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Thirty-year recovery of mollusc communities after nuclear experimentations on Fangataufa atoll (Tuamotu, French Polynesia)

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Abstract. A 30-year study of temporal changes in gastropod community structure on the reefs of a Pacific Ocean atoll (Fangataufa, Tuamotu Archipelago) subjected to atmospheric nuclear tests during the 1960's offered the opportunity for an unthinkable field experiment that could help ecologists understand mollusc primary succession. Reef molluscs were partly or entirely wiped out by the heat of the nuclear tests and the reefs were recolonized by ocean larvae. On all reefs, community composition before the tests was very different from what it evolved to afterwards. A new method of analysis was developed to study the temporal variation in community composition before versus after the tests (temporal beta diversity). Analyses showed that community compositions diverged through time among the reefs. Only some species can survive the harsh conditions of supralittoral zones, so the same species recolonized them; environmental filtering controlled the development of the new communities. In the reef flat and edge zones, differences in community composition seem to be the result of neutral stochastic colonization by larvae coming from the open ocean. All reefs developed a community composition quite different from that before the nuclear tests.

1. Introduction

Are ecological communities structured by internal or external forces, or by random processes? Internal forces include species interactions, e.g. competition and predation; external forces refer to environmental factors filtering species according to their niches; among random processes, random dispersal is most important in ecology.

To answer that question, one ideally has to compare communities before and after a major catastrophic event that wipes out communities and restarts primary succession. In nature, this happens after landslides, earthquakes or volcanic eruptions, for example. In this paper, we will take advantage of atmospheric nuclear tests conducted on an atoll in the Pacific

Ocean for which we were invited to conduct ecological monitoring; the tests offered the occasion for an otherwise impossible field experiment. The nuclear tests annihilated previous reef communities. The new communities that developed on the exposed reefs were compared to the communities surveyed before the tests to assess hypotheses about recolonization mechanisms of the reefs.

A long-debated question is whether species assemble into communities following describable rules, or if the assemblages are formed by random ecological processes. Much theoretical work has been published during the last quarter of the 20th century. Studying birds, Diamond [1] provided rules describing mechanisms through which competition and niche overlap determined species assemblages. Connor and Simberloff [2] criticized this approach by showing that many of Diamond's rules were tautological and did not lead to predictions that can be tested against empirical evidence. Some of the rules led to predictions that could be tested, though. The proposed mechanisms behind assembly rules are now usually tested using null models [3,4]. In opposition to assembly rules, Hubbell [5] proposed in his neutral theory that the diversity of species in a community is determined mostly by random dispersal (e.g. of larvae in animals, or propagules in plants), speciation, and extinction.

Fangataufa atoll (22° 14' S, 138° 43' W, figure 1a), located in the Tuamotu Archipelago in south-central Pacific (French Polynesia), has been used as a nuclear testing site. Four atmospheric nuclear tests were conducted between 1966 and 1970, followed by underground tests until 1996. The French *Direction des Centres d'Expérimentations Nucléaires* asked ecologists to survey the evolution of the mollusc communities on reefs impacted by the nuclear tests. Monitoring the ecological impact of this experiment will hopefully help marine ecologists understand the primary succession and the following structuring of mollusc communities on reefs after they were partly or entirely wiped out by the nuclear tests.

This paper compares the observations across surveys over 30 years and makes comparisons between reefs to assess hypotheses about the mechanisms that determined

78   recolonization. We will determine whether the mollusc assemblages found on three reefs after

79   the tests were the same or different from those found before. Recurrence of similar

80   assemblages before and after the tests would support environmental control (species sorting),

81   whereas different assemblages would indicate random (neutral) processes, which may include

82   replacement by ecologically equivalent or different species.

83   **2. Surveys on Fangataufa atoll**

84   Surveys were done on the supralittoral zones, reef flats and reef edges of two outer reefs and

85   one inner reef of the atoll (figure 1).

86   Transect Terme Sud (35 quadrats, see section 4), located on the outer reef on the

87   southern side of the atoll, is highly exposed to the swell. The original transect that was

88   surveyed from 1968 to 1987 was located at 22° 16' 30" S, 138° 44' 48" W (position of a steel

89   peg cemented on the conglomerate in 1987, quadrat 23). In July 1996, a storm with strong

90   southerly winds (25 knots) hit Fangataufa, causing strong swell and 8-m waves on the

91   southern side of the atoll, including the Terme Sud site. The swell broke coral colonies from

92   the outer slope and transported coral blocks that covered the Terme Sud transect that had been

93   surveyed from 1968 to 1987. Considering the geomorphologic homogeneity of the zone, a

94   new transect was established 30 m to the east, at 22°16' 30-31" S and 138°44' 48-50" W, and

95   used for the May 8, 1997 survey.

