure that the methodological approach developed in this study, which combines a sampling plan, a field method using circular plots and a geostatistical analysis, can be reused in a monitoring network, we had to find a compromise between the station densities to be assessed per reef zone and the level of precision of the interpolation.

Parsimony between sampling effort and spatialisation quality on reef zones

Spatial correlation analyses were used to associate interpolation quality with station densities per hectare for each BBV by comparing parsimonious models with the initial complete model. We can formulate recommendations based on two quality thresholds. The first for "excellent quality" based on the initial sampling effort and the second for "very satisfactory quality". For these two thresholds, we propose respectively monitoring densities of 1.0 station.ha^{-1} and 0.3 station.ha^{-1} for the outer slope and 3.7 stations.ha-1 and 1.0 station.ha-1 for the reef flat, respectively. At the habitat scale, the outer slope is more homogeneous than the reef flat. For an excellent quality threshold, we propose 1.2 station.ha-^{1} for the outer slope and 4.3 station.ha^{-1} for the reef flat respectively. For a very satisfactory quality threshold, we propose 0.5 station.ha^{-1} for the outer slope and 1.5 station.ha^{-1} for the reef flat respectively.

Whether using a BBV or habitat approach, the suggestions for station density are more or less the same. The station density recommendations are based on the mean of all the BBVs or habitats studied, but the details of each BBV or habitat show variability around this mean. As the amplitude of this variation is relatively small, the use of the mean of all BBVs or habitats per zone remains coherent. Under these conditions, a stratified sampling plan, homogeneous within reef zones and differentiated between reef zones, can be designed (Table. 3).

Recommendations must be considered in the light of our knowledge of spatial homogeneity within the reef habitats studied. As Andréfouët and Guzman (2005) point out, habitat heterogeneity provides a better explanation of spatial distribution than geomorphological diversity. Our proposals must therefore be considered in the context of a relatively homogeneous outer slope and a reef flat that is heterogeneous in terms of the studied BBVs. Spatial correlations show that the areas with the lowest correlation coefficients are located close to anthropogenic pressures (e.g. stormwater discharges) or at the boundary between two reef habitats with different benthic compositions (e.g. between a reef flat with transverse stripes and a channel). If these zones are already predefined, a higher station density could be applied. Moreover, the fringing reefs on Reunion Island are recent (Montaggioni 1974). The reef flat is poorly developed with numerous small habitats (Montaggioni and Faure 1980; Nicet et al. 2016) and is subject to strong watershed pressure (Cuet 1989; Tedetti et al. 2020). All these factors combine to produce a highly heterogeneous ecological status (Bajjouk et al. 2019). Older, more developed reefs and less subject to watershed pressure, have a more homogeneous ecological status, which may influence the station densities to be proposed. In general, the station density needs to be considered in the context of each study goal, taking into account human and financial resources, accessibility of the study area and other constraints that may not allow such densities. Based on our study, we can estimate the level of reliability required for different reef areas and habitats (Fig. S3 and S4). These densities are also valid for a fringing reef, with stations close to 100 m².

Table 3

Comparison of sampling effort in terms of station densities, human time and cost between the three cases studied (Optimal Sampling Effort “OSE”, Recommended Sampling Effort according habitat approach with the 0.9 threshold “RSE(0.9)” and 0.7 threshold “RSE(0.7)”. The time required to assess an *in situ* station and set up a database is estimated at 5 minutes. The cost is estimated at 80 USD per hour. However, in the cost estimate, only human time is considered, whereas on the outer slope, boat hire should be added.

Reef zone	Area (ha)	Stations.ha^{-1}			Time (h)			Cost ($)			Cost.ha^{-1} ($.$ha^{-1}$)		
		OSE	RSE (0.9)	RSE (0.7)	OSE	RSE (0.9)	RSE (0.7)	OSE	RSE (0.9)	RSE (0.7)	OSE	RSE (0.9)	RSE (0.7)
Outer slope	401	1.6	1.2	0.5	59	33	17	4,720	2,640	1,360	12	7	3
Reef flat	250	7.6	4.3	1.5	157	90	31	12,560	7,200	2,480	50	29	10

