# Assessing key ecosystem functions through soundscapes: A new perspective from coral reefs

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Original Articles

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ABSTRACT

The functioning of tropical coral reefs is imperilled by climate change, overfishing, and decreasing water quality. Maintaining their capacity to provide goods and services will critically depend on our ability to monitor their functioning at appropriate spatial and temporal scales. Given the constraints of traditional methods to respond to those needs, the potential of complementary tools such as Passive Acoustic Monitoring (PAM) is emerging. Coral reef soundscapes (i.e. ambient sound) encompass sounds produced by numerous organisms. Soundscape characteristics quantified by ecoacoustic indices have been found to reflect general ecosystem properties, such as diversity and abundance of fishes, and coral cover. The present study tested, on the virtually pristine coral reefs around Europa Island, South-West Indian Ocean, the capacity of acoustic indices to assess key ecosystem functions. Soundscapes were recorded during 2 h, and ecosystem functions were evaluated using video footage of the fish assemblages and underwater photogrammetry of the benthic landscapes. We found significant and strong correlations between six ecoacoustic indices and six key ecosystem functions, including habitat features and fish assemblage characteristics. The six ecoacoustic indices were representative of several combinations of frequency, amplitude and time analysis domains, highlighting the diversity of the functional information conveyed by soundscapes. Our findings reveal that a 2 h daytime recording on a coral reef could provide sufficient acoustic information to characterise major ecosystem functions of a site. This should facilitate the detection of functional disturbances at temporal and spatial scales adapted to the rapidity of upcoming climate changes. Our results also highlight the potential of ecoacoustics to bring novel and relevant insights in the functioning of ecosystems.

## 1. Introduction

In the context of worldwide ecological disruption and decline of coral reef ecosystems (Hughes et al., 2017), conservation strategies presently focused on the preservation of biodiversity should integrate the identification and maintenance of the ecosystem functions that are crucial for sustaining coral reefs (Hughes et al., 2017; Bellwood et al., 2019). Also, notwithstanding the utmost importance of conserving marine biodiversity, it is critical to secure the services that even altered reef ecosystems can continue to provide to humans in the future (Hughes et al., 2017). These benefits mostly rely on ecosystem

functioning which is particularly imperilled by climate change, but also by local pressures like fishing and decreasing water quality (Bellwood et al., 2012; MacNeil et al., 2015; Harborne et al., 2016). Thus, maintaining productive coral reefs will depend on our ability to rapidly detect functional disturbances and losses across multiple spatial scales, and respond in a time-effective manner with locally-adapted conservation measures involving human interventions (Hughes et al., 2017; Hoegh-Guldberg et al., 2018). A first issue to solve is the deficit of operational methods and indicators for monitoring ecosystem functions. These should be simultaneously: i) well correlated to the functions evaluated; ii) easy to understand for management applications; iii)

rapid to assess and reliable; iv) replicable across multiple spatial and temporal scales.

In this study, we considered that an ecosystem function was "the movement or storage of energy or material within an ecosystem" as defined by Bellwood et al. (2019); we focussed on the key functions identified by Harborne et al. (2016) in their review: corals, algae, habitat complexity, plankton, invertebrates, plankton feeders, herbivores, and tertiary consumers.

As primary ecosystem engineers, scleractinian corals directly control processes as diverse as providing habitat for associated reef organisms, generating sand and promoting the recycling of organic matter (Wild et al., 2011). Darling et al. (2012) consider coral growth form as one of the most important coral life history traits, determining the ecological functions fulfilled by corals (Bellwood et al., 2019). This implies that the functional characteristics of coral communities strongly depend on the relative abundance of the different coral growth forms present (González-Barrios and Álvarez-Filip, 2018). The diversity of coral growth forms, more than total live coral cover *per se*, also determines habitat complexity (Darling et al., 2017; González-Barrios and Álvarez-Filip, 2018) which is a strong predictor of the taxonomic and functional structure of fish (e.g. Graham and Nash, 2013; Darling et al., 2017) and invertebrate assemblages (Idjadi and Edmunds, 2006), as well as the recruitment of fish species (e.g. Pratchett et al., 2008). Like corals, fleshy algae partake in bio-chemical cycles and play a significant role in shelter provision and habitat choice for reef organisms (Afeworki et al., 2013; Fulton et al., 2019). Growing faster, they permanently compete with corals for space, inducing a dynamic spatio-temporal equilibrium between coral-dominated states and states dominated by macroalgae (Hughes et al., 2017; Fulton et al., 2019).

Fish grazing on hard substrates, and particularly parrotfishes, contribute to four main benthic ecosystem processes: removal of algae, external bioerosion, coral predation and redistribution of sediments (Bellwood et al., 2012). Most, but not all of grazing fishes are herbivores. We chose "grazers" as a generic term, even if this word may designate a more restricted group of herbivorous fishes (Green and Bellwood, 2009). By capturing zooplankton, planktivores introduce and sequester nutrients from both oceanic and lagoon ecosystems to the reef food web (Hamner et al., 2007), while tertiary consumers are essential for food web stability (Bascompte et al., 2005).

These ecosystem functions can be evaluated by traditional survey methods such as underwater visual census, photography and video footage, which produce both detailed (i.e. to species level) and quantitative assessments (i.e. substrate cover, abundance and biomass of mobile organisms). However, such surveys are limited in spatial and temporal coverage as they require high amounts of expert time in the field and for analysis, involving logistical constraints and elevated costs. Moreover, the presence of divers and variations of visibility can introduce sampling biases (Emslie et al., 2018), while Bellwood et al. (2019) argue that ecosystem functions are likely to be significantly underestimated using visual census. For these reasons, traditional methods should be combined with other tools to implement time and spatially efficient monitoring networks.

Passive Acoustic Monitoring (PAM) has great potential to help responding to the current marine conservation challenge. In fact, it requires low sampling efforts (Elise et al., 2019), and can be implemented from the surface without specific technical skills (e.g. Kennedy et al., 2010), using recorders moored on the seafloor (e.g. this study) or drifting buoys (e.g. Lossent et al., 2017), drastically reducing human costs and avoiding monitoring biases due to divers' presence. In addition, sampling schemes can be repeated identically across multiple spatial and temporal scales and the fully digital raw data produced can be easily compared among localities, stored, exchanged, and re-analysed when needed (Gibb et al., 2019).

By recording ambient sound on a site (i.e. the soundscape), PAM captures a multitude of soniferous activities (feeding, courtship, spawning, defence, escape, etc.), some of which are intimately related with ecosystem functions (e.g. parrotfishes scraping the substrate). As such, PAM could be a particularly relevant tool to assess these functions. While cataloguing and automatic classification of the sounds produced by individual species have made considerable progress over the last decade (see Tricas and Boyle, 2014; Ibrahim et al., 2018), Gibb et al. (2019) argue that this approach may be best suited to species-focused assessments rather than broader scope ecological monitoring, for which they recommend the use of ecoacoustic indices, especially in highly diverse ecosystems.