96   Transect Hélène (42 quadrats), located on the outer reef on the western side of the atoll,

97   is moderately exposed to the swell. The position of a steel peg located between the reef flat

98   and the supralittoral zone is 22° 15' 28" S, 138° 45' 42" W.

99   Transect Manchot (60 quadrats), located on the inner reef on the northwestern side of the

100 atoll, is sheltered from the swell. At high tide, waves breaking on the outer reef supply it with

101 ocean water. The position of a steel peg cemented on the reef flat in 1987 at quadrat 40 is 22°

102   12' 45" S, 138° 46' 99" W.

103   Eight field surveys were conducted on the three reefs from 1967 to 1997. Reef Hélène

104   was sampled in October 1967 and the other two (Terme Sud, Manchot) in March 1968. During

105   the 1969 expedition, there was only time for the survey of two reefs, Hélène and Terme Sud.

106   In 1972, 1974, 1977, 1987 and 1997, all three reefs were surveyed.

107   The field surveying methods were the same during all surveys. The transects, marked by

108   metal posts, were the same except for a small change in the position of Terme Sud in 1997,

109   described above. Descriptions of the geomorphology of the transects can been found in [6,7].

110   The transect profiles are shown in figure 1b-d. The Terme Sud and Hélène transects present a

111   high reef edge forming an algal crest beaten by strong waves and swell from the ocean,

112   followed by a reef flat and a supralittoral zone of grey coral blocks cemented together, called

113   conglomerate. The Manchot reef is located inside the lagoon. Its edge is low, mostly

114   consisting of coral instead of massive red calcareous algae, followed by the reef flat, without a

115   supralittoral zone. Preliminary results of the 1967 to 1977 observations were published in the

116   scientific literature by [7].

117   3. Nuclear tests and other anthropogenic impacts on the reefs

118   The following atmospheric nuclear tests were conducted by the French *Direction des Centres*

119   *d'Expérimentations Nucléaires* between 1966 and 1970:

120   • On September 24, 1966, the *Rigel* test (125 kt) was conducted on a barge anchored in the

121   lagoon. It had little impact on the outer reefs of the atoll.

122   • On August 24, 1968, *Canopus* (2.6 Mt, on a platform held by a moored balloon) was the

123   most powerful test in French Polynesia. The blast, conducted at low tide, burned all vegetation

124   on the atoll and caused important damages to the supralittoral zone, reef flat and reef edge

125   (algal crest) mollusc communities, which were mostly eliminated.

126   • May 30, 1970, *Dragon* (945 kt, on a platform held by a moored balloon) also had major

127   effects on communities.

128   • August 2, 1970, *Orion* (72 kt) had more limited effects.

129   Another man-made perturbation affected the inner reefs in 1965. See Appendix S3.

130   **4. Surveying method**

131   Molluscs were selected as the target taxonomic group to survey the effects of atmospheric

132   nuclear tests on reefs because they are unmoving or slowly moving organisms. After

133   disturbance or annihilation, populations can be replenished by larvae living in the ocean and

134   the lagoon, which settle in suitable locations. Another interesting aspect of mollusc

135   communities is that they can be sampled on outer reefs without recourse to boats and other

136   heavy equipment.

137   Molluscs that were emerged at low tide were unprotected against the heat of nuclear

138   blasts. On the reef flat, molluscs living in puddles where water remained at low tide were

139   protected by seawater. On the reef edge (algal crest) and in the supralittoral zone, the heat

140   flash was also very destructive.