We also emphasize that by representing field values by habitat (choropleth map, Fig. S5), we lose the granularity of interpolations to obtain a landscape vision of the ecological state of a coral reef. However, the habitat map, if it has already been produced, makes it possible to optimize the effort of acquiring *in situ* data. A stratified sampling plan with a predefined station density can be proposed. Interpolations or choropleth maps can then be produced. Where habitat information is not available, a systematic sampling plan may be more appropriate. Thus, depending on the sampling plan defined according to this approach, it becomes possible to move from the mesoscale, useful in particular for areas of high preservation concern, to the macroscale, useful for a landscape vision of a coral reef and the environmental factors that control the spatial distribution of benthic communities (Loiseau et al. 2021; Lutzenkirchen et al. 2024). Thus, the three spatial scales can be studied on a reef unit, moving from the microscale (station scale, Fig. 4 - E1), to the mesoscale achieved by coupling the circular plot and ordinary kriging (interpolation, Fig. 4 – E2) and to the macroscale by averaging field values by habitats (choropleth map, Fig. 4 – E3).

Conclusions, perspectives and limitations

The main novelty of this study was the integration of circular plot with geostatistical techniques to produce reliable interpolation maps of the spatial distribution of nine essential benthic biodiversity variables (BBVs) related to coral reef health. To ensure the accuracy of the results, the sampling effort can be reduced by a factor of 2 for maintaining general reliability, and by a factor of 5 for achieving very satisfactory accuracy. The transition from microscale (station level), mesoscale (interpolation) to macroscale (choropleth map) appears to address the needs of managers, particularly in studying cause-and-effect relationships between environmental pressures and the spatial distribution of the health status of a reef zone. Spatialisation of ecologically sensitive areas can aid public authorities in land-use planning by preventing development near sensitive or vulnerable areas.

Following spatialisation, it may be possible to calculate area ratios and monitor these ratios over time (e.g. calculate the area with more than 50% live coral cover). Given the recommendations on station density, it is feasible to monitor the studied BBVs diachronically, with a fixed sampling plan over time. Additionally, developing indicators based on these BBVs could facilitate tracking their evolution, thereby quantifying and localizing the impacts of human projects. However, distinguishing the drivers of the spatial and temporal distribution of a coral reef's ecological status remains a crucial step for achieving this objective.

We finally emphasize that the recommendations provided should be interpreted for the purposes of locating and quantifying areas of ecological concern, and are not intended for detailed descriptions of benthic populations. The circular plot method is a visual estimation method that can lead to estimation errors, and its accuracy is estimated to be medium to high (Hill and Wilkinson 2004). For such detailed assessments, classical methods (i.e. Line Intercept Transect) are more suitable. Lastly, the use of ordinary kriging requires meeting specific conditions, such as a minimum number of stations in a given area and conducting spatial autocorrelation analysis of the ecological variables studied, which can be restrictive.

Declarations

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Author Contribution

L.B. collected the data, carried out the analyses and drafted the manuscript. M.P. and B.B. provided strong support during the drafting process and made several revisions.M.P., R.C. and T.R. helped with data collection.T.B. provided detailed proof-reading, particularly on the statistical approach to spatialisation.N.N. and E.C. contributed synthesising thoughts, such as the idea in Figure 4, and corrected the English.All authors reviewed the manuscript

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Data Availability

The field data are currently being entered into BD Récif (the national database for coral reef observation and monitoring data under IFRECOR) and the maps produced into Sextant (https://sextant.ifremer.fr/Donnees/Catalogue#/search?isTemplate=n&from=1&to=30&sortBy=dateStamp&sortOrder=desc&languageStrategy=searchInDetectedLanguage&any=UTOPIAN).

Supplementary Information:

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Figures

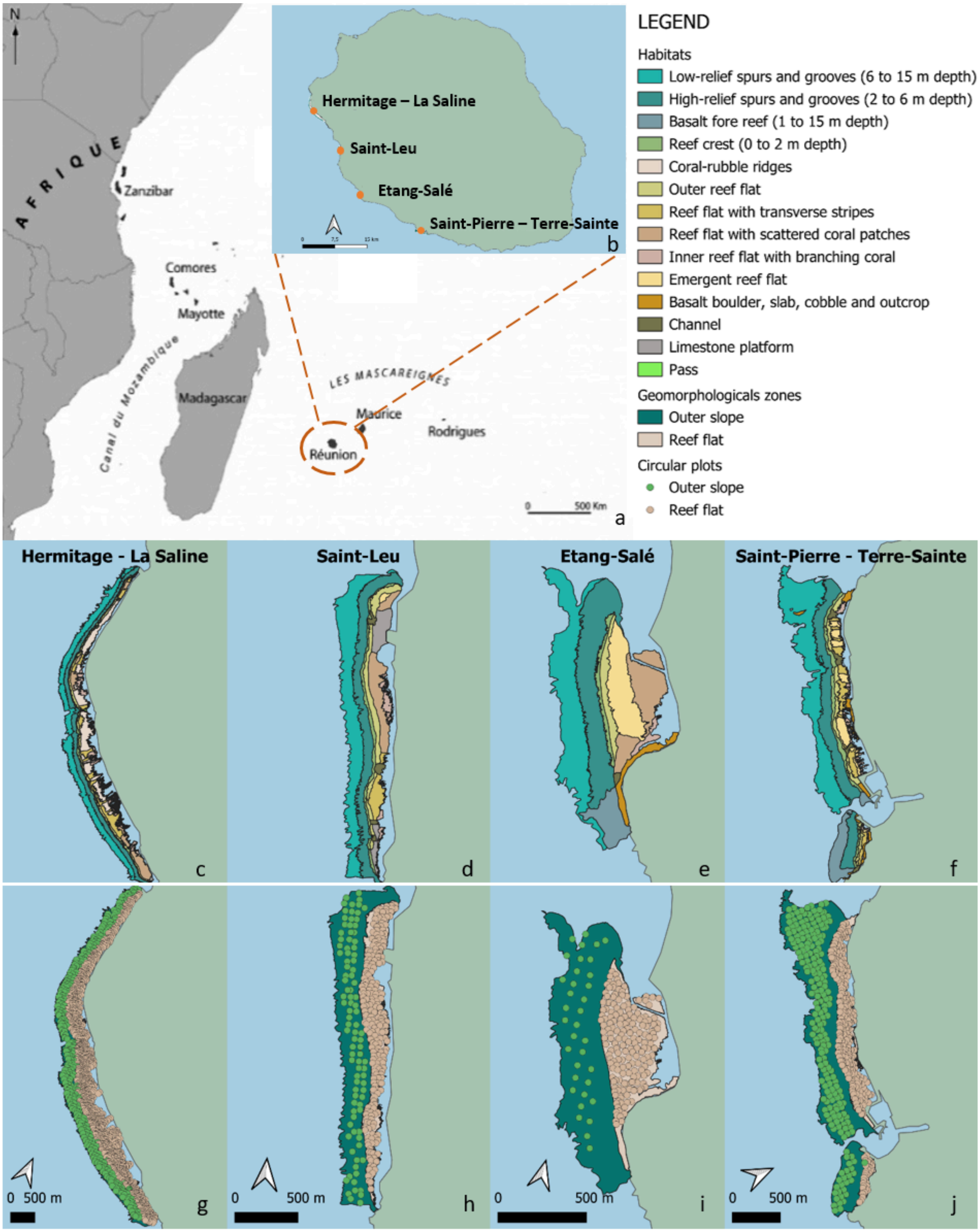

Figure 1

Reunion Island and sampling effort at the four sites according to the 14 habitats defined by Nicet and Andres (in press). a: Location of Reunion Island, b: Location of the four study sites, c to f: Reef habitats of l'Hermitage - La Saline (c), Saint-Leu (d), Etang-Salé (e) and Saint-Pierre - Terre-Sainte (f). g to j: Geomorphological zone and circular plots, with the outer slope in green and the reef flat in pink.

