



Diversity and assemblage structure of tropical marine flora on lava flows of different ages



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ABSTRACT

Recent volcanic lava flows extending into the ocean represent an ideal opportunity to study the long-term successional development of marine floral assemblages on the bare new substratum. We describe the floral assemblages of nine lava flows of different ages (prehistoric to 2007) at Piton de la Fournaise (Reunion Island, Indian Ocean) based on a survey of 37 stations. We identified 159 species including 148 macroalgae, 1 seagrass, and 10 cyanobacteria. Fifty-one of those represent new records for Reunion Island, and at least 9 taxa were identified as new to science. Recent lava flows were characterized by the dominance of ephemeral, opportunistic species, such as *Pseudobryopsis hainanensis* and *Acrocladus dotyanus*, while prehistoric lava flows were mainly characterized by perennial species, particularly *Sargassum portierianum* and *Turbinaria ornata*. A canonical correspondence analysis revealed that the environmental factor that most significantly correlated to the variation in floral assemblages was the distance to the most recent lava flow (2007). This factor was also highly correlated to coral cover. The composition of the different floral assemblages is discussed in relation to abiotic and biotic factors to explain ecological succession in a tropical environment.

1. Introduction

Macroalgae are a key component of coral reef communities providing crucial ecological functions such as stabilization of reef structure, production of carbonate sediment, nutrient retention and recycling, primary production and trophic support (Fong and Paul, 2011). Faced with hazards of various origins, coral reefs are one of the most threatened marine ecosystems on earth (Bellwood et al., 2004; Hoegh-Guldberg and Bruno, 2010; Graham et al., 2015). The loss of coral reef resilience can lead to dramatic changes in benthic structure (regime shifts), which significantly alter ecosystem processes and functioning. The critical consequences of these regime shifts on ecosystem services

and their profound management implications, calls for a better understanding of the processes that drive alternative reef regimes and ecological successions.

In many instances, coral reefs have shifted from coral to algal dominance (Bruno et al., 2009) due increased anthropogenic activities, including overfishing (review by Jackson et al., 2001), nutrient enrichment (Carilli et al., 2009), coral diseases and global climate change (Hughes et al., 2007; Anthony et al., 2008). Benthic algae are known to be rapid and efficient initial colonizers on almost any area of coral reefs that have been cleared by disturbances (e.g. Rogers et al., 1991; Hughes, 1994; Schroeder et al., 2008). The successional sequence of algae and invertebrates and the role of abiotic and biotic factors in

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mediating (facilitating or inhibiting) the succession of species after disturbances have been studied in experimental/artificial setups (e.g. Littler and Littler, 1980; Humphries et al., 2014; Doropoulos et al., 2017). But the processes and patterns of colonization of newly available surfaces by macroalgae in nature are less well understood.

The bare new submerged substratum produced during volcanic eruptions of the Piton de la Fournaise volcano offers an ideal setting for the study of developmental stages and ecological successions that can lead to complex ecosystems such as coral reefs. Marine ecosystems close to active volcanic areas are regularly exposed to natural hazards such as incandescent lava flows, landslides caused by micro-seismic events, and changes in physicochemical conditions (e.g. water warming or acidification) (Okubo and Clague, 2009). Both the frequency and the intensity of these disturbance events can impact the structure of the communities, including species richness (Connell, 1978), life-history strategies (Odum, 1969; Leps et al., 1982) or trophic structure (Odum, 1969; Sandin and Sala, 2012; Schils, 2012).

Reunion Island (Indian Ocean) is one of the few places where volcanic activity is frequent. The mean frequency of eruptive phases was 9 months over the past century (27 eruptions from 1998 to 2007; Tanguy et al., 2011). It is also one of the rare localities where lava frequently flows into the ocean (Michon and Saint-Ange, 2008). In April 2007, lava from a continuing eruption of the Piton de la Fournaise volcano entered the ocean at Saint Philippe (southeast coast). The underwater section of the flow created an area of new substratum of several hundred meters in width. This event presented an ideal opportunity to study the development of new floral assemblages on the new bare submerged flows in comparison to older flows.

The species diversity of marine macroalgae of Reunion Island is known mainly from the works by Montagne and Millardillet (1862), Jadin (1894, 1935), Payri (1985) and Ballesteros (1994). In addition, some studies have looked into particular groups such as *Sargassum* (Mattio et al., 2013), turf algae (Lison de Loma, 2000) and Cyanobacteria (Charpy et al., 2010; Echenique-Subiabre et al., 2015). Thanks to these floristic studies exclusively based on morphological analyses, the marine flora of Reunion Island is relatively well known and a total of 243 currently accepted species names are recorded in AlgaeBase (Guiry and Guiry, 2017) including 38 brown algae, 63 green algae, 128 red algae and 14 cyanobacteria. The collecting effort, however, at Reunion Island, has been significantly less than in some of the neighbouring countries and islands states (see Mattio et al., 2013, 2016). For example, Mauritius, which is of similar size, accounts for 435 currently accepted species names (Bolton et al., 2012; Guiry and Guiry, 2017). Past inventories at Reunion Island focused on easily accessible areas of the island, mainly on reef areas of the West Coast (e.g. Saint Gilles, Saint Leu), and no record is available for the exposed southeast coast directly off the Piton de la Fournaise volcano.

In this study, we investigated the pattern of tropical macrophytes (macroalgae and seagrasses) and benthic cyanobacteria on submerged lava flows of Piton de la Fournaise. Specifically, we aim to achieve three objectives: (i) provide a species inventory of marine macrophytes and cyanobacterial communities of the lava flows, (ii) compare these assemblages between lava flows of different ages and (iii) highlight the environmental factors that affect the differences in floral assemblages.

2. Material and methods

2.1. Description of the study area

Reunion Island, located 690 km east of Madagascar, is part of the Mascarene Archipelago along with Mauritius and Rodrigues (Fig. 1). These three young geological oceanic islands are entirely of volcanic origin. Reunion Island is about 3 million years old (McDougall, 1971) and originated from two volcanoes: Piton des Neiges and Piton de la Fournaise. The former has been extinct for ca. 70,000 years, while the latter is still active with effusive activity (Michon et al., 2013; Lénat,

2016). The coastline of Reunion Island is characterized by a narrow insular shelf and steep slopes. The west and southwest coasts are urbanized, with fringing coral reefs extending about 25 km (12% of the total coastline) (Tessier et al., 2008). The north coast, relatively sheltered from the effects of trade winds, is also densely populated. It receives 9 of the 13 perennial river mouths of the island and is characterized by turbid waters and a high proportion of soft substratum. The southeast region of the island is deeply marked by recent and ongoing volcanic activity of the Piton de la Fournaise volcano, is sparsely inhabited (Pinault et al., 2013a). Two main sectors have been studied: (i) inside the volcanic enclosure and (ii) outside the volcanic enclosure (Fig. 1). The first sector included the flows younger than 10 years (eruptions from 2002, 2004, 2005, 2007: recent lava flows), while the second sector included the lava flows older than 30 years (eruption from 1977 and prehistoric flows: ancient lava flows) (Fig. 1).