141   In this study, a sampling unit is a portion of a transect: either the supralittoral zone, or

142   the reef flat and reef edge together. A rope ladder was positioned on the reefs forming a

143   transect perpendicular to the shoreline with three parts on Terme Sud and Hélène (reef edge,

144   reef flat and supralittoral zone) and two parts on Manchot (reef edge and reef flat). The ladder

145   delimited 6-m^2 quadrats (3 m long × 2 m wide). All gastropods present in each quadrat were

146   collected, identified to species and counted, except for Vermetids (tube worms) and

147   Hipponicids (Gastropods), which could not be accurately counted.

148   Bivalves were only found on the Manchot reef flat (*Chama croceata* and *Tridacna*

149   *maxima*, Table S1.5, Appendix S1), except for a few *Isognomon isognomum* (Isognomonidae

150 family) found on the reef flat bordering the conglomerate on Terme Sud and Hélène. The

151 *Isognomon* were not counted because they were attached under decimetre-length erratic blocs

152 transported across the flat by waves when the swell is important at high tide. In addition to

153 molluscs, a sea cucumber (echinoderm) species was found in fair abundance on Manchot

154 (Table S1.5). Manchot is an inner reef where sea cucumbers are not washed away by the surf

155 and can maintain a population. The counts of that species were kept in the data subjected to

156 the analyses because they were part of the sedentary reef fauna.

157 **5. Statistical methods**

158 The following methods were used in the analyses.

159 (a) *Alpha diversity*

160 Alpha diversity for the various transects and years was estimated by the species richness, the

161 Shannon diversity index H, and the exponential of H which is Hill's [8] diversity number N_1.

162 N_1 is a more easily interpretable estimator of alpha diversity than H [9].

163 (b) *Redundancy analysis*

164 Redundancy analysis (RDA [10]; see also [11]) is an extension of multiple regression that

165 allows one to explain (in the same sense as in regression analysis) the variation of a

166 multivariate response data table (here, mollusc community composition data) using

167 explanatory variables (here, a 2nd-degree polynomial function of time). A linear function of

168 time would only have allowed us to model the variation in community composition among

169 years as a straight line, whereas a 2nd-degree polynomial function allowed the community time

170 series to double back upon itself, as will be seen in the results. In the analyses made separately

171 for the three transects, the linear and quadratic functions of time were both significant

172 explanatory variables of the community variation among years. RDA produces the same sort

173 of test of significance as linear regression analysis. It also produces ordination plots that allow

174   one to visualize the relationships between the observations (sampling years in our study) and

175   the species. RDA were computed on log-transformed data, $y' = \log(y + 1)$.

176   (c) *Beta diversity for surveys along time*

177   Beta diversity is the variation in community composition among sites in a study area, or

178   among survey times for a survey across years. The total variance of the community

179   composition data is a convenient and flexible measure of that variation if the community

180   composition data have been transformed in an appropriate way [12]. The Hellinger

181   transformation [13] is a widely used befitting transformation; it consists of dividing all

182   abundances by the sampling unit (row) sum and taking the square root of the result. After that

183   transformation, the Euclidean distance among the rows of transformed data is the Hellinger

184   distance among the original data, and that is one of the distances suitable for beta diversity

185   studies [12]. The total variance, or total beta diversity (BD_{Total}), computed on Hellinger-

186   transformed data is a value between 0 and 1, which is comparable among study sites provided

187   that the sampling units are of the same size; that is the case in this study.

188   (d) *Local contributions to beta diversity for surveys along time*

189   BD_{Total} can be partitioned into contributions of individual sampling units, called *Local*

190   *contributions to beta diversity* (LCBD indices, [12]). These indices, which sum to 1 for a

191   given data matrix and can be tested for significance, indicate how exceptional each sampling

192   unit is, compared to a synthetic unit with mean species composition. Legendre & Gauthier

193   [14] have shown that BD_{Total} and LCBD indices can also be computed for repeated surveys

194   forming a time series. In the present study, these indices will be computed separately for each

195   transect (Terme Sud, Hélène and Manchot) across the surveys that took place between 1967

196   and 1997. The tests of significance of the LCBD indices will indicate which years were

197   significant, thus exceptional in community composition, compared to the other survey years

198   on each transect.

199   (e) *Before-after analyses*

200   We analysed the survey data (Appendix S1) to answer the following question: after the nuclear

201   tests, were the assemblages generated during primary succession similar to those found before

202   the tests? Strong similarity (i.e. small dissimilarity) would support the hypothesis of

203   environmental control (species sorting by environmental conditions). Or were the assemblages

204   different, and if so, were some (or many) species replaced by functionally similar or different

205   species? A mixture would be in agreement with the hypothesis of random (neutral) processes,

206   partly or entirely independent of the environmental conditions. Neutral primary succession can

207   produce species replacement by functionally equivalent or non-equivalent species.