A suite of such indices has been developed to evaluate global ecological features through ecosystems' soundscapes (e.g. Sueur et al., 2014). These indices have been shown capable of reflecting differences in species richness, phylogenetic diversity, or ecological state (see Gasc et al., 2017 for terrestrial examples; Lindseth and Lobel, 2018 for marine examples). On coral reefs, amplitude (estimated by either Sound Pressure Level -SPL- or Power Spectral Density -PSD-) and Acoustic Complexity Index (ACI; Pieretti et al., 2011) have been the mostly used acoustic indices. High values of these indices in the lower frequencies (< 1 kHz) indicate diverse and abundant reef fish assemblages, high coral cover and richness, high crustose coralline algae cover, high structural complexity or high density of mobile macro-invertebrates (Kennedy et al., 2010; Kaplan et al., 2015; Bertucci et al., 2016; Freeman and Freeman, 2016; Staaterman et al., 2017). Conversely, elevated levels of these indices in the higher frequencies (> 2 kHz) usually indicate more degraded ecological states, with high dead coral cover (Nedelec et al., 2015), abundant photosynthetic macroalgae (Freeman and Freeman, 2016; Freeman et al., 2018) and high densities of snapping shrimps, which are the dominant sound producers of higher frequencies (e.g. Radford et al., 2014; Kaplan et al., 2015; Lillis and Mooney, 2018). The ecoacoustic indices that have been developed hitherto on coral reefs are more oriented towards ecological state assessments than to monitoring functions. Apart from Freeman and Freeman (2016) and Freeman et al. (2018), who highlighted indices correlated with habitat complexity and macroalgal photosynthetic activity, respectively, we found no study describing links between explicitly identified ecosystem functions and ecoacoustic indices calculated from soundscape recordings, whereas this potential has been emphasized by Blumstein et al. (2011) and Gasc et al. (2017).

The main objective of the present study was to evaluate the potential of Passive Acoustic Monitoring to reliably identify and evaluate specific key ecosystem functions, based on a coral reef study. We examined correlations between key functions assessed by imagery and a suite of acoustic indices, including some that have not been used in the marine realm to date. To focus strictly on the relationship between biophony and ecosystem functions, we conducted this study on the nearly pristine coral reefs of Europa Island (Fig. 1), an isolated no-take area where anthrophony would not affect the recordings. In addition, soundscapes were recorded under particularly quiet conditions in terms of waves, wind and rain, to minimise the influence of geophony.

## 2. Material and methods

### 2.1. Study area

In April 2018, we conducted image-based ecological surveys and acoustic recordings at nine sites on the slopes of Europa Island's fringing reefs, in the southern Mozambique channel (Fig. 1). Europa Island is a near-pristine and isolated atoll (about 300 km from the nearest shore of Madagascar), whose access has been restricted by military presence for almost 50 years, and protection by statute (no-take area) for over 20 years (Chabanet et al., 2016). Its coral reefs comprise a planar area of 18 km², characterised by an exceptionally high biomass of fishes, including sharks, high live coral cover, locally exceeding 80%, and low algae cover (Chabanet et al., 2016). The presence of large piscivores, herbivores and large schools of planktivores, as well as the contrasts in fish assemblages and benthic communities
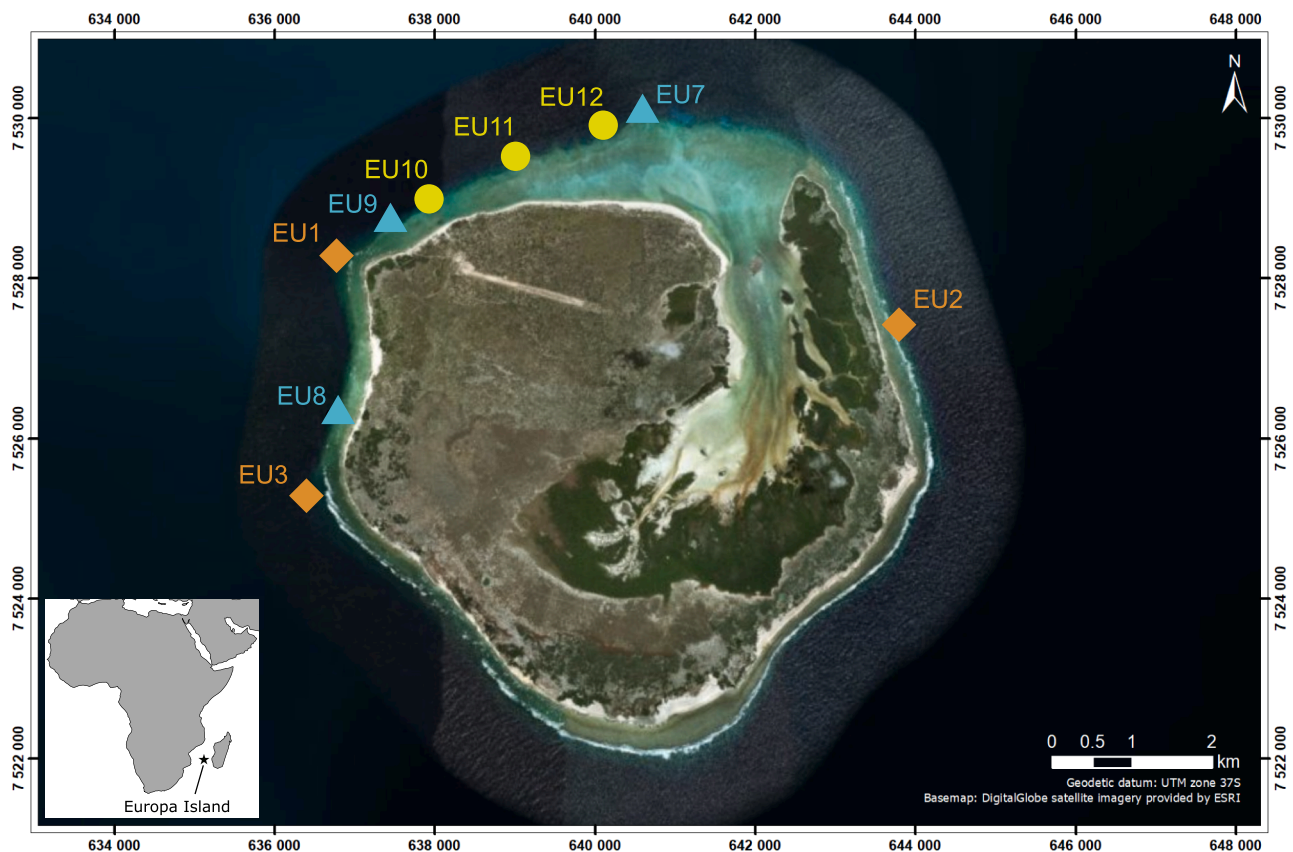
**Fig. 1.** Location of the nine sites sampled on the outer reef slopes of Europa Island. Orange diamonds (EU1, EU2, EU3) indicate gentle slope sites exposed to wave action; yellow circles (EU10, EU11, EU12) correspond to sheltered gentle slope sites; blue triangles (EU7, EU8, EU9) correspond to steep slope sites.

among sites reported by Chabanet et al. (2016) were of particular interest for our study. All sites were between 10 and 15 m depth, and were selected to reflect the diversity of reef slope habitats found around Europa Island (Fig. 1 and Table S1):

- EU1, EU2, EU3: exposed sites with gentle slopes and high cover of living substrate (> 50%);
- EU7, EU8, EU9: sites with steep slopes and high cover of living substrate (> 50%);
- EU10, EU11, EU12: sheltered sites with gentle slopes and relatively low cover of living substrate (< 45%).

### 2.2. Evaluation of key ecosystem functions

#### 2.2.1. Benthic functions

At each site, a pair of divers carried out an image acquisition procedure designed to cover an area of 150 m$^2$ (15 × 10 m). Each diver was equipped with a Sony Alpha 7II camera with Sony FE16-35 mm F4 lens in a Nauticam NA-A7II housing and 180 mm glass dome port. Photographs were taken while swimming in a boustrophedonic pattern 3 m above the substrate with cameras pointing downwards. Additional pictures were taken closer to high-complexity landscape components to capture parts that were invisible from above. Depth of eight ground control points placed across the surveyed area was measured with a dive computer, while their geographical coordinates were recorded with a GPS at the water surface, allowing to orient and georeference the site. Three scale bars were placed in the area for accurate scaling during photogrammetric processing. Depending on topography and structural complexity, between 500 and 1300 images were taken at each site.