2.1.1. Inside the volcanic enclosure: recent lava flows

Most of the recent eruptions of the Piton de la Fournaise (2002, 2004, 2005, 2007) resulted from vents located inside the walls of the current caldera or volcanic enclosure (Fig. 1), at various elevations along the rift zone. This volcanic area is exposed to trade winds and recurrent, sometimes strong, oceanic swell particularly during the austral winter and impacted by widespread runoff and percolation following heavy rainfall (Pinault et al., 2013a). The shoreline of the volcanic enclosure, which forms the southern area of the study site, consists of sea cliffs 3–8 m high that extend vertically underwater to depths of 3–5 m. The deeper areas of the flows consist largely of unconsolidated lava boulders, loose rocks, and rubble, with the bottom sloping into deep water at an angle of c.a. 30°.

2.1.2. Outside the volcanic enclosure: ancient lava flows

The area immediately to the north of the volcanic enclosure, which forms the central area of the study site, is a prehistoric flow of undetermined age (Fig. 1). First evidence of an eruption of the Piton de la Fournaise dates from 1640, but many flows occurred before that date (McDougall, 1971). The northern area of the study site consists of the 1977 flow (Fig. 1), which entered the sea outside the volcanic enclosure, creating a shoreline c. 750 m wide with sea cliffs 3–5 m high and narrow black sand beaches. The substratum immediately offshore, deposited by the prehistoric lava flows and the 1977 flows, consists of 1–3 m diameter angular boulders and steep slopes down to 8 m. Between 8 and 20 m deep, the bottom slopes downward more gradually; beyond the 20 m contour, the bottom once again drops down at a steep angle. The substratum between 8 and 20 m consists of compact wave-smoothed lava with dense algal cover. Well-developed coral communities were found between 10 and 25 m north of the study site on the 1977 flow and at the Caesari Rock and Waterfalls Bay areas (Fig. 1) (Pinault et al., 2013b, 2014).

2.2. Sampling sites and stations

Most of the data used in this study were sampled during the BIOLAVE expedition (November–December 2011), which the overall aim was to study species and habitat diversity along the coastal marine section of the Piton de la Fournaise volcano. The Piton de la Fournaise lava flows were also regularly sampled for species inventories on several other occasions between 2006 and 2013 by ARVAM (Association pour la Recherche et la Valorisation Marines) team. A total of 13 sampling sites were studied from lava flows both inside (7) and outside (6) the volcanic enclosure. Sampling sites are represented in Fig. 1 and listed in Table A1 (Appendix A).

2.3. Sampling strategy

Two types of sampling were designed to (i) provide a species inventory of marine macrophytes and cyanobacterial communities of

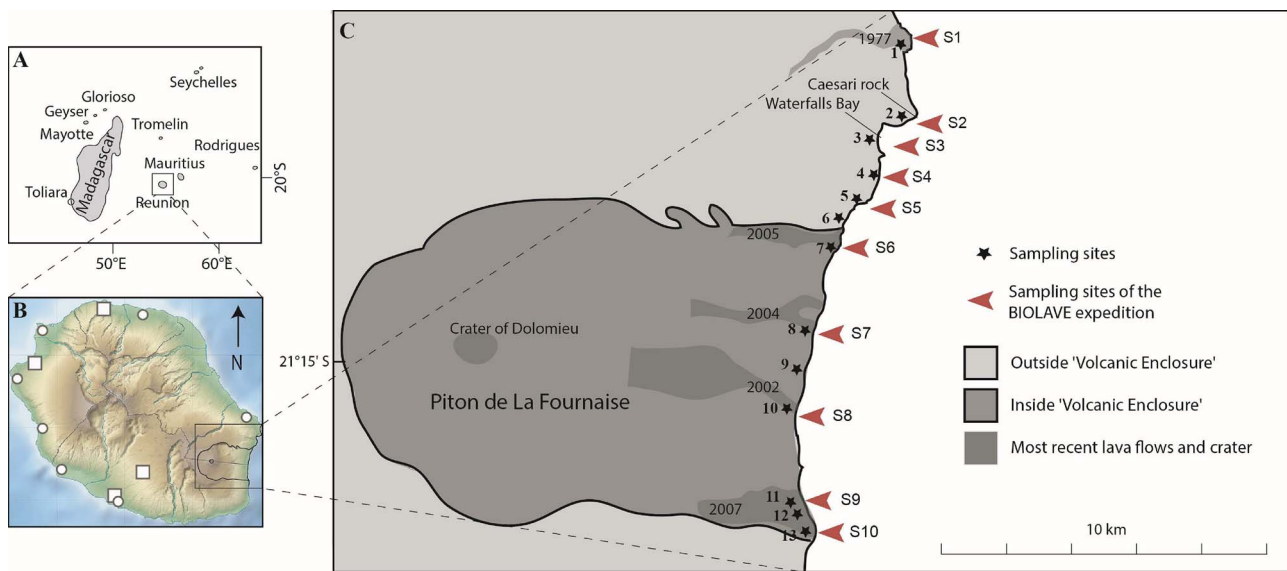


Fig. 1. A- The location of Reunion Island in the southwest Indian Ocean; B- The location of the study area in the southeast coast of Reunion Island; C- The location of the different lava flows (Prehistoric, 1977, 2002, 2004, 2005 and 2007) along the slope of Piton de la Fournaise. All sampling sites were specified with black stars and the ten sampling sites (S1–S10) explored during the BIOLAVE expedition were indicated in this figure with red arrows. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

submerged lava flows of Piton de la Fournaise, and (ii) compare these assemblages between lava flows of different ages (from prehistoric to 2007).

2.3.1. Species inventory

The species inventory was compiled from all samples collected along the coast of Piton de la Fournaise volcano (Fig. 1, Table A1). Samples were randomly collected from subtidal (0–30 m) and intertidal habitats (basaltic rocks and intertidal pools) over a total of 13 sites at different seasons.

2.3.2. Comparisons between lava flows

The comparison of marine flora assemblages (macroalgae, seagrasses and cyanobacteria) of the different lava flows of the Piton de la Fournaise volcano was based on the data collected in November–December 2011 during the standardized sampling of the BIOLAVE expedition (Pinault et al., 2013b, 2014; Table A1).

Surveys were conducted only at 10 sites located in the two sectors (Fig. 1): (1) inside the volcanic enclosure (S6–S10) and (2) outside the volcanic enclosure (S1–S5), on lava flows of different ages. At each site, four sampling stations delimited by depth (5–10, 11–15, 16–20, and 21–30 m) were explored, except for S2, S3 and S10, where only three sampling stations (10–15, 16–20, and 21–30 m) were studied because of difficult swell conditions. In total, 37 sampling stations were explored randomly by two trained divers over an estimated area of 300 m² for 20 min (Table A1).