208   We examined the data of the reef flat and edge zones of the three transects (Tables S1.1,

209   S1.3 and S1.5). We compared the pre-test data (1967 or 1968) to the 1972 to 1998 post-test

210   data in turn. We did not use the 1969 data from Terme Sud because additional nuclear tests

211   took place in 1970 (see Section 3); we used only the pre-*Canopus* and post-test surveys in

212   these analyses.

213   For each comparison of two survey vectors, $\mathbf{y}_1$ and $\mathbf{y}_2$, we computed the following

214   indices for the herbivore and carnivore feeding categories (Appendix S1). Results for the

215   detritivores and filter feeders are not reported because there were too few species.

216   • a_j is the part of the abundance of species j that is common to the two survey vectors: $a_j =$

217     $\min(y_{1j}, y_{2j})$. A is the sum of the a_j values for all species in the functional group under study. It

218   represents the unscaled similarity between two surveys.

219   • b_j is the part of the abundance of species j that is higher in survey 1 than in survey 2:

220     $b_j = y_{1j} - y_{2j}$. B is the sum of the b_j values for all species in the functional group under study. It

221   is the unscaled sum of species losses between time 1 and time 2.

222   • c_j is the part of the abundance of species j that is higher in survey 2 than in survey 1:

223     $c_j = y_{2j} - y_{1j}$. C is the sum of the c_j values for all species in the functional group under study. It

224   is the unscaled sum of species gains between time 1 and time 2.

225   The values A, B and C are the building blocks of well-known quantitative dissimilarity

226   coefficients used in community analysis to estimate beta diversity, in particular the Ružička

227   (D_R) index (B+C)/(A+B+C) and the percentage difference ($D_{\%diff}$) index (B+C)/(2A+B+C),

228   described for example in Legendre (2014) [15]. B and C express the directionality of the

229   process of losses and gains of individuals between two surveys. The graphs in the Results

230   show B and C scaled by division by (A+B+C), as well as the D_R dissimilarity, which measures

231   temporal beta diversity. Values of these three indices are in the [0,1] range. When applied to

232   presence-absence data, D_R becomes the Jaccard dissimilarity index and $D_{\%diff}$ becomes the

233   Sørensen index.

234   We carried out the before-after analysis of the supralittoral zone data of the two outer

235   reefs by visual inspection. That was sufficient to draw conclusions because only a few species

236   were capable of surviving in the harsh conditions of water shortage found therein. Analysis

237   did not require computation of the indices described in the previous paragraph.

238   (f) *Software*

239   The calculations were performed in the R language [16]. Alpha diversity indices were

240   computed using the *diversity()* function of the *vegan* package [17]. Redundancy analyses were

241   computed   with   the   *rdaTest*   package   available   on

242   http://adn.biol.umontreal.ca/~numericalecology/Rcode/. BD_{Total} and LCBD indices were

243   computed with function *beta.div()* [12, Appendix S4]. A simple *ad hoc* R function was written

244   to compute indices for the before-after comparison.

245   **6. Results**

246   Gastropod counts along the sampling years on the three transects are presented in Appendix

247   S1. Table S1.6 reports the scientific names of species collected on the transects following

248 current nomenclature, the synonyms used in [7], as well as the species feeding categories.

249 (a) *Reef flats and edges of the outer reefs (Terme Sud and Hélène)*

250 Alpha diversity values and total numbers of animals are reported in Table 1. On Terme Sud,

251 fewer animals were found after the *Canopus* test (August 1968) than before; numbers

252 increased again during the following surveys. On both reefs, species richness was higher after

253 *Canopus* than before, indicating that the reefs were again suitable habitats for the fauna and

254 that primary colonization by larvae brought in a good diversity of molluscs. On both reefs, the

255 N_1 diversity number was higher or about equal in 1972 than in 1967 or 1968.

256 After Hellinger transformation of the data, BD_{Total} among years was 0.162 on Terme Sud

257 (7 data years) and 0.107 on Hélène (6 data years). For both transects, yearly LCBD indices

258 were high and significant for the first year only, which is, before the *Canopus* nuclear test in

259 August 1968 (Table 2).

260 The RDA biplots show the among-year variation (figure 2a,b). Different species

261 displayed different patterns of variation along the years:

262 • *Scutellastra flexuosa* was a characteristic species on Terme Sud in 1968, where it was found

263 exclusively on the reef edge. It had completely disappeared during the 1969 to 1977 surveys,

264 to reappear in 1987 and 1997. On the reef flat, a group of species increased in abundance from

265 1969 to 1977 and a few species, not seen or rarely seen previously, appeared in 1987 (*Nerita*

266 *plicata*) and 1997 (e.g. *Mancinella armigera*, *Drupa morum*) (Figure 2a, Table S1.1).