A three-dimensional model of each site was constructed by photogrammetry using Pix4Dmapper Pro software (v4.2.26). The spatial resolution of the models (i.e. the ground sampling distance – GSD) was < 1 cm. Orthomosaics (geometrically rectified photographic projection) and Digital Surface Models (DSM; projection of the bottom elevation) were exported from the 3D models in order to evaluate different coral growth form covers and habitat complexity. Prior to analyses, the orthomosaics and DSMs were clipped to a plane area of exactly 150 m$^2$ in Global Mapper v19.0 software (Blue Marble Geographics, 2018). Three-dimensional surface was computed from the DSM with the "Surface Volume" tool (3D Analyst Extension) in ArcGIS 10 (ESRI, 2018). Habitat complexity was calculated as the ratio of 3D surface to 2D surface (i.e. 150 m$^2$).

Cover of seven different coral growth forms (Table S1; Veron, 2000) was estimated on the orthomosaic. Individual live coral colonies were delineated as polygons and the area of each polygon computed in QGIS (QGIS Development Team, 2018). Polygons were classified according to growth form, their areas summed and converted to percentage of total surface area. For simplicity, we focussed on the two most contrasting forms (i.e. suggesting contrasting functions) that were well represented in the benthic communities across the study sites (Table S1): i) encrusting and ii) laminar, foliose, helmet-shape (LFH) corals. Three "benthic functions" were thus considered: encrusting corals, LFH corals and habitat complexity.

#### 2.2.2. Fish functions

Video footage was used to evaluate the diversity, abundance and biomass of fish assemblages at each site (e.g. Myers et al., 2016). Stereo-cameras (two GoPro cameras, San Mateo, USA) affixed 50 cm above the substrate filmed during 90 min. Cameras were oriented so that footage captured half substrate and half the water column above. We identified individual fish and estimated an index of abundance and biomass for each species, using the software EventMeasure (SeaGIS,

**Table 1**

List of the six key ecosystem functions considered in this study (from Harborne et al., 2016) and the twelve corresponding variables tested. DIV: diversity; ABUND: abundance; Log BIOM: natural logarithm of biomass.

| Key ecosystem function | Variable tested |
|---|---|
| Encrusting corals | Encrusting coral cover |
| Laminar, foliose, helmet-shape (LFH) corals | LFH coral cover |
| Habitat complexity | Habitat complexity |
| Herbivores | Grazers (DIV) |
| | Grazers (ABUND) |
| | Grazers (Log BIOM) |
| Planktivores | Planktivores (DIV) |
| | Planktivores (ABUND) |
| | Planktivores (Log BIOM) |
| Tertiary consumers | Tertiary consumers (DIV) |
| | Tertiary consumers (ABUND) |
| | Tertiary consumers (Log BIOM) |

Bacchus Marsh, Australia). The maximum abundance "MaxN" for a species was calculated as the maximum number of individuals of this species that can be observed on a single frame of the footage. Size of these individuals was measured, and their biomass evaluated, to calculate the maximum biomass "MaxB" of this species. Diet and size class, based on maximum recorded total length (FishBase, 2018), were compiled for each species.

Diversity, abundance and biomass (logarithm) were calculated for three functions: grazers, planktivores, and tertiary consumers. Grazers included the scrapers/small excavators and grazers/detritivores species described in Green and Bellwood (2009). Planktivores were defined relying on species diet only. Tertiary consumers were defined as piscivorous and mobile invertebrate feeding species whose maximum recorded total length is > 50 cm. Species corresponding to these three functions are indicated in Table S2. As these functions can be considered alternatively in terms of diversity, abundance or biomass, each fish function was initially represented by three variables in our analyses.

Among the key functions highlighted by Harborne et al. (2016), algae, plankton and invertebrates could not be assessed. Indeed, the orthomosaics generated by photogrammetry are not well suited to assess algal abundance, while due to logistical constraints we could not assess plankton and invertebrate abundances. Hence our study focussed on six key functions represented by twelve variables (Table 1).

### 2.3. Evaluation of coral reef soundscapes

Underwater soundscapes were recorded using a TC 4014–5 omnidirectional hydrophone (linear Frequency range: 30 Hz to 100 kHz ± 2 dB; sensitivity: − 186 dB re 1 V μPa$^{-1}$; RESON, Slangerup, Denmark) fixed to a large aluminium tripod and connected to an acquisition chain (preamplifier with gain set at 20 dB, acquisition card, and PC inside a waterproof container) designed by NORTEKMED S.A.S (Toulon, France). The hydrophone was fixed at the top of the tripod (approx. 1.5 m above the substrate), facing downwards to reduce the capture of ambient sea surface noise. The tripod was tied to the reef to prevent any movement during acoustic recordings. The recording system was calibrated with a Brüel & Kjaer 4229 hydrophone calibrator (Nærum, Denmark), and programmed to record continuously at a sampling rate of 100 kHz and 16 bits-depth, providing an analysis range of 0–50 kHz.

At each site, soundscape was recorded for a minimum of two hours between 9:30 am and 3:30 pm, a time slot identified to present relatively constant reef organisms' activities (e.g. Myers et al., 2016), as well as stable soundscapes (Elise et al., 2019). Sound recordings were performed at the same sites where benthic habitat was assessed, simultaneously to video footage assessing fish assemblages, with no divers present in the vicinity of the video or audio recording systems. Sound recording malfunction necessitated resampling four sites in the days following the video footage of fish assemblages. Given the short-term stability of soundscapes and biological activities we consider that this inconvenience did not jeopardize the validity of the study.

The continuous acoustic recording from each deployment was divided into 5 min samples, a duration that we found adapted to coral reef soundscapes' analyses in a previous study (Elise et al., 2019). Each acoustic sample was individually inspected using spectrograms, and also listened to when necessary, to eliminate samples containing wave or boat noise, or noise of animals probing the hydrophone. Spectrograms were visualised using a software developed by NORTEKMED S.A.S (FFT size 131,072 points, no overlap, hamming window; rms of SPL are calculated for each second to be displayed). Due to favourable meteorological conditions, only very few samples were eliminated. Twenty-four "clean" 5 min sound samples (.wav) were available for all sites except two (EU1 and EU12, twenty-three samples per site).

For each sample, we calculated three ecoacoustic indices commonly used in marine studies (SPL, H and ACI) and three less known indices (BI, sh and th) (Table 2). SPL was computed with a software developed by NORTEKMED S.A.S (Toulon, France); H, ACI, sh and th were calculated using R package 'seewave' (Sueur et al., 2008), and BI was calculated using R package 'soundecology' (Villanueva-Rivera and Pijanowski, 2016). See Supporting Information for details on the calculation of these acoustic indices. Apart from SPL which measures sound amplitude, these indices evaluated the acoustic diversity of a site in various ways.