2.4. Environmental factors

Several environmental factors were either measured *in situ* or extracted from available mapping documents, according to the methods described by Pinault et al. (2014). For each station, the following variables were recorded: (1) depth, (2) substratum rugosity, (3) percentage of soft substrate, (4) coral cover, (5) macroalgal cover, (6) width of the island shelf and (7) distance to the most recent lava flow (2007).

Substrate rugosity, percentage of soft substrate, coral and macroalgal cover were estimated *in situ* using the habitat assessment score described by Pinault et al. (2013a) (Appendix A, Table A2). The width of the island shelf in meters and the distance from the most recent lava

flow (2007) in kilometers were estimated using the MapInfo GIS software (MapInfo Corporation, 1999). The width of the insular shelf was measured transversely to the shore from the high tide line to the –100 m isobath using the bathymetric map of the naval hydrographic and oceanographic service (SHOM).

2.5. Species identification

At each station, marine macrophytes and cyanobacteria were photo-documented *in situ* and as many different species encountered as possible were collected, with the exception of crustose coralline algae. At the laboratory, subsamples of each specimen were preserved in a solution of buffered formaldehyde in seawater (3%) for later microscopic examination, and in 70% ethanol or silicagel for DNA analyses.

2.5.1. Cyanobacteria

Samples of cyanobacteria were analyzed immediately following the collection. Incident light microscopy (Wild M5A, Zurich, Switzerland) was used to locate representative subsamples and taxonomically uniform colonies and for the preparation of fresh and semi-permanent slides. Slides were observed using a transmission light compound Zeiss Universal Research Microscope (Zeiss, Oberkochen, Germany) equipped with Phase Contrast and Differential Interference Contrast (DIC) optics. The magnifications used subsequently at 100, 400 and 1000× according to needs for identification. In semi-permanent slides, the organisms were embedded in glycerol, the specimens covered with cover slip and sealed with Canada Balsam. Measurements were carried out with Sigma-Scan Image analytical software (Sausalito, CA) and Motic Images Plus (Motic Group, China), measured from calibrated ocular micrometer, and from in-scale projections and photo-micrographs.

The systematics of cyanobacteria is complex and currently in the process of revision (Komárek, 2016). The present contribution only deals with phenotype determination using the available monographs and identification manuals following the botanical tradition as in Zubia et al. (2016). Currently accepted names were checked in AlgaeBase (Guiry and Guiry, 2017).

2.5.2. Macrophytes

Macrophytes specimens were sorted, photographed, given

preliminary identifications and pressed as herbarium vouchers on the day of collection. Detailed morphological and anatomical examinations were made using pressed and formaldehyde-preserved samples. Slides preparations were made from hand sections or squashed specimens and then stained with 1% aniline blue. Observations and measurements were made using a binocular loupe and a light microscope (Leica MZ6 and D2000 respectively; Leica Microsystems, Wetzlar, Germany; magnifications x10 to x400), equipped with a Canon EOS 600D camera. Species identifications were done using Indo-Pacific floras (e.g. De Clerck et al., 2005; Oliveira et al., 2005) and the most recent taxonomic treatments of specific algal taxa. The voucher collection was deposited in the Herbarium of Reunion University (REU), France. For taxa in which species identification based on morphological data has been shown to be problematic, DNA-assisted analyses were used to increase the accuracy of the identifications. These include species in the green algal genera *Codium*, *Halimeda*, and order Cladophorales, the brown algal order Dictyotales (*Dictyota*, *Lobophora*, *Padina*) and family Sargassaceae, and the red algal genera *Portieria*, *Dichotomaria*, *Liagora*, and the *Laurencia* complex.

2.6. Data analysis

Species accumulation curves were calculated based on inventory data, using 200 permutations using the “specaccum” function of the vegan package of the software R (Gotelli and Colwell, 2001).

Analyses of Similarity (ANOSIM) based on untransformed data and Bray-Curtis distance measures were used to statistically test for differences in the relative composition of marine floral assemblages between the prehistoric (S2–S5) and more recent (S1, S6–S10) lava flows. An additional analysis was performed, excluding the S1 (1977) lava flow. Analyses of Contribution to the Dissimilarity (SIMPER) were used to identify the taxa responsible for differences in assemblage composition. ANOSIM and SIMPER analyses were performed with PRIMER 6 (Clarke and Gorley, 2006).

The relationships between algal assemblage structure (species occurrences) and environmental variables were investigated using a canonical correspondence analysis (CCA) (Ter Braak, 1986). It is a fact that rare species are often positioned as outliers in correspondence analysis ordinations (Greenacre, 2013) and statistical estimation problems are posed by multicollinearity (Ter Braak, 1986). In this sense, species occurring at less than 2 stations and significantly correlated with environmental variables (correlation test — Pearson 1957) were omitted from analysis prior to conducting CCA. A Monte-Carlo randomization test (1000 permutations) was used to assess the probability of the observed pattern being due to chance (McCune and Grace, 2002).

Student's *t*-test was also used to identify statistically significant differences between the lava flows at a 95% confidence level for some environmental factors.

3. Results

3.1. Macrophyte and cyanobacteria inventory

A total of 407 specimens (34 cyanobacteria, 372 macroalgae and 1 seagrass) were collected on the volcanic habitats of Piton de la Fournaise between 2006 and 2013. A total of 159 species was identified including 10 cyanobacteria, 148 macroalgae and 1 seagrass (Appendix B). Twenty specimens have been sequenced and the Genbank accession numbers of some generated sequences are given in Appendix C.

The 407-species-sample accumulation curve (Fig. 2) did not reach its asymptote, implying that an increased sampling effort would likely yield a larger number of species for the area.

The 10 species of Cyanobacteria belonged to four genera of the families Microcoleaceae and Oscillatoriaceae in the order Oscillatoriales (Appendix B). Three species represent new records for Reunion Island: *Lyngbya sordida*, *Leptolyngbya hendersonii* and *Phormidium laysanense*

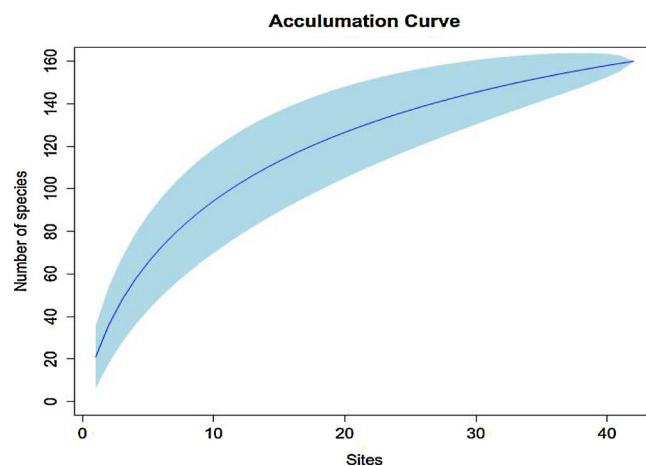


Fig. 2. Species accumulation curves (SAC). The solid line represents the mean SAC with its standard deviation from random permutations of the data.