267 • On Hélène, *Scutellastra flexuosa* was also a characteristic species of the reef edge in 1967. It

268 had nearly disappeared at the time of the 1972 to 1977 surveys, to reappear in 1987 and 1997.

269 On the reef flat, a group of species increased in abundance from 1972 to 1987 (*Mitra litterata*,

270 *Tenguella granulata*, *Morula uva*) and a few species not seen previously appeared in 1997

271 (e.g. *Cerithium sp.*, *Monetaria caputserpentis*) (Figure 2b, Table S1.3).

272   Additional canonical analyses (RDA) compared temporal community evolution on the

273   two outer reefs, Terme Sud and Hélène, after the *Canopus* nuclear test. The explanatory

274   variables were again a 2nd-degree polynomial function of time, plus a factor identifying the

275   two transects. The differences in community composition between the two reefs were

276   significant in the supralittoral zone and on the reef flats and edges. The results, detailed in

277   Appendix S2, clearly indicate that after the *Canopus* test, community compositions evolved

278   differently on the two reefs. Significant indicator species [18,19] were identified in the reef

279   flat and edge data (figure S2.2); three species were specific to Terme Sud and four to Hélène.

280   (b) *Reef flat and edge of the inner reef (Manchot)*

281   Fewer animals were found after the *Canopus* nuclear test than before; numbers increased

282   during the four following surveys (Table 1). Species richness was about the same in all

283   surveys. The N_1 diversity number was higher in 1972 than in 1968.

284   In the RDA biplot displaying among-year variation (figure 2c), different species had

285   different patterns of variation along the years. *Cerithium echinatum* and the echinoderm

286   *Halodeima atra* were very abundant in 1968; they nearly disappeared from that reef during all

287   following surveys. A group of species increased in abundance from 1968 to 1997 (*Tenguella*

288   *granulata*, *Drupa ricinus*, *Imbricaria conovula*, *Mitra litterata*, *Conus sponsalis*). *Morula uva*

289   was high in 1968, then low, then very abundant in 1997. *Dendropoma maxima* and *Chama*

290   *croceata* had medium abundances in 1968, then low, then medium again. Other species

291   remained stable during the six surveys (*Conus ebraeus*, *Conus miliaris*, *Conus nanus*) (Figure

292   2c, Table S1.5).

293   The bivalves *Chama* and *Tridacna* completely disappeared from Manchot after the

294   *Canopus* test. *Chama* came back to pre-test levels in 1977 and increased even more in 1997.

295   The gastropod *Cerithium echinatum* also nearly disappeared after *Canopus*.

296   (c) *Before-after comparisons for the reef flat and edge data*

297   Carnivores dominated on all three reefs: their proportions were 0.794 on Terme Sud, 0.865 on

298   Hélène and 0.767 on Manchot (over 6 surveys: 1 before *Canopus* and 5 after).

299   Let us examine the graphs for Terme Sud (figure 3a,b) in detail to understand how to

300   extract information. The left-hand graph concerns the 10 herbivorous species whereas the

301   right-hand graph deals with the 14 carnivores. The abscissa indicates which surveys are being

302   compared: the 1968 pre-*Canopus* survey is compared in turn to the five post-test surveys

303   conducted from 1972 to 1997. The D_R (temporal beta) index computed for all species (grey

304   circles) is shown in both graphs; it is fairly constant over the five comparisons, representing an

305   average change of 62% in community composition. We see that the change among the

306   herbivores (closed circles, left) is more important (86% on average) than among the carnivores

307   (right, 48% on average). Among the herbivores (left), the abundance losses of several species

308   (squares) of the pre-*Canopus* survey are large whereas the gains (triangles) of other species in

309   the second survey are small. The opposite is true for carnivores (right), although the difference

310   is smaller. In each graph, the losses and gains (squares plus triangles) sum to the

311   dissimilarities (filled circles).