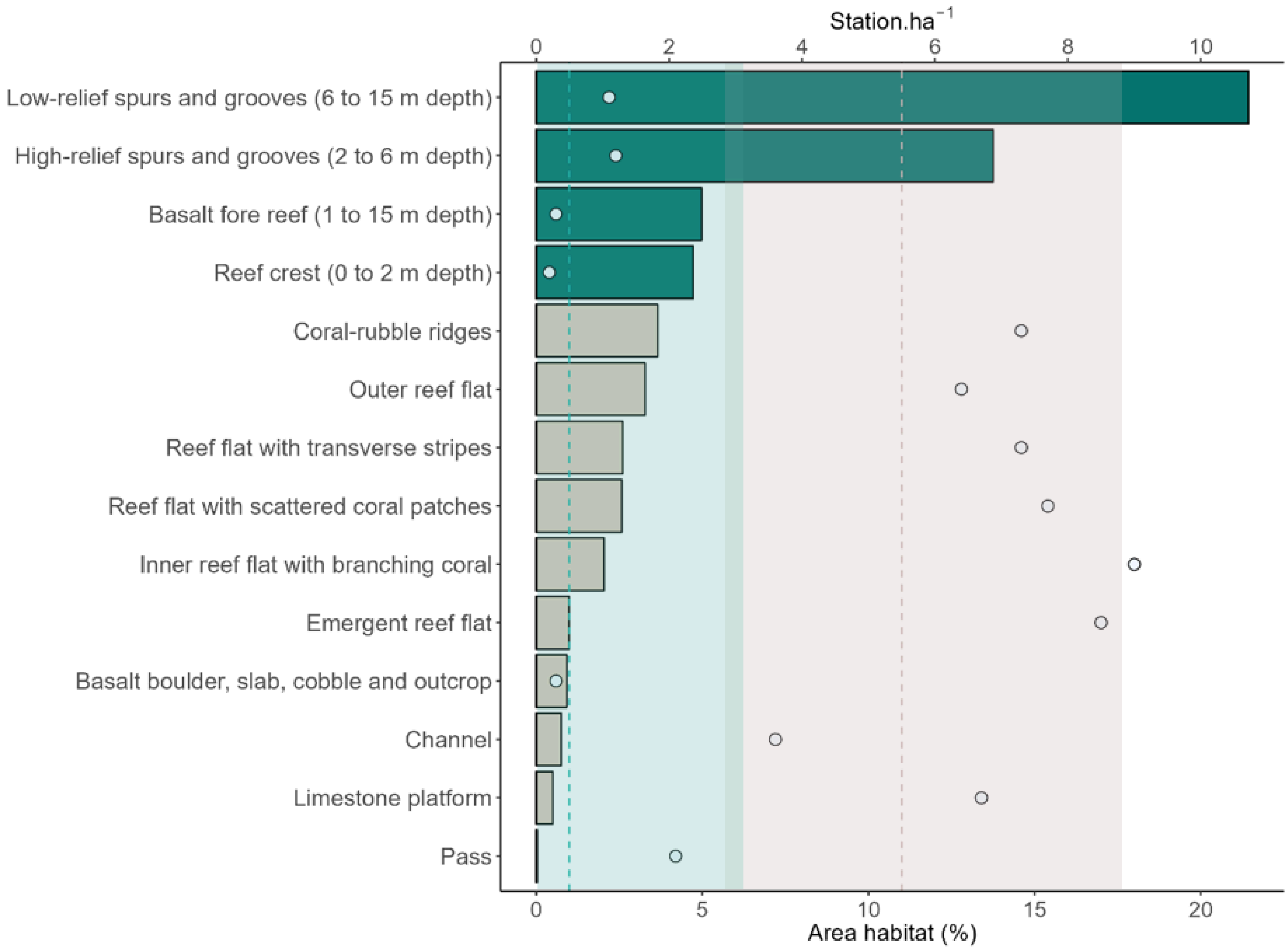

Figure 2

Proportion of area of the 14 habitats (Nicet and Andres, in press) in the study area (green bars: outer slope; gray bars: reef flat) and station density (station.ha-1) in each habitat (dots). Green: outer slope, pink: reef flat. Dotted green line: mean station densities for outer slope habitats; dotted pink line: mean station densities for reef flat habitats. Greenish zone: standard deviation of station densities for outer slope habitats; pinkish zone: standard deviation of station densities for reef flat habitats.