(Fig. 3). One species of *Lyngbya* sp1 could not be identified.

The 149 species of marine macrophytes belonged to 24 orders, 51 families and 82 genera. The Rhodophyta were the more diverse group with 87 species belonging mainly to Ceramiales (28 species) and Nemaliales (14 species). The Chlorophyta accounted for 31 species and were mainly represented by the orders Bryopsidales (14 species) and Cladophorales (11 species). The main representatives of the Phaeophyceae (30 species) were the genera *Dictyota* and *Lobophora* (Dictyotales) accounting for 18 species in total. The seagrass was the least diverse group with only one species collected: *Syringodium isotifolium*.

52% of all species were confidently assigned to known species names (Rhodophyta 48%, Chlorophyta 59%, Phaeophyceae 55% and one seagrass, *Syringodium isotifolium*) (Appendix B). The rest of the species level taxonomic units is still awaiting final name confirmation, particularly for groups that are difficult to identify without DNA analyses such as e.g. *Amphiroa* (Rösler et al., 2016) or *Peyssonnelia* (Gabriel et al., 2015) and/or that may contain some level of cryptic diversity (e.g. Payo et al., 2013). At least 9 taxa (6%) likely represent species new to science, but remain undescribed (*Codium arabicum* 6, *Codium* sp. ID73, *Codium* sp. ID74, *Dictyota friabilis* 1b, *Lobophora* sp12, *Lobophora* sp70, *Lobophora* sp76, *Portieria* sp63, *Stypopodium* sp1) and 51 species represent new records for Reunion Island (Appendix B, Fig. 4).

3.2. Marine floral assemblages analysis

The floral assemblages of the lava flows of the Piton de la Fournaise volcano were described from 9 different lava flows inside and outside the volcanic enclosure (Fig. 1, Table 1). A total of 93 species were recorded for all lava flows with an average number of species of 18 ± 6 per stations (mean \pm SD, Table 1). The richest site was S5, with 43 species, whereas the lowest specific richness was observed at S1 and S2 (17 and 21 species respectively), which are the sites the farthest away from the 2007 lava flow (Table 1). The floral assemblages of the different sites have been synthesized in Fig. D.1 (Appendix D). The red and green algae were observed more frequently in recent lava flows (172 and 117 observations respectively) than in ancient lava flows (115 and 75 observations respectively) (Table D1, Appendix D). Nine species (10% of the total number of species) were observed with a frequency of occurrence above 50%: two Cyanobacteria (*Lyngbya sordida* and *Symploca hydroides*), three Chlorophyta (*Codium arabicum* 6, *Halimeda discoidea* and *Anadyomene wrightii*), one Phaeophyceae (*Lobophora* sp.) and 3 Rhodophyta (*Actinotrichia fragilis*, *Amansia dietrichiana* and *Carpopeltis* sp1) (Table D1). Conversely, 34 species (37% of the total number of species) were observed with a frequency of occurrence < 5% including species that were observed only once: *Blennothrix cantharidosma* (S9),

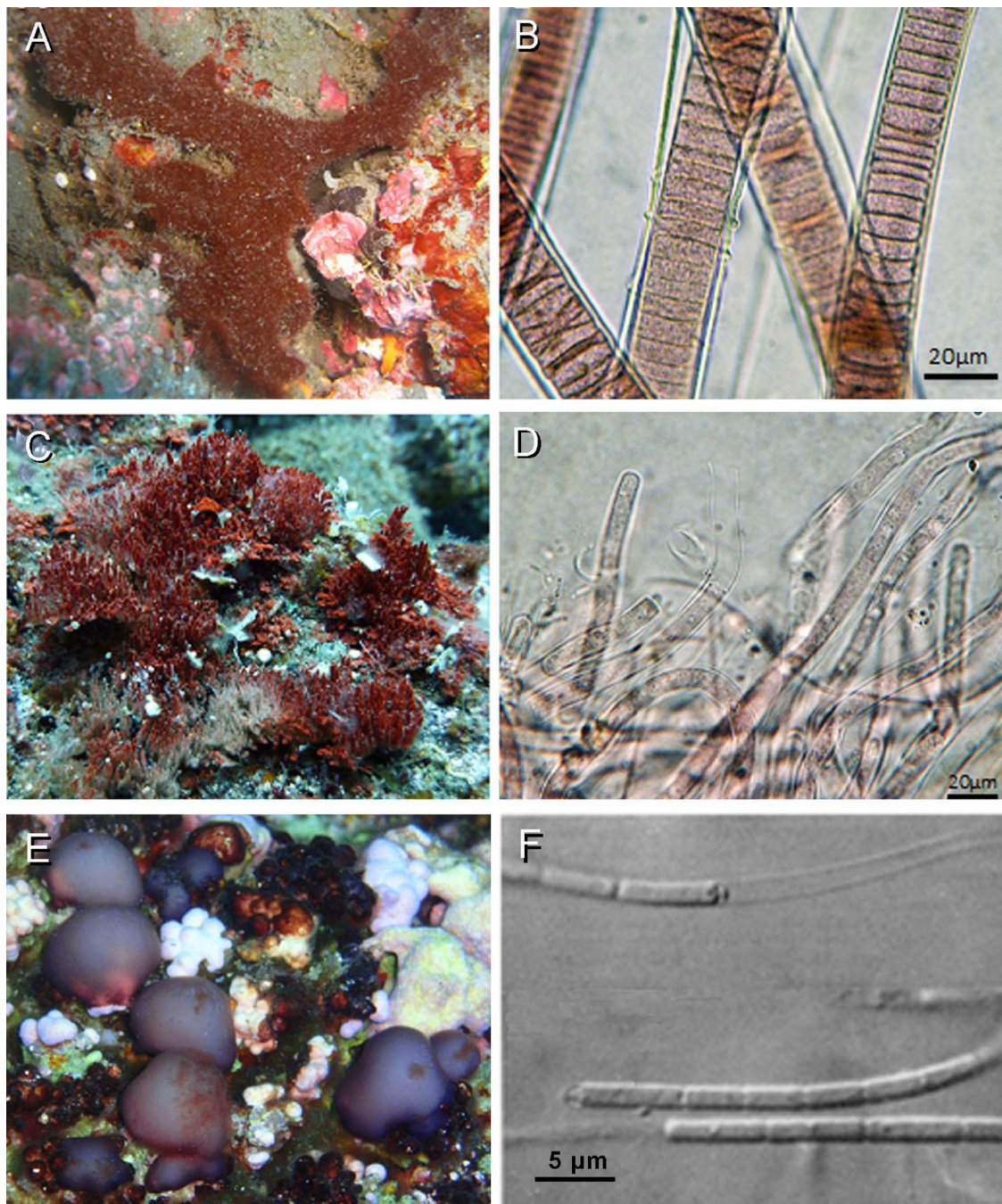


Fig. 3. Illustrations of some cyanobacterial species collected in volcanic habitats of Piton de la Fournaise. A–B: *Lyngbya sordida* Gomont; C–D: *Symploca hydroides* Gomont; E–F: *Leptolyngbya hendersonii* (Howe) Anagnostidis & Komarek.

the seagrass *Syringodium isoetifolium* (S3), *Sargassum obovatum* (S5) and 16 species of Rhodophyta (Table D1).