While several studies on coral reefs have considered relatively wide frequency bands for indices calculations (i.e. 0–1 or 0–2 kHz versus > 2 kHz; e.g. Bertucci et al. 2016; Staaterman et al., 2017), others have focussed on more limited bandwidths (e.g. Kennedy et al., 2010; Kaplan et al., 2015; Freeman and Freeman, 2016). The results of these studies suggest that the key functions targeted in the present

**Table 2**

List of the acoustic indices calculated (more details in Sueur, 2018).

| Sound-analysis domain | Acoustic index | Definition |
|---|---|---|
| Frequency - amplitude | Sound Pressure Level (SPL) | Ratio of the absolute local sound pressure (caused by a sound wave) and the reference level (P*ref* underwater = $10^{-6}$ Pa) on a logarithmic scale (in dB), between two frequency limits |
| | Bioacoustic Index (BI) | Area under the curve of the dB mean spectrum between two frequency limits |
| | Spectral entropy (sh) | Shannon evenness of the frequency spectrum. sh was converted to spectral variability (sv) with the relation sv = 1 – sh |
| Time - amplitude | Temporal entropy (th) | Shannon evenness of the amplitude envelope. th was converted to temporal variability with the relation tv = 1 – th |
| Frequency - time -amplitude | Acoustic entropy index (H) | Multiplication of sh by th |
| | Acoustic Complexity Index (ACI) | Measure of the complexity of Short-time Discrete Fourier Transform matrix, giving more importance to sounds that are modulated in amplitude and, hence, reducing the importance of sound with a rather constant amplitude |

study (Table 1) may be related with acoustic activities below 1 or 2 kHz. For completeness, each of the six indices was calculated on five bandwidths: 0.1–0.5 kHz; 0.5–1 kHz; 1–2 kHz; 2–7 kHz; and the full bandwidth 0–50 kHz. Reef organisms' acoustic activities have been reported below 0.1 kHz (see e.g. Lobel et al., 2010). However, the 0–0.1 kHz band is heavily subject to perturbations by waves – even under globally calm conditions - or commercial shipping, as these low frequencies propagate over long ranges (Hildebrand, 2009). Hence, we excluded frequencies below 0.1 kHz from our analyses.

We thus examined 30 different acoustic combinations (six indices × five bandwidths) in this study. Each index was averaged across the twenty-four 5 min samples available to obtain a single value for each site.

### 2.4. Statistical analyses

All statistical analyses were performed with R software (Version 3.5.0, R core Team 2018), with all tests at 0.95 significance level.

We first visualised the functional differences among the nine sites with three Principal Component Analyses conducted on the variables representing ecosystem functions.

We then examined the correlations among the twelve variables representing the six ecosystem functions (Table 1) and the 30 acoustic combinations. For each "benthic function", we retained the best correlated acoustic index (i.e. with the highest significant Pearson correlation coefficient). For each "fish function" (i.e. grazers, planktivores, tertiary consumers), we retained the highest coefficient amongst

diversity, abundance or biomass. We thus obtained six ecosystem function-acoustic index associations.

Values of the six functions on the one hand, and the six acoustic indices on the other hand, were visualised with a radar plot for each site. Radar plots of ecosystem functions and acoustic indices were superimposed. As a radar plot surface area depends on the order of the vertexes of the polygon, we calculated the mean surface area obtained across all possible permutations. We finally compared the mean plot area values for functions and acoustic indices to evaluate the potential of the suite of acoustic indices to reflect general ecosystem functioning.

## 3. Results

The sites revealed marked differences in their functional aspects as evaluated with the six key functions (Fig. 2 and Table S3), corresponding to three different habitat types. Results were consistent regardless whether "fish functions" were considered in terms of diversity, abundance or biomass (Fig. 2). Exposed gentle slopes were characterised by higher encrusting coral cover and lower habitat complexity, while sheltered gentle slopes presented lower LFH coral cover. All key ecosystem functions values except encrusting coral cover were higher on the steep slopes sites (Fig. 2).

A comparison of two 5 min sound samples, representative of the soundscapes of the most functionally contrasted sites EU3 and EU7 (Fig. 2), illustrates how acoustic characteristics may differ among sites. In this example, global sound energy was higher at the gently sloping site EU3 (Fig. 3A and D), but spectrograms and frequency spectra
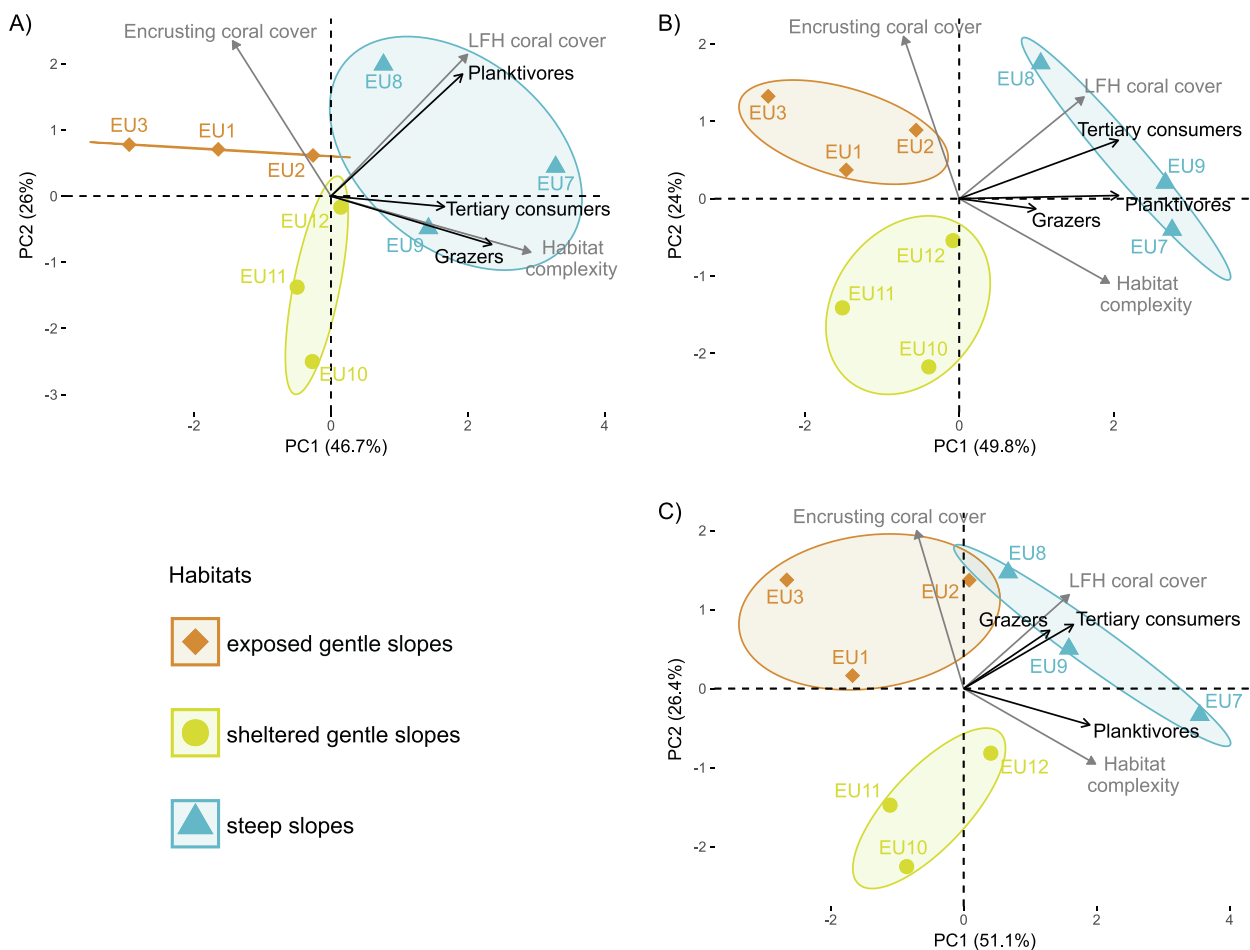