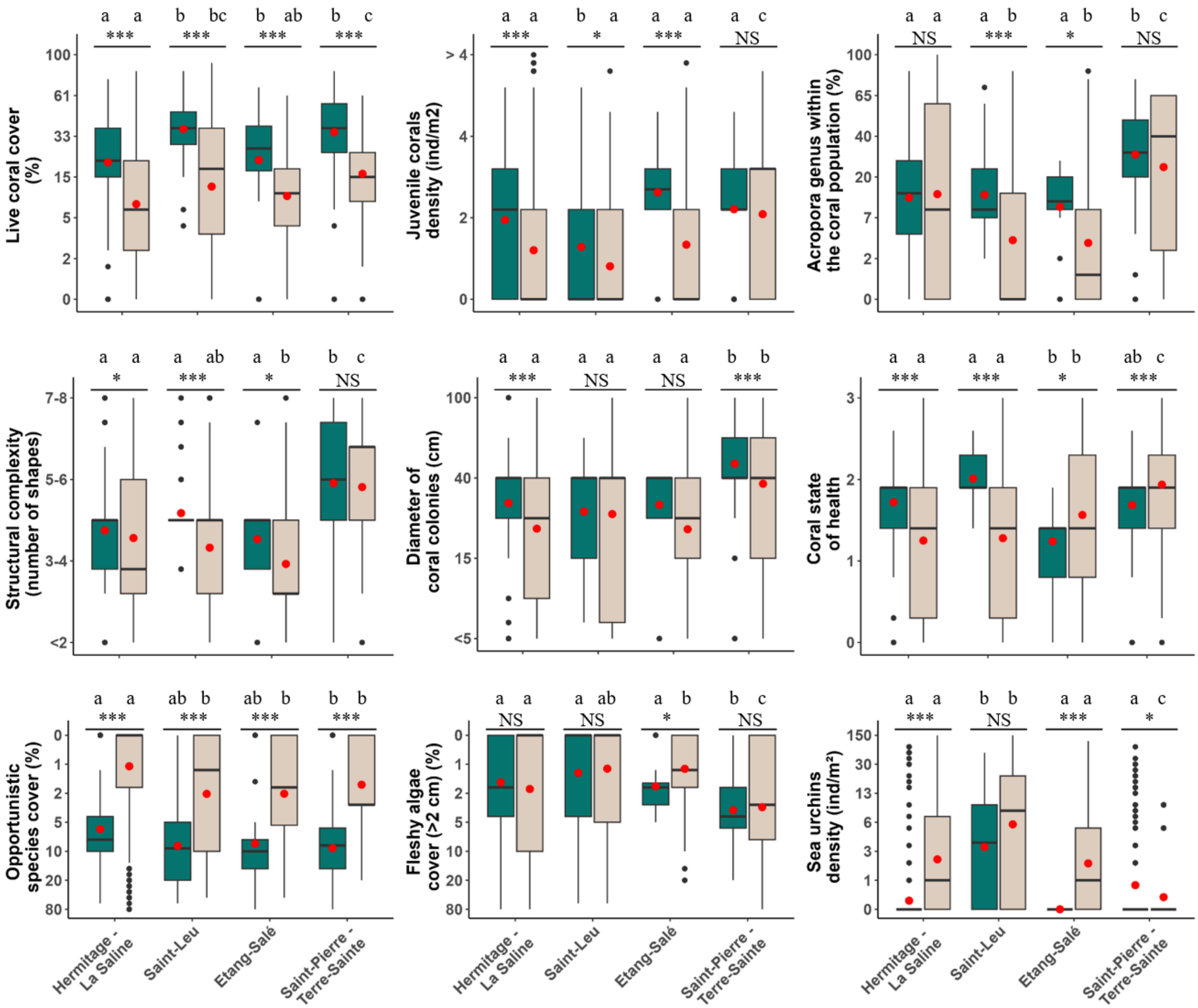

Figure 3

Comparisons of values for each BBV between sites and zones (green: outer slope, pink: reef flat). Red dots represent the mean value per reef zone. Significant differences between sites per zone are represented by a letter (ANOVA tests with Bonferroni corrections, p-value threshold = 0.008). Significant differences between zones per site are represented by an asterisk (NS: p-value > 0.05, *: p-value < 0.05, **: p-value < 0.01 and ***: p-value < 0.001). Coral health assessment 0: dead communities, 1: poor condition, 2: satisfactory condition, 3: very good condition.