3.2.1. Analysis of similarities between lava flows

The results of the one-way ANOSIM test showed a significant difference ($R = 0.463$, $p = 0.016$) in floral composition between the groups of the recent (S6–S10) and the prehistoric lava flows (S2–S5). The SIMPER analysis (Table 2) showed that two green algae species (*Caulerpa mexicana* and *Neomeris vanbosseae*), three brown algae species (*Dictyopteris delicatula*, *Dictyota friabilis* 1b, *Lobophora* sp.), one cyanobacterium (*Phormidium laysanense*) and five red algae species (*Amansia dietrichiana*, *Carpopeltis* sp1, *Dasya mollis*-Fig. 4E, *Dudresnaya* cf. *hawaiiensis* and *Neurymenia fraxinifolia*) contributed the most to the dissimilarity of the assemblages between the prehistoric and the recent

lava flows. *Dictyopteris delicatula*, *Dictyota friabilis* 1b and *Phormidium laysanense* were more commonly collected in prehistoric lava flows while the other species were more commonly found in recent lava flows (Table 2, Fig. D1, Table D1).

3.2.2. Environmental factors

The environmental factors, measured during the BIOLAVE expedition have been previously published by Pinault et al. (2014) and are summarized in Table A3 (Appendix A). The main difference in the habitats between recent (S6–S10) and ancient (S1–S5) lava flows is coral cover: the lava flows outside the volcanic enclosure present a significant higher coral cover (6.2–43.1%), compared to the lava flows inside the volcanic enclosure (1.9–8.7%) (Table A3; t -test, $p < 0.05$).

Coral cover was positively correlated with distance to the most

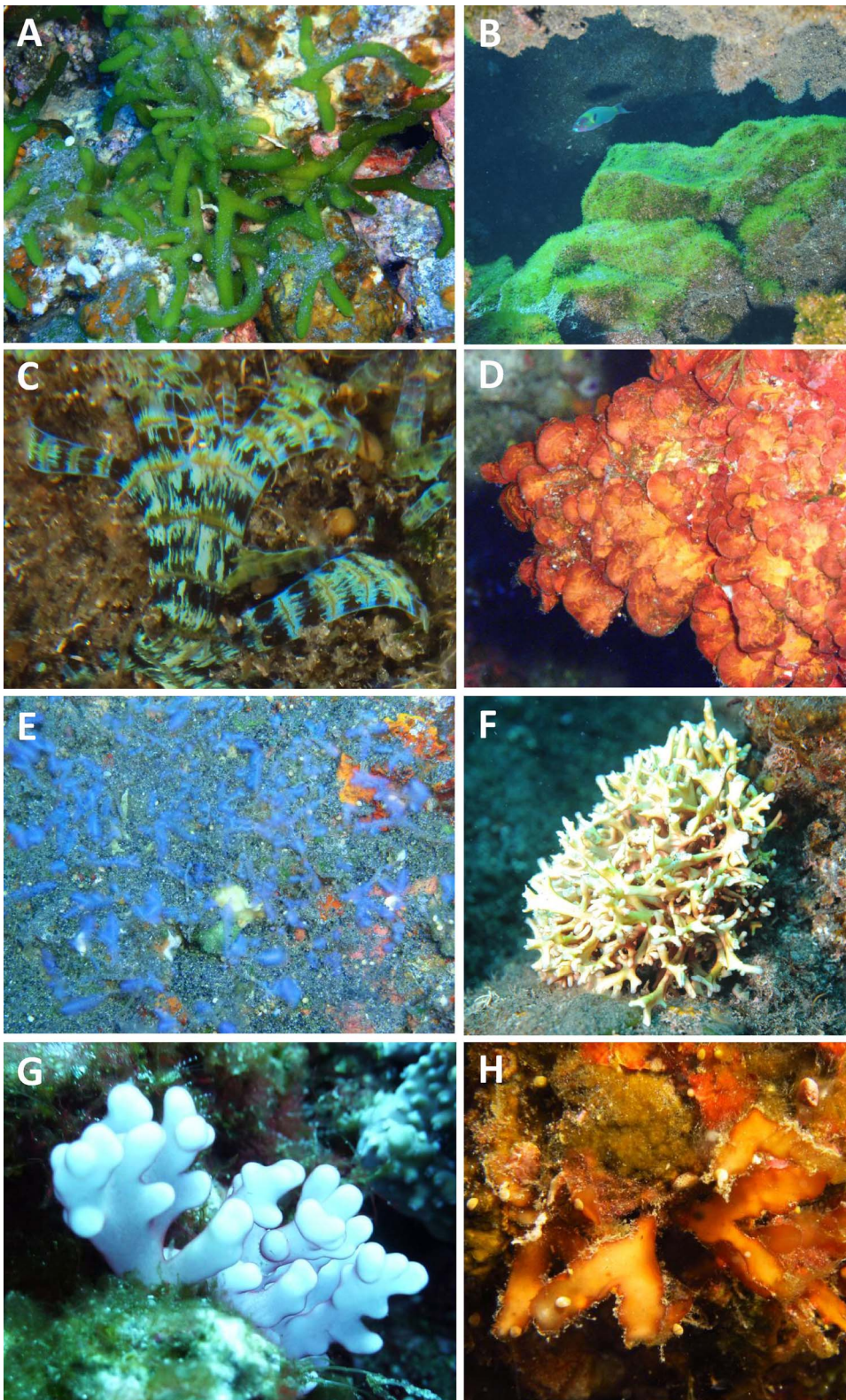


Fig. 4. Illustrations of some macroalgal species collected in volcanic habitats of Piton de la Fournaise: *Codium* sp. ID74 (A); *Pseudobryopsis hainanensis* C.K.Tseng covering basaltic substrate on lava flows (B); *Styopodium* sp1 (C); *Peyssonnelia* sp2 (D); *Dasya mollis* Harvey (E); *Titanophora pikeana* (Dickie) Feldmann (F); *Renouxia* sp1 (G) and *Cryptonemia* cf. *crenulata* (J.Agardh) J.Agardh (H).

recent lava flow ($p < 0.001$), with rugosity ($p < 0.05$) and negatively correlated with soft substratum ($p < 0.001$) (Table 3). Width of the insular shelf and distance to the most recent lava flow were highly correlated ($p < 0.001$) meaning that for recent lava flows the slope from the shoreline to 100 m deep was steeper than for ancient lava flows (Table 3). Finally, macroalgal cover was negatively correlated with rugosity ($p < 0.01$) (Table 3). Because these relationships caused

multicollinearity issues, the width of the insular shelf, the percentages of soft substrates and the coral and macroalgal covers were excluded from further analyses.