**Fig. 2.** Principal Component Analyses performed on the six ecosystem functions with fish functions considered: A) in diversity; B) in abundance; C) in biomass (logarithm). LFH: laminar, foliose, helmet-shaped. Confidence ellipses at 0.95 significance level are indicated, i.e. ellipses would include 95% of the observations.
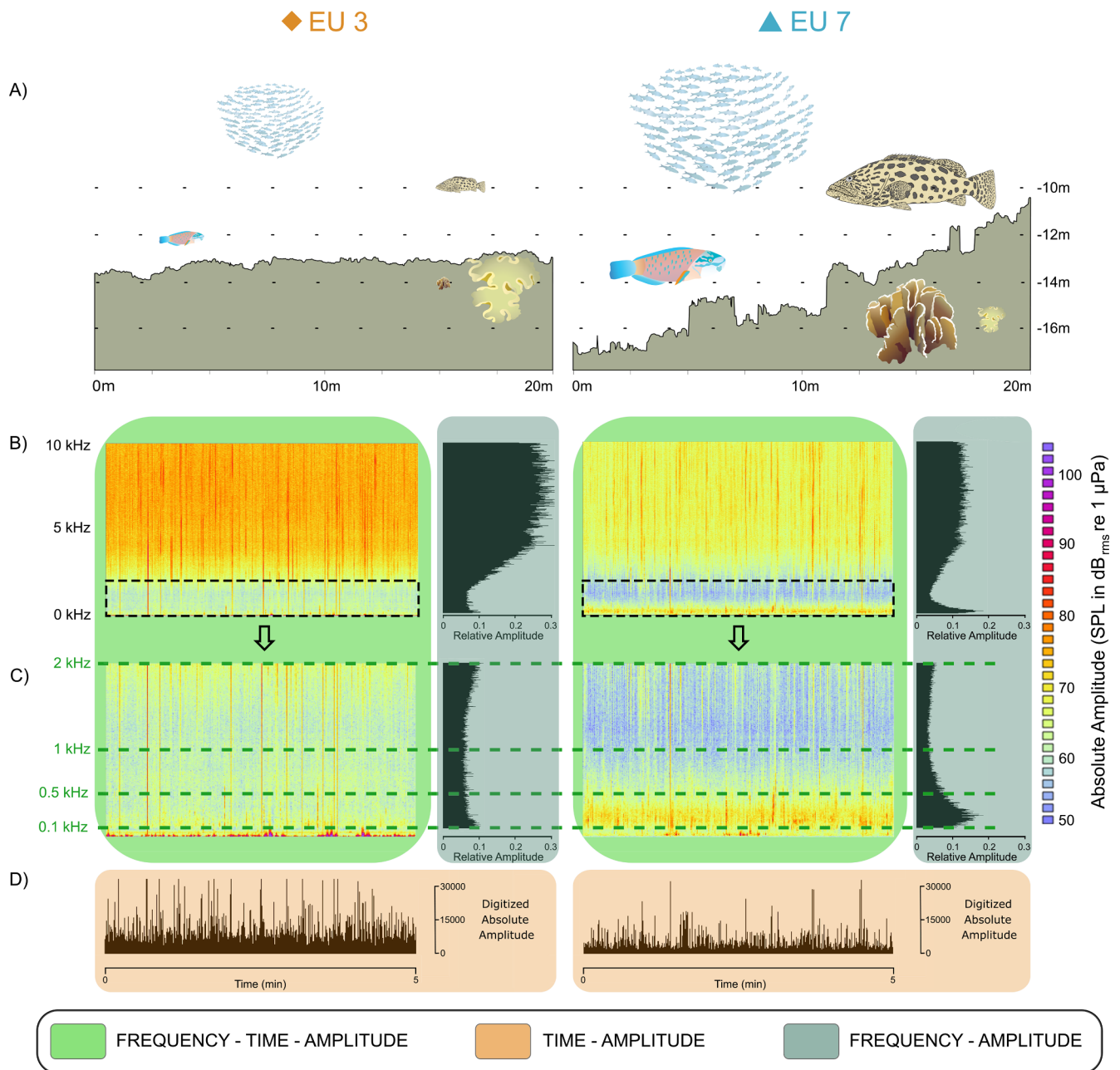
**Fig. 3.** Key ecosystem functions and associated soundscapes at two contrasted sites (EU3 and EU7). A) Habitat complexity profile and the other five key functions. The size of icons is proportional to the function represented (encrusting coral cover, LFH coral cover, log biomass of planktivores, log biomass of grazers, abundance of tertiary consumers); B) Spectrogram and corresponding frequency spectrum shown for the 0–10 kHz bandwidth to highlight site contrasts; C) Spectrogram and corresponding frequency spectrum for the 0–2 kHz bandwidth; D) Amplitude envelope. Icons courtesy of Joanna Woerner, Dieter Tracey, Kim Kraeer, Lucy Van Essen-Fishman, and Tracey Saxby (Integration and Application Network of the University of Maryland Center for Environmental Science, http://ian.umces.edu/imagelibrary/).

revealed that this energy was mostly contained in the higher frequency band (> 2 kHz) (Fig. 3B). In contrast, the steeply sloping site EU7 exhibited more energy than EU3 in the lower frequency bands (0.1–0.5 kHz, and, to a lesser extent, 0.5–1 kHz; Fig. 3C). Frequency spectra (Fig. 3B) also revealed that energy was more balanced between low and high frequency bands at EU7 than at EU3, the latter presenting higher spectral variability (Fig. 3B).

Several acoustic indices were able to detect these types of contrasts among soundscapes. The highest correlation coefficients between acoustic indices and ecosystem functions across the nine sites were obtained for acoustic indices encompassing the three sound-analysis domains, on various bandwidths (Table S4 and Fig. 4):

- Frequency-amplitude: SPL 0.1–0.5 kHz; bioacoustic index 0.5–1 kHz; bioacoustic index 1–2 kHz, spectral variability 0–50 kHz
- Time-amplitude: temporal variability 0–50 kHz
- Frequency-time–amplitude: ACI 1–2 kHz

Values of spectral variability 0–50 kHz, and temporal variability 0–50 kHz were significantly different among the three habitat types (Fig. 5). Values of bioacoustic index 1–2 kHz, and ACI 1–2 kHz were similar among sheltered and exposed gently sloping habitats, whereas values of SPL 0.1–0.5 kHz, and bioacoustic index 0.5–1 kHz significantly differed among these habitat types (Fig. 5).