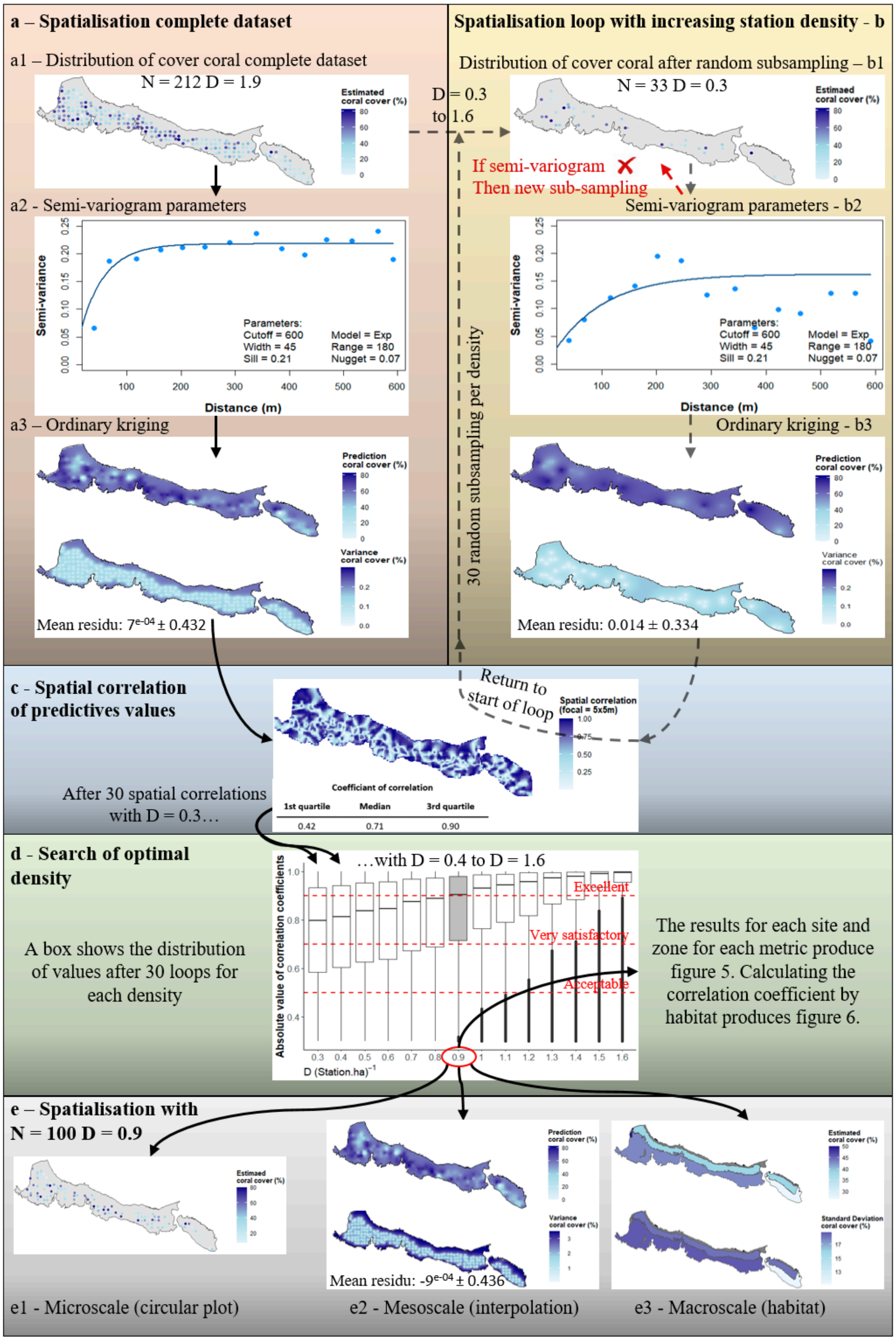

Figure 4

Graphical summary of the coral cover on the outer slope of Saint-Pierre - Terre-Sainte, from the search for optimal station density to the use of spatialisation at different spatial scales. Box a is the reference step. a1: Distribution of coral cover using the complete database (1.9 station.ha^{-1} corresponding to 212 stations). a2: Definition of semi-variogram parameters. These parameters will be used for semi-variograms generated from reduced station densities. a3: Ordinary kriging with predicted and variance values and cross-validation analysis between estimated and predicted values, with mean and standard deviation of residuals tabulated. Box b is a loop, represented by the dotted arrows, repeated 30 times for station densities from 0.3 to 1.6 with a step size of 0.1. b1: Distribution of coral cover with 0.3 station.ha^{-1} (corresponding to 33 stations). b2: Semi-variogram with fixed parameters. Red dotted arrow: if the parameters of the semi-variogram do not follow the distribution of the sub-sampled data, a new sub-sample is generated (step b1) until the semi-variogram is validated. b3: Ordinary kriging. Box c is the spatial correlation step. Each prediction map generated by the loop is spatially correlated with the prediction map generated from the entire database. Box d generates a graph showing the distribution of the correlation coefficient of the 30 spatial correlations for each station density. The three dashed red lines are the thresholds of 0.5 (acceptable), 0.7 (very satisfactory) and 0.9 (excellent). The gray box represents the optimal station density for excellent spatial correlation with the map generated from the complete database. Box e shows the different spatial scales examined from a random sub-sample corresponding to 0.9 station.ha^{-1} (100 stations). e1: Distribution of coral cover with 0.9 station.ha^{-1} (circular plot of 100m²). e2: Ordinary kriging with cross-validation analysis for spatialisation at mesoscopic scale (reef zone). e3: Choropleth map by reef habitat of mean and standard deviation of coral cover for spatialisation at macroscale (reef habitat).