The CCA analysis (Fig. 5) revealed a projection of the sites along the vector “distance to the most recent lava flow”, with S1 being the most distant site (10.73 km; Table A3), and S9 and S10 the closest site to the recent lava flow (0 km; Table A3). At a smaller scale, the sites were also

Table 1Number of species per stations (N_{MS} ; mean \pm S.D) and number of species per site for the BIOLAVE expedition.

Sectors	Age of the lava flows	Sites	Number of stations	N_{MS}	N_{TS}^a	Numbers of species per site				
						Cyanobacteria	Seagrass	Green algae	Brown algae	Red algae
Outside the volcanic enclosure “Ancient lava flows”	1977	S1	4	12 \pm 1	17	4	0	4	4	5
	Prehistoric	S2	3	12 \pm 3	21	6	0	4	2	9
	Prehistoric	S3	3	18 \pm 8	38	6	1	9	3	19
	Prehistoric	S4	4	18 \pm 6	40	4	0	10	7	19
	Prehistoric	S5	4	23 \pm 6	43	7	0	9	8	19
Inside the volcanic enclosure “Recent lava flows”	2005	S6	4	19 \pm 6	39	5	0	9	5	20
	2004	S7	4	21 \pm 4	28	4	0	7	2	15
	2002	S8	4	21 \pm 5	39	2	0	14	4	19
	2007	S9	4	18 \pm 4	36	6	0	11	3	16
	2007	S10	3	19 \pm 6	31	5	0	8	4	14
Total	9 lava flows	10	37	18 \pm 6	93	10	1	16	12	54

^a N_{TS} : total numbers of species per site.

segregated based on depth and rugosity (Fig. 5). Shallower stations were positively correlated to rugosity, while deeper stations appeared negatively correlated with rugosity (Fig. 5).

The CCA analysis also revealed a strong correspondence between these environmental factors and the presence of different groups of species (Fig. 5B).

The communities associated with the recent lava flows S7, S8, S9 and S10 (Group I; negatively correlated to the distance to the most recent lava flow) were characterized by high frequency of the following species: *Acrocladus dotyanus*, *Caulerpa mexicana*, *Caulerpa serrulata*, *Codium* sp. ID73, *Cryptonemia* cf. *crenulata*, *Dasya mollis*, *Dudresnaya* cf. *hawaiiensis*, *Halimeda gracilis*, *Halymenia jelinkii*, *Neomeris vanbosseae*, *Pseudobryopsis hainanensis* and *Polysiphonia* sp1 (Fig. 5B).

Communities associated with ancient volcanic formations (S1–S5, Group II; positively correlated to the distance of the most recent lava flow) were distinguished by the frequent occurrence of the following species: *Amphiroa* sp2, *Dictyota fragilis* 1b, *Dictyosphaeria versluysii*, *Dictyopteris delicatula*, *Gracilaria canaliculata*, *Leptolyngbya hendersonii*, *Phormidium laysanense* and *Turbinaria ornata* (Fig. 5B).

This “ancient” group could be subdivided in two main subgroups with: (i) floral assemblages of sites S1 and S2 characterized by high rugosity, high coral cover (see Table 3) and shallow habitats, and (ii) floral assemblages of sites S3, S4 and S5 characterized by low rugosity and deeper habitats. The coral cover appeared as a significant factor for explaining these two distinctive floral assemblages in our study (Table A3, Table 3). Then, two additional groups of species stand out (Fig. 5B): Group III (*Blennothrix glutinosa*, *Blennothrix majus*, *Microdictyon* sp1 and *Symploca hydnoidea*) which appeared positively correlated to rugosities and shallower habitats, whatever the distance to the most recent lava

flow; and Group IV (*Amansia rhodantha*, *Ceratodictyon scoparium*, *Dasya stanleyi*, *Dichotomaria marginata*, *Dictyota pfaffii* 2, *Galaxaura rugosa*, *Peyssonnelia* sp2 and *Sargassum portierianum*) which was positively correlated to deeper stations.

4. Discussion

4.1. Macrophyte and cyanobacteria inventory

We identified 159 species of macroalgae, Cyanobacteria and seagrass in the different lava flows of the Piton de la Fournaise volcano (Table 1). Our sampling effort resulted in the identification of 51 new records for Reunion Island, and at least 9 taxa that likely represent species new to science.

The benthic Cyanobacteria collected during this study are generally common in the coral reef ecosystems of the southwest Indian Ocean (Bauer et al., 2008; Palinska et al., 2015), including Reunion Island (Echenique-Subiabre et al., 2015), Mayotte and Madagascar (Charpy et al., 2010), and the Iles Eparses (Zubia et al., 2016).

Syringodium isoetifolium represents the only record of seagrasses for Reunion Island and, prior to this study, had been observed only from the reef flat of Hermitage on the west coast of the Island (Ballesteros, 1994).

Nine species of green algae were found to represent new records for Reunion Island, and three species of the genus *Codium* represent undescribed species new to science (Appendix B, Fig. 4A). Within the Phaeophyceae, the Dictyotaceae were the most diverse family. Two species of *Dictyota* represent new records for Reunion Island: *Dictyota hamifera* and *Dictyota stolonifera*. Among Dictyotales, 4 new species

Table 2

Results of the SIMPER analysis of algal species contribution (> 2%) to the different floral assemblages. The table displays the average abundance of the species contributing the most to the dissimilarity between the prehistoric (S2–S5) and the recent (S6–S10) lava flows (Average dissimilarity = 62.08).

	Species	Group “prehistoric” Average abundance	Group “recent” Average abundance	Contrib.%
Cyanobacteria	<i>Phormidium laysanense</i>	1.50	0.80	2.17
Green algae	<i>Caulerpa mexicana</i>	0.50	3.20	3.26
	<i>Neomeris vanbosseae</i>	0.50	2.80	2.76
Brown algae	<i>Dictyopteris delicatula</i>	2.00	0.40	2.09
	<i>Dictyota friabilis</i> 1b	2.25	0.00	2.61
	<i>Lobophora</i> sp.	1.50	3.80	3.15
Red algae	<i>Actinotrichia fragilis</i>	2.00	2.80	2.00
	<i>Amansia dietrichiana</i>	1.50	2.80	2.39
	<i>Carpopeltis</i> sp1	2.00	3.20	2.00
	<i>Dasya mollis</i>	0.25	2.20	2.41
	<i>Dudresnaya</i> cf. <i>hawaiiensis</i>	0.00	1.60	2.03
	<i>Neurymenia fraxinifolia</i>	0.75	2.20	2.17

Table 3

Pearson correlation matrix for the environmental factors: depth, substrate rugosity, percentage of soft substrates, coral cover, macroalgal cover, width of the island shelf (Width) and distance to the most recent lava flow (Distance).