The simultaneous assessment of the six ecoacoustic indices provided
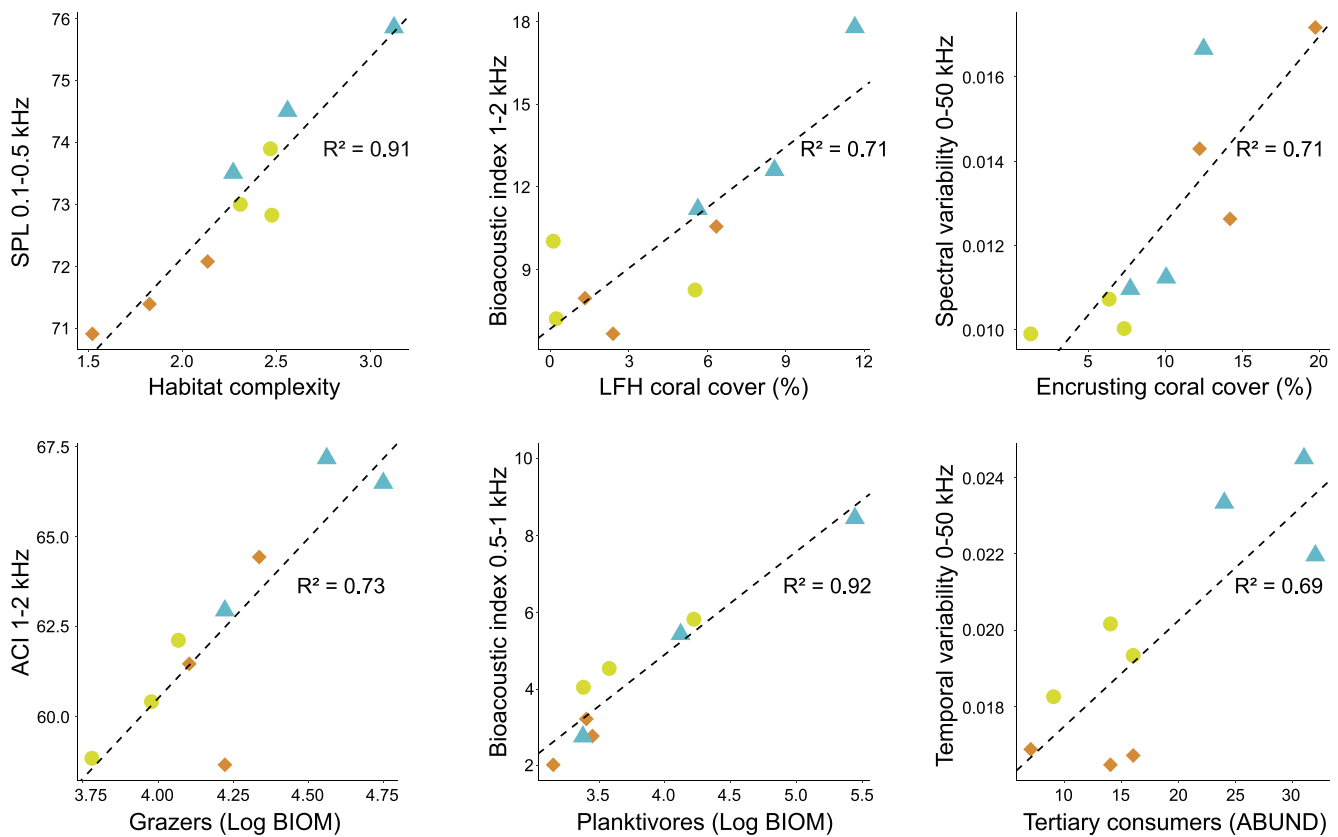
**Fig. 4.** Graphical representations of the highest correlations found between acoustic indices and ecosystems functions. SPL values are in dB$_{rms}$ re 1μPa, the other indices have no units. Orange diamonds (EU1, EU2, EU3) indicate gentle slope sites exposed to wave action; yellow circles (EU10, EU11, EU12) correspond to sheltered gentle slope sites; blue triangles (EU7, EU8, EU9) correspond to steep slope sites.
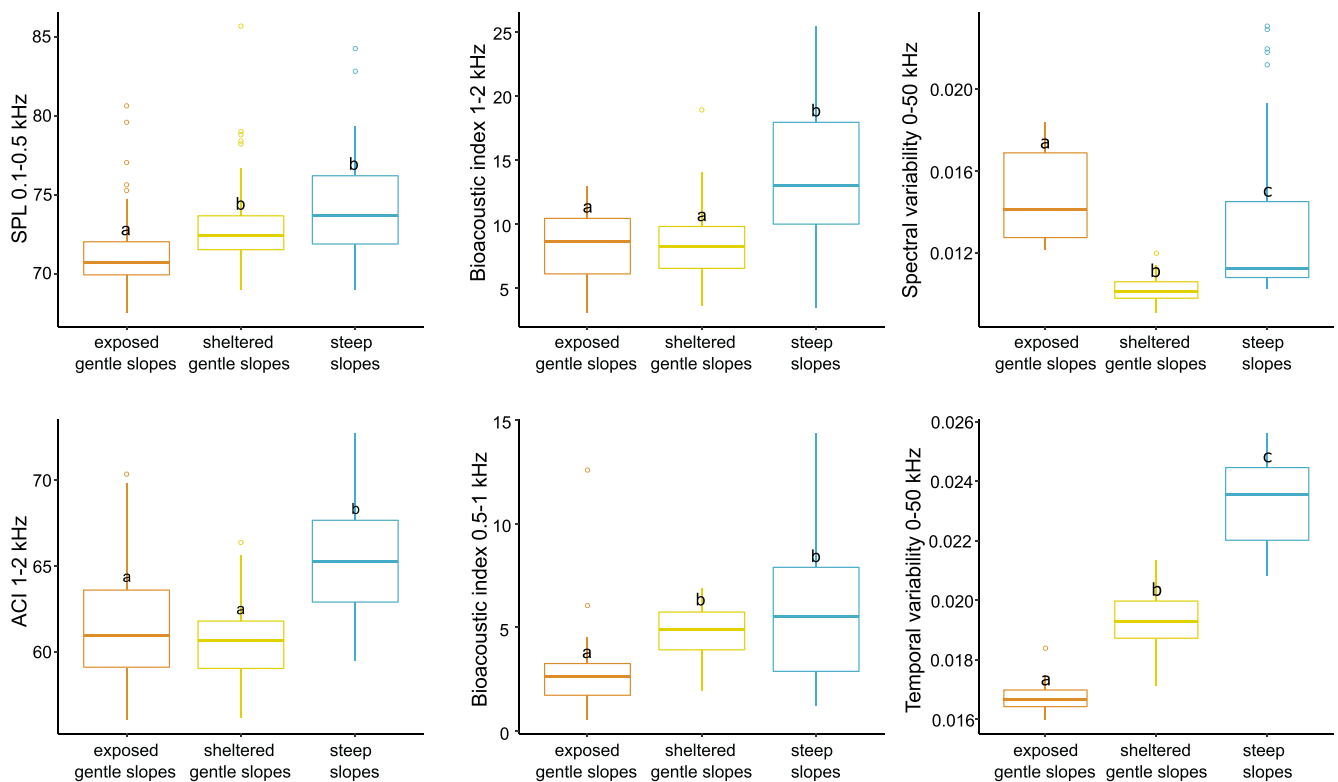