312   On Hélène (figure 3c,d), the overall dissimilarity between surveys (grey circles) is

313   higher than on Terme Sud, representing a change of 77% on average, with a peak for the

314   1967-1977 comparison. Here, changes in herbivore abundances were higher during the first

315   two comparisons than for carnivores (closed circles), nearly equal in the 1967-1977

316   comparison, and lower in the last two comparisons (on average, 72% for herbivores and 78%

317   for carnivores). Among the herbivores, two species found in 1967 were present again in 1972

318   with reduced abundances; they increased to higher abundances as time went by, and were

319   joined by 4 other herbivore species (Table S1.3). This resulted in a decreasing curve of

320   herbivore losses (squares) and an increasing gain of these and other herbivore species

321   (triangles). Among the carnivores, the abundance losses (squares) of the 9 species present in

322   the pre-test survey were small whereas the gains in the post-test surveys (triangles) were large.

323   The gains and losses of the detritivores are not plotted because they involved a single species.

324   On inner reef Manchot (figure 3e,f), the overall dissimilarity between surveys (grey

325   circles) is the highest of three surveyed transects, representing a change of 80% on average.

326   The changes in herbivore abundances were higher in all survey pairs (closed circles, 98% on

327   average) and lower for carnivores (66% on average). Among the herbivores, the losses of

328   several species (squares) found in the pre-*Canopus* survey are very high for all survey pairs

329   (91 to 98%), whereas the gains during the second survey of each pair (triangles) are very small

330   (1 to 5%). Among the carnivores, the losses of some species found in the pre-*Canopus* survey

331   (squares) are small and decreasing from 16 to 2%, whereas the gains in the second survey of

332   each pair (triangles) go increasing from 28 to 79%. The gains and losses of detritivores and

333   filter feeders are not shown because they only involved two species in each case.

334   (d) *Supralittoral zones of the outer reefs (Terme Sud and Hélène)*

335   Most animals found in the supralittoral zone were killed by the heat flash of the nuclear tests.

336   With time, the surviving individuals were joined on the conglomerate by new ones that settled

337   as larvae (Tables S1.2 and S1.4).

338   On Terme Sud, alpha diversity measured by H and N_1 increased with time (Table 1).

339   This is because the dominant gastropod, *Tectarius grandinatus*, decreased noticeably in

340   abundance after the *Canopus* nuclear test, increasing the evenness of the distribution of the

341   community composition, which was only composed of 2 to 5 species. On Hélène, alpha

342   diversity was much more variable through time, with no clear trend (Table 1). *Tectarius*

343   *grandinatus* decreased noticeably in abundance after *Canopus* and *Littoraria coccinea*

344   disappeared completely from the surveys until 1977.

345 **7. Discussion**

346 Reef molluscs are long-living animals. In the portion of Polynesia south of the equator, most

347 species reproduce during the austral summer. They can live several years, even decades; they

348 are not necessarily replaced on a yearly basis. Newcomers slowly replace animals found on a

349 reef when some die for natural causes, generating temporal autocorrelation in our survey data.

350 Reef carnivorous molluscs do not eat herbivorous molluscs; they eat small prey, including

351 polychaete worms, living in the algal turf.

352 (a) *Temporal variation on the reef flats and edges*

353 On Terme Sud and Hélène, species richness increased during the years following the nuclear

354 tests. On Manchot, it remained at the level it was before the tests although species composition

355 was strongly modified.

356 Total community variation among years (BD_{Total}) was fairly similar on the two outer

357 reefs (0.162 on Terme Sud and 0.107 on Hélène), but it was higher on the Manchot inner reef

358 (0.221); the BD_{Total} values are bounded between 0 and 1 and are comparable among reefs [12].

359 Species richness was also higher on Manchot than on the outer reefs, especially before the

360 *Canopus* test (Table 1). The Manchot inner reef offered more sheltered living conditions than

361 the outer reefs. Furthermore, Manchot was located about 6.5 km from the nuclear firing

362 platform (Fig. 1a), so that the frying effect of the nuclear tests was likely less important on the

363 Manchot fauna than on Terme Sud (3.5 km) and Hélène (3 km).

364 Only the LCBD indices corresponding to the first survey years (1967 on Hélène, 1968

365 on Terme Sud and Manchot), before the main nuclear test (Canopus, August 1968), were

366 significant (Table 2). This result indicates that community composition before the main test

367 was very different from what it became afterwards on each reef. So the end effect of the

368 nuclear tests was not to reduce species richness, but to allow the establishment of a mollusc

369 community largely different from what it had been before the tests.