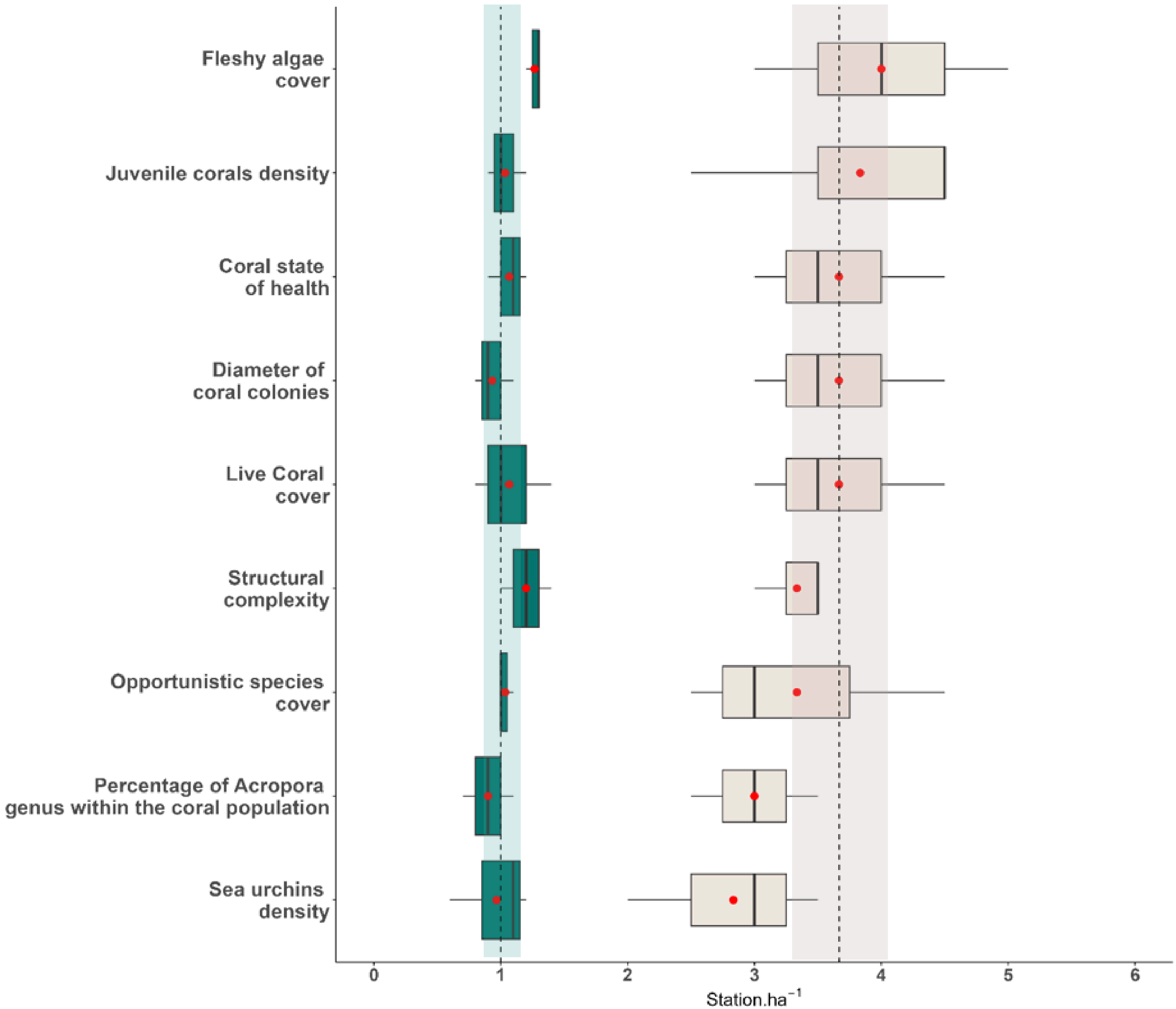

Figure 5

Minimum station densities required to obtain a mean correlation coefficient of 0.9 with the model produced from the complete database for each BBV. Red dots represent the mean value. Green graphs: outer slope; pink graphs: reef flat; dotted lines: mean of station.ha^{-1} per zone for all parameters (greenish zone: standard deviation for outer slope; pinkish zone: standard deviation for reef flat).