**Fig. 5.** Boxplots showing the values of the six selected ecoacoustic indices for the three habitats (n = 72 for each habitat type). Effects of habitat type was tested using Kruskal-Wallis and corresponding post-hoc tests, as the assumption of parametric tests were not met. Significant differences (p < 0.001) among habitats are indicated with different letters.
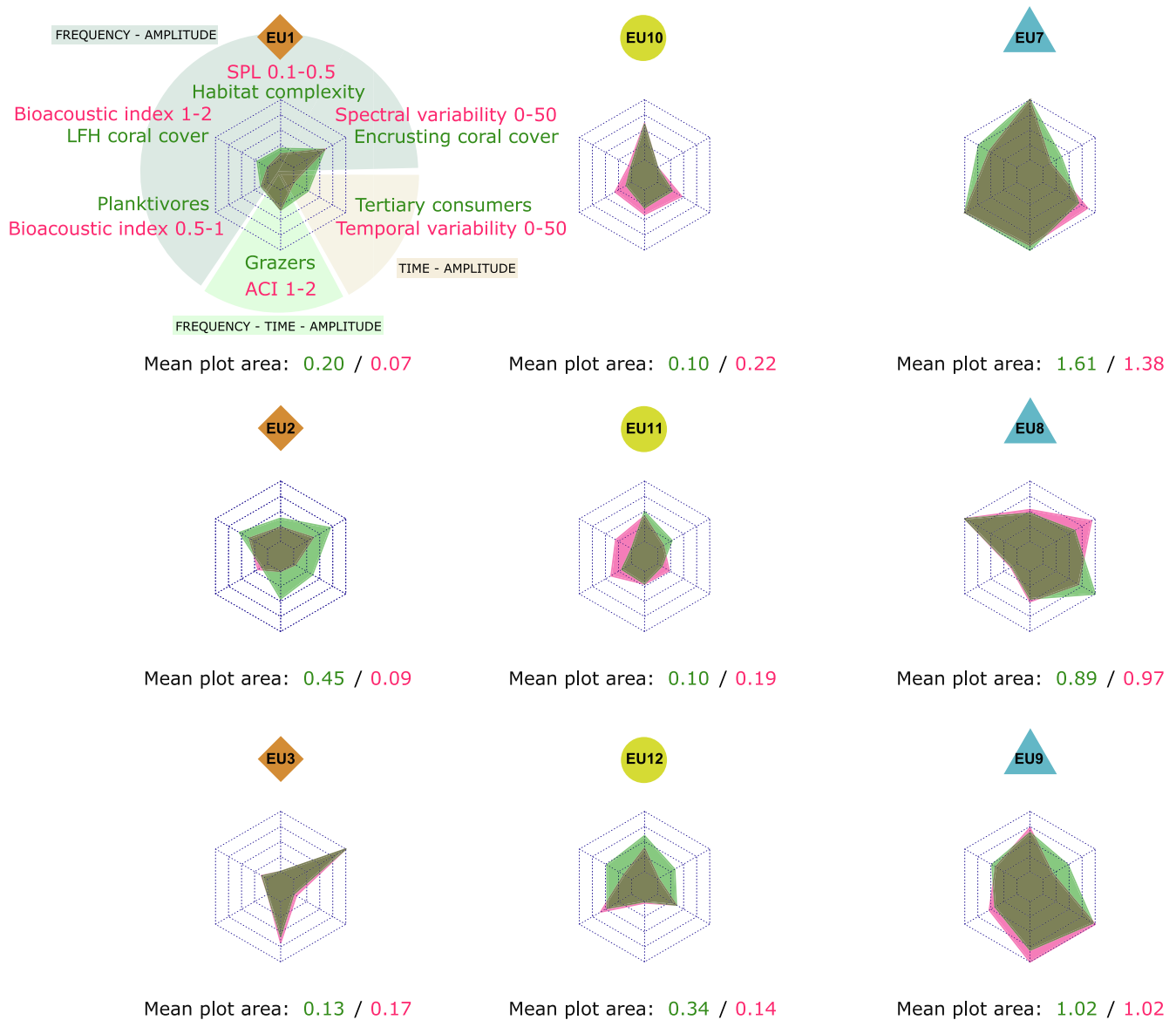
**Fig. 6.** Radar plots representing the values of the six ecosystem functions (green) and the six corresponding acoustic indices (pink) for each site. Matching between functional and acoustic areas result in brown. Mean plot areas are calculated as the mean area of the 720 plots resulting from all the permutations of the six vertexes of the polygon.

a perception of general ecosystem functioning. The steep slopes sites (EU7, EU8 and EU9) presented higher functional and acoustic areas than the other sites (Fig. 6), whereas differences among the gentle slope sites were more ambiguous. In most cases, the shape of the polygons obtained with ecosystem functions closely matched those obtained with ecoacoustic indices (EU3, EU10, EU11, EU7, EU8, EU9). This was, however, not the case for sites EU1, EU2, EU12. The high correlation between mean areas of functional and acoustic plots (Fig. 7) suggested the possibility of an ecoacoustic assessment of general ecosystem functioning. However, mean areas of functional and acoustic plots were not well correlated for the functionally closest sites (i.e. gently sloping sites; Fig. 7). In other words, sites that are functionally similar could not be discriminated using the six ecoacoustic indices simultaneously, whereas they could be discriminated when using indices SPL 0.1–0.5 kHz, spectral variability 0–50 kHz, temporal variability 0–50 kHz and bioacoustic index 0.5–1 kHz separately.

## 4. Discussion

Climate change impacts coral reefs with variable intensities among regions, countries and localities (Hughes et al., 2017; Hoegh-Guldberg et al., 2018). The amplitude of the expected changes calls for an adjustment of management and conservation goals towards more pragmatic strategies which prioritise the sustainability of ecosystem functions and services (Hughes et al., 2017). This will require regular functional feedback from the field at multiple spatial scales to prioritise and monitor conservation areas, and readjusting conservation policies when necessary. While traditional methods (UVC, photo and video surveys) have limited capacities to respond to such monitoring needs, the utility of PAM in both spatially-extended surveys and long-term monitoring is increasingly recognised (see Lindseth and Lobel, 2018). As important components of coral reef ecosystem functioning (e.g. removal of carbonate or turf algae; Bellwood et al., 2019) intuitively
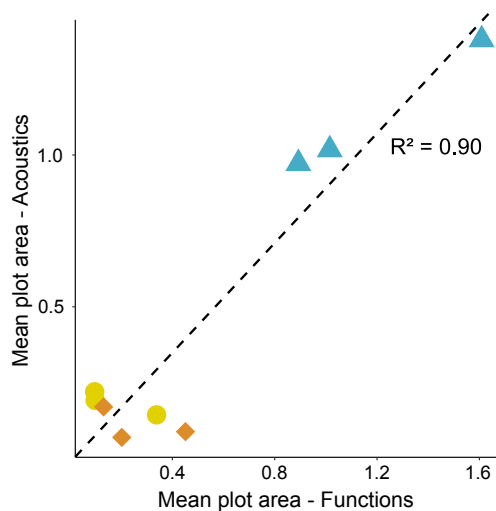
**Fig. 7.** Correlation between mean areas of functional and acoustic plots.

imply sonorous processes, the present study explored whether acoustic indices were able to reflect several key ecosystem functions.

By including a sound-analysis domain (time–amplitude) and acoustic indices (temporal variability, bioacoustic index, spectral variability), to our knowledge not previously used on coral reefs (see Lindseth and Lobel, 2018), we disentangled the main acoustic features of the soundscapes recorded around Europa Island, and explored a novel characterisation of ecosystem functions by means of ecoacoustic indices.

Several studies suggested the potentially strong influence of habitat complexity on the soundscape (e.g. Kennedy et al., 2010; Radford et al., 2014), but only Freeman and Freeman (2016) showed SPL 0.1–0.5 kHz to be related to reef habitat complexity, which they assessed using chains and counting of holes. The present study also found SPL 0.1–0.5 kHz to be strongly correlated with habitat complexity, which was quantified using highly accurate underwater photogrammetry (e.g. Burns et al., 2015). We concur with the hypothesis of Freeman and Freeman (2016) that structurally complex habitats accommodate a high diversity of organisms (e.g. fishes), whose activities produce low frequency sounds (Tricas and Boyle, 2014). Nonetheless, Lugli (2012) has highlighted the role of cavities in low frequency sound amplification. We therefore further suggest that, at the landscape scale, complex underwater structures could amplify low frequency sounds produced on site or coming from the surroundings, hence increasing low frequency sound levels. Less complex habitats would not obstruct the propagation of low frequency sounds, while sediments absorb them (Hughes et al., 1990). Further studies will be needed to disentangle the influence of the physical structure itself and the activity of sheltered organisms on low frequency soundscapes.