370   The RDA biplots (figure 2) illustrate that process in terms of the changes in species

371   composition. On each reef, the surveys form an ordered sequence starting before *Canopus* and

372   moving on to 1972, 1974, 1977 and 1987, with species (arrows) changing in importance along

373   the years. The 1997 survey is in a position orthogonal to the line joining the 1967-68 to 1987

374   surveys, which shows that it is not a simple linear extension of that sequence. The circular (or

375   arched) arrangement of the survey years is due to gradual changes in species composition

376   (Tables S1.1, S1.3 and S1.5).

377   The before-after analyses of the flat and edge portions of the three reefs (figure 3)

378   indicate that after the molluscs were wiped out of the reefs by the *Canopus* and *Dragon* tests,

379   primary succession, which was initiated by larvae coming from the ocean during the following

380   years, caused community composition to vary a lot from transect to transect. Comparing the

381   reefs,

382   • on Terme Sud, all carnivorous species found before the tests were also found after, in

383   reduced abundances at first; carnivore losses were replaced by individuals of other carnivorous

384   species that were partly new to the reef (Table S1.1). By opposition, two abundant species of

385   herbivores were replaced largely, but not entirely, by other species of herbivores and by

386   carnivores after the tests. The community increased in richness (Table 1) along the years after

387   the tests;

388   • on Hélène, new herbivorous species were found on the reef after the tests; most species

389   (herbivores and carnivores) increased in numbers, forming a community that increased in

390   density (Table 1) during the years of surveys after the tests. The species composition changed

391   without significant change in species richness;

392   • on Manchot, all carnivorous species found before the tests were also found after, some in

393   reduced abundances at first. The herbivores were more strongly affected (losses: squares) as

394   the single dominant species, *Cerithium echinatum*, nearly disappeared from all surveys from

395   1972 to 1997; it was replaced by a sparse representation of other herbivorous species and a

396   strong increase in several carnivorous species, in particular *Mitra litterata* (Table S1.5). The

397   community strongly increased in density along the years following the tests (Table 1).

398   Focussing on the two major trophic groups, it is clear that herbivores, which were found

399   in greater abundances before *Canopus*, did not recover their pre-test abundances and were

400   replaced by carnivores (Terme Sud, Manchot) or by other species of herbivores and by

401   carnivores (Hélène) during the post-test surveys.

402   Larvae coming from the surrounding ocean recolonized the reefs. On the reef flats and

403   edges of the two external reefs (Terme Sud and Hélène) and of the internal reef (Manchot),

404   herbivores were replaced after the nuclear tests either by species of the same (herbivores) or a

405   different feeding group (carnivores). That mixture is consistent with the hypothesis of neutral

406   dynamics, partly or entirely independent of the environmental conditions on the reef flats and

407   edges of Fangataufa atoll.

408   (b) *Supralittoral zones*

409   Few gastropod species can survive the harsh conditions of the supralittoral zone on a

410   tropical atoll; species have different types of shells and different habitats. *Nerita plicata* and

411   *Tectarius grandinatus* have strong, heavy shells. *Nerita* lives in crevices and near water,

412   *Tectarius* is found on conglomerate or coral blocs covered by endolithic *Entophysalis* algae

413   that give the blocs a grey colour. *Littoraria coccinea* has a thin and tiny shell and lives

414   exposed to the sun. On Hélène transect, populations of *L. coccinea*, directly exposed to the

415   flash of the *Canopus* nuclear explosion (August 1968), were completely eliminated. Some new

416   individuals were found on the supralittoral blocks ten years later and the population recovered

417   after ten more years (Table S1.4, Appendix S1). The populations of *N. plicata*, whose

418   individuals are always found in crevices, were not eliminated and those of *T. grandinatus*,

419   whose individuals are found both in crevices and exposed, were partly eliminated (Table

420   S1.4). The picture was almost the same on the Terme Sud supralittoral zone (Table S1.2)

421   except for the total absence of *L. coccinea* due to frequent strong currents during strong swell.

422   In summary, community composition did not change much on the supralittoral zones, where

423   only a few species can survive. Strong species filtering by environmental conditions clearly

424   dominated during recolonization of the supralittoral zone on both reefs.