	Depth	Rugosity	Soft substrates	Coral cover	Macroalgal Cover	Width	Distance
Depth	1.000						
Rugosity	0.024	1.00					
Soft substrates	-0.014	-0.523***	1.00				
Coral cover	-0.165	0.352*	-0.620***	1.00			
Macroalgal cover	0.004	-0.508**	0.100	0.021	1.00		
Width	0.036	-0.103	-0.041	0.556***	0.116	1.00	
Distance	0.051	-0.032	-0.238	0.691***	0.276	0.928***	1.00

Correlation is significant at * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$ (in bold).

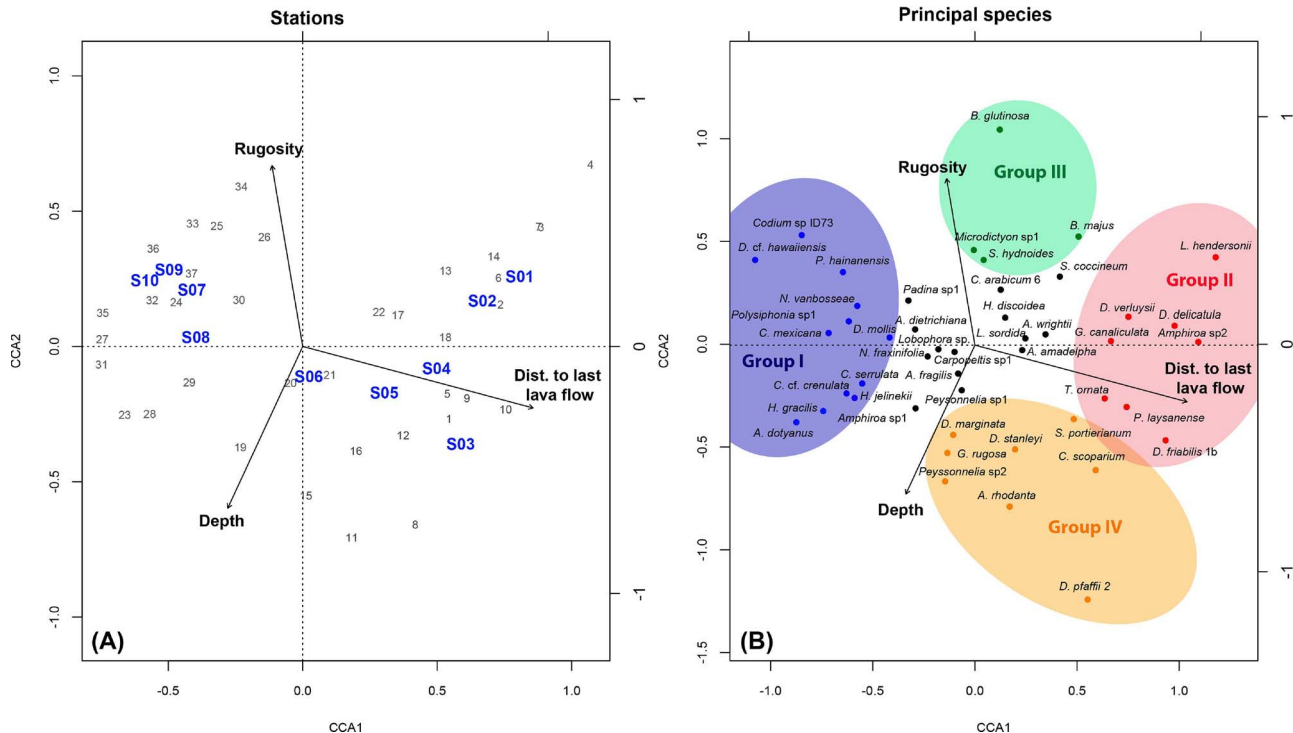


Fig. 5. (A) Biplot canonical correspondence analysis (CCA) of environmental variables and sites/stations, and (B) Biplot CCA of environmental variables and characteristic species. Eigenvalues: axis 1, 0.27; axis 2, 0.12. Proportion of total explained variance: axis 1, 48.7%; axis 2, 21.5%. Species-environmental variable correlation: axis 1, 87.4%; and axis 2, 89.8%. Monte-Carlo test of all canonical axes is significant ($p = 0.001$), 1000 permutations.

remain to be described: *Dictyota friabilis* 1b, *Lobophora* sp70, *Lobophora* sp76 and *Stypopodium* sp1 (Fig. 4C). This large proportion of new species is a result of molecular work done recently for the genus *Lobophora*, which has uncovered a large number of cryptic species (Vieira et al., 2014, 2016a). The Rhodophyta represent the most diverse group with 55% of the species collected during this inventory. The majority of the species collected during this study could not be assigned to known species names (39 species), or their identification remained uncertain (5 species). Based on our results, however, we found that 28 species represent new records for Reunion Island (Appendix B). Among these species, many are characteristic of the deepest habitats (e.g. *Acrosymphyton* sp1, *Dudresnaya* cf. *hawaiiensis*, *Platoma* sp1, *Predaea* *weldii*, *Renouxia* sp1) (Appendix B), which have been little explored in previous studies in Reunion Island.

Our species accumulation curve indicates that many more species may occur in the study area if sampling effort was increased and if molecular analyses were generalized to the whole specimen collection. The high proportion of new records may be further explained by the molecular work that unveiled greater species diversity than based solely on morphology (reviewed in Cianciola et al., 2010; De Clerck et al., 2013).

4.2. Marine flora succession

Our data showed that the marine floral assemblages were significantly different between the lava flows of different ages.

The recent lava flows (S6–S10) were characterized by the high occurrence of filamentous and/or opportunistic species (*Acrocladus dotyanus*, *Amansia dietrichiana*, *Caulerpa mexicana*, *Caulerpa serrulata*, *Dasya mollis*, *Pseudobryopsis hainanensis*). This observation is in accordance with the successional development demonstrated in other studies (Littler and Littler 1980; McClanahan 1997; Titlyanov et al., 2008). After the disturbances, the bare substratum is generally rapidly overgrown by biofilms consisting of organic matter and microorganisms, such as bacteria and diatoms, which serve as a substrate for colonization by filamentous cyanobacteria and turf algae (Rogers et al., 1991). These pioneer species are characterized by high rates of reproduction and growth, and thalli with large surface to volume ratios (Odum 1969; Littler and Littler 1980). A good example of such species is *Pseudobryopsis hainanensis*, a distinctive opportunistic green algal species known to form blooms on coral reefs following disturbances like cyclones and hurricanes (Pauly et al., 2011). At the Piton de la Fournaise, we found this species covering large areas in some of the recent lava flows (S9 and S10).

The first successional stages were observed at sites S9 and S10. A dense turf covered all the lava flows and a very high cover of Liagoraceae was observed during the austral winter of 2007, eight months after the lava flow was created. Similar Liagoraceae blooms have been observed following hurricane disturbances in Palau and the Caribbean (e.g. Woodley et al., 1981; Edmunds and Witman, 1991; Fenner, 1991). At Reunion Island, Liagoraceae blooms are usually seasonal and occur at the start of the austral summer (November–December–January) so the link with the volcanic eruption is debatable.