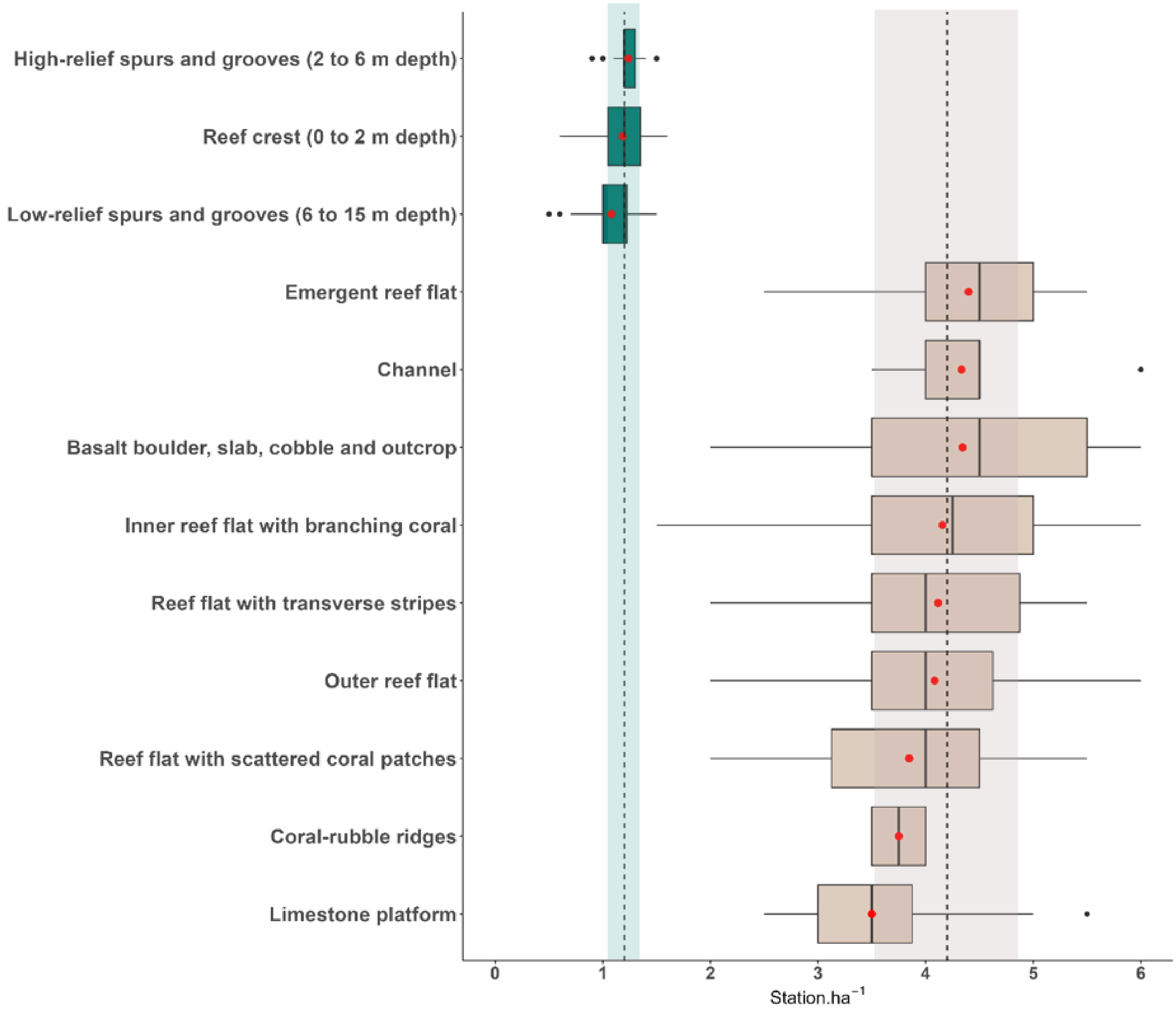

Figure 6

Minimum station densities required to obtain an average correlation coefficient of 0.9 with the model produced on the basis of the complete database for each habitat. Red dots represent the mean value. Green graphs: outer slope; pink graphs: reef flat; dotted lines: mean of station.ha^{-1} per zone for all habitats (greenish zone: standard deviation for outer slope; pinkish zone: standard deviation for reef flat).

Supplementary Files

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