Previous studies have found several acoustic indices to be related with total live coral cover (Kennedy et al., 2010, Kaplan et al., 2015; Bertucci et al., 2016), but such a coarse evaluation without distinguishing growth forms can lead to an oversimplification of ecosystem functioning (Darling et al. 2012; González-Barrios and Álvarez-Filip, 2018). Indeed, the diversity of coral growth forms strongly influences associated communities (e.g. fishes) by providing a variety of food and shelter opportunities (Pratchett et al., 2008; Wilson et al., 2008). Here we detected that coral growth forms were linked to diverse aspects of the soundscape.

On the one hand, cover of LFH corals was correlated to bioacoustic index 1–2 kHz. This frequency band is known to be related with invertebrate sounds (Radford et al., 2008; Freeman and Freeman, 2016), but also some fish sounds (e.g. Lobel et al., 2010; Tricas and Boyle, 2014). As the bioacoustic index considers both the sound level and the number of frequency bands used (Boelman et al., 2007), its value in the

1–2 kHz band could reflect both diversity and abundance of the organisms that find shelter in the habitat provided by LFH corals.

On the other hand, encrusting coral cover was correlated with spectral variability, which is driven by the variability of sound amplitude across frequency bands. Sites with high encrusting coral cover, such as EU3, revealed marked differences between sound amplitude in high and low frequency bands, resulting in high spectral variability on the 0–50 kHz bandwidth. This variability could reflect the vacancy of numerous acoustic niches, as sites with high encrusting coral cover are less attractive to a diversity of reef organisms (e.g. Wilson et al., 2008). We suggest that bioacoustic index 1–2 kHz and spectral variability 0–50 kHz represent proxies for the evaluation of different coral functions.

Earlier ecoacoustic studies have emphasized links between soundscapes and global diversity and abundance of fishes (Kennedy et al., 2010; Kaplan et al., 2015; Bertucci et al., 2016; Staaterman et al., 2017). However, biomass and functional traits are recognised as more accurate descriptors of the state and functioning of fish assemblages (e.g. MacNeil et al., 2015). The only ecoacoustic study on coral reefs that included fish biomass did not detect a significant relationship with soundscape characteristics, possibly because they evaluated overall mobile fish biomass rather than the biomass of particular functional groups (Staaterman et al., 2017). Biomass may have specific characteristics linked to the size distribution of fishes and the distinctive sounds produced by fish of various sizes within a species (e.g. Amorim and Hawkins, 2005). As large fishes may fulfil important roles for coral reef functioning (Bascompte et al., 2005; Lokrantz et al., 2008) and are known to be highly vulnerable (e.g. Mellin et al., 2016), the ability to detect high fish biomass, and therefore likely large fishes, could be an important contribution of ecoacoustics.

Among grazing fishes, parrotfishes (i.e. *Scarus* spp and *Chlorurus* spp) are particularly noisy when feeding by scraping teeth on hard substrates, producing a broad bandwidth sound from a few dozens of Hertz to about 9 kHz (Lobel et al., 2010, Tricas and Boyle, 2014). However, in the present study, biomass of fish grazers was correlated with ACI calculated on the narrower 1–2 kHz bandwidth. As this frequency band is less energetic than other bandwidths on coral reefs (e.g. Kaplan et al., 2015; Freeman and Freeman, 2016), ACI calculated between 1 and 2 kHz could be well suited to detect scraping events, which stand out from background noise. Indeed, ACI was originally developed to detect transient, fast modulating and highly energetic events, in contrast to more sustained background noise (Pieretti et al., 2011). Bohnenstiehl et al. (2018), and Bolgan et al. (2018) have emphasized the necessity of a careful choice of the frequency-time resolution settings to calculate ACI. In our case, the time resolution was 82 ms, which is the lower limit of the duration of a scraping event (Tricas and Boyle, 2014), and could be well adapted to reflect the intensity of grazing activity.

Nearly all plankton feeding fishes form schools, whether they are sedentary or mobile, gathering at times in huge numbers. Sedentary planktivores are always small and were represented in our study by several species of *Chromis* (Pomacentridae) and *Pseudanthias* (Serranidae). Mobile planktivores are larger and comprise several major groups such as Caesionidae, Acanthuridae and Balistidae. They may represent a sizeable proportion of the abundance and biomass of fishes, but because they roam over large areas their presence at a given place is highly variable, with soundscapes varying accordingly. Tricas and Boyle (2014) have recorded the *in situ* acoustic activity of *Pseudanthias bicolor* when schooling, with a maximum frequency of 793 Hz. During the analysis of the video footage, we observed numerous events of rapid movements of schools of planktivores, particularly when chased by predators. These produced clearly audible sounds characterised by highly energetic frequency peaks between 0.5 and 1 kHz, which could explain the correlation of planktivores' biomass with bioacoustic index 0.5–1 kHz.

The abundance of tertiary consumers was correlated with temporal

variability on the 0–50 kHz bandwidth. We suggest that tertiary consumers preferentially target sites where numerous acoustic events occur, traducing activity by a variety and/or abundance of potential prey. In turn, their chasing activity itself could contribute to the temporal variability of the soundscapes on these sites. Most tertiary consumer fishes are highly mobile and usually roam widely. Therefore, their abundance and biomass on one spot of the reef may vary greatly during the day, and soundscapes may vary accordingly. Sites with high temporal acoustic variability could thus reflect the movements of predators and/or their prey.

Our results were based on a single day assessment by site, though they might have benefited from video and acoustic data recorded over several days to strengthen the correlations found. Nevertheless, an earlier study (Elise et al., 2019) showed that ranking of sites based upon SPL 0.1–0.5 kHz remained stable even when soundscapes were recorded during different days and moon phases. As data were collected over a ten days' period at Europa Island, we can reasonably assume that variations over this period were higher among than within sites for SPL 0.1–0.5 kHz. Further studies could test the temporal stability of the other indices used in the present study. In addition, the robustness of our "functional" ecoacoustic indices to meteorological or anthropogenic disruptions should be evaluated, as these particularly affect the frequency bands below 2 kHz (Hildebrand, 2009).

Our study showed that even in a long-term protected locality like Europa, without fishing, land run-off or significant local human activity, the levels of various ecosystem functions vary substantially among reef sites. We found PAM able to capture these spatial variations, highlighting the sensitivity of this tool. To further assess the relevance of the "functional" ecoacoustic indices here described, regional studies should record soundscapes across natural and anthropic gradients, combined with visual surveys (Gibb et al., 2019). Once achieved this calibration phase, ecoacoutic information could assist managers to identify priority conservation areas and define management targets. Moreover, real-time monitoring of functional ecoacoustic indices may improve our comprehension of the impact of disturbances and the temporal dynamics of ecosystem responses.

This study revealed that a simple 2 h-recording of ambient sound could be sufficient to provide a snapshot of the functioning of a coral reef site. Without the need for divers' interventions, this could enable the deployment and retrieval of tens of recording devices in a single day, making possible the "acoustic functional mapping" of a large area within a short time span. The combination of traditional visual surveys with complementary methods such as remote sensing, environmental DNA surveys, and PAM opens novel perspectives in terms of management of coral reefs from local to regional scales, overriding the usual limits of traditional visual assessments.

## Data accessibility

## Acknowledgements

## Declaration of Competing Interest

The authors declare that they have no competing interests.

## Authors' contribution

SE, MK and JHB conceived the ideas; SE, JHB, IUB, RP, VM, LP, and MA designed methodology; SE, IUB, VM, JHB and SB collected the data; SE, IUB, RP and VM performed data handling; SE, IUB and RP analysed the data; SE, MK and JHB led the writing of the manuscript and all authors contributed critically to the drafts and gave final approval for publication.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2019.105623.

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