The floral assemblages of the ancient lava flows (S1–S5) did not constitute a homogeneous group. Sites S1 and S2 form coral-dominated systems with low algal diversity, mainly including species from nearby coral reefs (e.g. *Dictyopterus delicatula*, *Dictyosphaeria verluysii*, *Gracilaria canaliculata*, *Leptolyngbya hendersonii*). At these sites, the competition between scleractinian corals and benthic algae is an important process determining the colonization patterns of algae (McCook et al., 2001). Algae are widely considered to be competing with corals for space or light using several mechanisms like overgrowth, shading, abrasion, chemical allelopathy, recruitment barrier (macroalgal canopy) and epithelial sloughing (McCook et al., 2001).

Conversely, the prehistoric sites S3, S4 and S5 are characterized by abundant perennial seaweed species with more complex and longer life histories like *Sargassum portierianum* and *Turbinaria ornata*. This observation is in accordance with the successional development shown in other studies where the first colonization step is followed in the successional development by larger macroalgae such as calcareous (e.g. *Halimeda*), crustose coralline (e.g. *Porolithon*) and fleshy brown algae (e.g. *Dictyota*, *Padina* and *Sargassum*) and sessile reef invertebrates such as soft and hard corals (reviewed in Littler and Littler, 1980; McClanahan, 1997).

Our analysis also revealed the influence of bathymetry in structuring floral assemblages at ancient lava flows (Groups II, III and IV), which was not found on recent lava flows (Group I). The assemblages of shallow habitats were characterized mainly by cyanobacteria (*Blennothrix majus*, *Blennothrix glutinosa* and *Symploca hydroides*), while the assemblages of deepest habitats were characterized by six red algae and two brown algae (*Dictyota pfaffi* 2, *Sargassum portierianum*) (Fig. 5B). The stronger community structure at ancient lava flows may be explained by the stability of these assemblages that are not affected by recent volcanic disturbance events and therefore favor “specialist” species. Natural selection induces more or less specialized strategies among species by evolutionary tradeoff: between specializing to performing a few activities well and generalizing to perform many activities reasonably well (Levins, 1968). Specialist species are expected to benefit from environments that are spatiotemporally homogeneous whereas ecological generalists should benefit from environments that are spatiotemporally heterogeneous (Odum, 1969; Connell and Slatyer, 1977; Whittaker et al., 2010). We assume that the ancient sites (S1–S5) have been little affected by volcanic activity in recent decades and that the assemblages have been relatively stable for at least 34 years. The more recent sites have frequently been affected by the volcanic activity over the last decade promoting the persistence of generalist species assemblages characterized by opportunistic species dominance, including green filamentous species and turf algae.

4.3. Environmental factors influence

Our data revealed that the most significant factors affecting the floral assemblages on lava flows are the distance to the most recent lava flow (2007). This distance was highly correlated with high coral cover. The negative influence of the most recent lava flow on coral communities may be the result of the stress suffered by the entire coastal ecosystem within the study area at the latest eruption of the Piton de la Fournaise in 2007. From our observations, the strong rugosities observed at sites farthest from the 2007 flow are likely associated with high coral covers (S2- Waterfall bay and S1-1977 flow sites) (Fig. 5). In

contrast, high rugosities measured near the 2007 flow were probably associated with recent volcanic formations (gratons) that have not yet been wave-smoothed (Fig. 5). The specificity and diversity of habitats is a key factor to explain the floral assemblages. High topographic complexity may promote high abundance and diversity because it provides more diverse substratum for colonization by algae (e.g. bare substratum, live corals, coral rubble) and promote the co-occurrence of the species that are specialised on different reef habitat features (e.g. vertical walls, soft substratum, corals) (e.g. S4 and S5). Depth was also a very influential variable on the floral assemblages of Piton de la Fournaise. Many factors such as grazing, wave energy, water desalination and oxygenation, can contribute to algal depth zonation (Gomez and Huovinen, 2011).

The environmental factors measured in our study are mainly linked with habitats characteristics. However, the distribution and abundance of macroalgae are influenced by many others factors like “supply-side” factors (fecundity, dispersal, settlement, recruitment), resource availability (light, nutrients, substrate), physical stress (temperature, freshwater, sediment deposition), species interactions (especially competition and herbivory) and the historical effects of these factors and interactions between them (McCook, 1999). In Piton de la Fournaise, the water quality may also influence the species composition of the different floral assemblages. The high occurrence of cyanobacteria and the characteristic macroalgal species of the ancient lava flows (e.g. *Dictyosphaeria verluysii*, *Gracilaria canaliculata*) could be related to water quality. The area outside the volcanic enclosure (S1–S5) is likely more impacted by anthropogenic inputs (Saint Rose town, rivers, agricultural activities) than the others sites situated inside the volcanic enclosure. The high occurrence of *Dictyosphaeria* and *Gracilaria* is characteristic of enriched water, as observed along the West Coast of Reunion Island in a previous study (Naim, 1993). In Kaneohe Bay (Hawaii), corals on the reef slopes and outer reef flats were overgrown by the green alga *Dictyosphaeria cavernosa* in 1960s and its persistence has been attributed to nutrient-rich sewage discharge in the bay (Stimson et al., 2001). The presence of Cyanobacteria in coral reefs is also associated with higher levels of nutrients (especially phosphate contents) (Paerl et al., 2011; O’neil et al., 2012). On the other hand, the specific chemistry of lava flows could also influence the floral assemblages inside the volcanic enclosure. In this perspective, it would be interesting to perform chemical analysis on seawater, sediment and lava flows. The top-down control (herbivores) also plays an important role in the distribution and abundance of seaweeds (reviewed in Fong and Paul, 2011; Vieira et al., 2016b). Coral reef herbivores can remove almost 100% of the biomass produced daily by marine algae in some reef habitats, and the feeding activities of marine herbivores are an important ecological force controlling the structure and dynamics of algal communities (reviewed in Fong and Paul, 2011). The fish community of Piton de la Fournaise has been described in previous studies (Pinaut et al., 2013a,b, 2014) and a future multi-taxon analysis would be needed to understand the influence of herbivory pressure on floral assemblages.

5. Conclusions

In this study, we provide a species inventory of marine macrophytes and cyanobacterial communities of submerged lava flows of Piton de la Fournaise (159 species identified). The successional series of the floral assemblages have been correlated to the age of the lava flows. Our analysis also revealed the influence of some environmental factors (coral cover, rugosity, depth and the distance to the last lava flow) in structuring floral assemblages.

Future studies on the marine floral assemblages of Piton de la Fournaise, preferably making use of permanent quadrats in the different successional states of corals settlement and development, could concentrate on the structuring effects of nutrient availability and grazing pressure. In addition, an approach that takes into account species richness, abundance and functional traits would provide useful

information regarding the influence of lava flow on marine macrophyte communities and re-colonization processes. Given the critical consequences of phase shifts for coastal ecosystems, a thorough understanding of these processes is essential for the development of environmental policies and management.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.aquabot.2017.10.005>.

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