425   (c) *Sampling issues*

426   Eight ecological surveys conducted across three decades represented an important effort to

427   follow the changes in community composition on a remote atoll of the tropical Pacific Ocean,

428   where transportation and logistic costs are high. In more accessible study sites, more surveys

429   could have been conducted. As a consequence, it is clear that we have only detected the main,

430   long-term trends in the changes of the Fangataufa mollusc communities following the nuclear

431   atmospheric tests. The data we collected do not allow us to say anything about shorter-term

432   variations in community composition, which must also have taken place between our surveys.

433   **8. Conclusion**

434   Our observations of reef recolonization by molluscs after the nuclear tests conducted on

435   Fangataufa allow us to understand the relative roles of neutral processes and environmental

436   filtering that both played a role, but in different portions of the reefs.

437   Our observations clearly show that environmental filtering played a dominant role on the

438   supralittoral zones. Only a few species can tolerate their harsh conditions, where they formed

439   species-poor communities, which greatly differed in composition from the richer communities

440   of the reef flats and edges. Differences observed between the two types of habitats are clearly

441   due to differences in environmental conditions.

442   In the reef flat and edge zones, however, neutral processes dominated. Quite different

443   communities developed on the three reefs after the tests, as the result of random settlement of

444 larvae from the open ocean. Differences between reefs were cumulative and increased from

445 year to year across 29 years of recolonization. Mollusc assemblages that developed on these

446 portions of the reefs are likely to be the result of a dynamics governed by stochastic

447 immigration of species that were ecologically equivalent within the herbivore and carnivore

448 trophic groups. This is an interesting case of neutral dynamics, which has been developed to

449 explain diversity patterns in tropical forests and coral reefs [5,20,21].

450 **Ethics.** This paper does not report research on human or animal experimentation.

451 **Data accessibility.** The Fangataufa atoll data are available in the electronic supplementary

452 material, appendix S1.

453 **Competing interests.** We have no competing interests.

454 **Authors' contributions.** BS designed the study and carried out the surveys reported in this

455 paper. PL participated in the 1997 survey, analysed the data and wrote the manuscript. BS

456 participated in the interpretation and discussion of the results. The two authors gave final

457 approval for publication.

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523

524 Table 1. Alpha diversity indices and total numbers of animals per year for the three transects.

525 Column headings: years and months of the surveys.

	1967	1968	1969	1972	1974.	1977	1987	1997
	Oct.	Mar.	Mar.	Jan.	Oct.	Sept.	Jan.	May
Terme Sud transect								
Reef flat and reef edge								
Richness	—	10	12	15	16	16	17	18
Shannon H	—	1.88	1.76	2.11	1.96	1.96	2.36	2.29
$N_1 = \exp(H)$	—	6.57	5.79	8.29	7.12	7.08	10.62	9.87
Total animals	—	446	163	342	489	361	335	332
Supralittoral zone								
Richness	—	2	—	2	2	3	2	5
Shannon H	—	0.20	—	0.39	0.63	0.55	0.69	0.69
$N_1 = \exp(H)$	—	1.22	—	1.47	1.88	1.74	1.99	2.00
Total animals	—	266	—	54	85	87	99	193
Hélène transect								
Reef flat and reef edge								
Richness	12	—	—	14	14	12	15	14
Shannon H	1.99	—	—	1.98	1.61	1.02	1.63	1.90
$N_1 = \exp(H)$	7.32	—	—	7.28	5.02	2.78	5.13	6.70

531 **Terme Sud transect**

532 *Reef flat and reef edge*

533 Richness

534 Shannon H

535 $N_1 = \exp(H)$

536 Total animals

538 *Supralittoral zone*

539 Richness

540 Shannon H

541 $N_1 = \exp(H)$

542 Total animals

544 **Hélène transect**

545 *Reef flat and reef edge*

546 Richness

547 Shannon H

548 $N_1 = \exp(H)$

Total animals	246	—	—	356	821	1259	1008	765

Supralittoral zone

Richness	3	—	2	2	2	3	3	3
Shannon H	0.58	—	0.68	0.58	0.44	0.31	0.91	0.74
$N_1 = \exp(H)$	1.78	—	1.97	1.78	1.55	1.36	2.48	2.10
Total animals	567	—	58	19	133	174	253	262

Manchot transect

Reef flat and reef edge

Richness	—	21	—	17	23	20	19	19
Shannon H	—	1.76	—	2.15	1.61	2.25	2.03	2.00
$N_1 = \exp(H)$	—	5.80	—	8.56	5.02	9.50	7.60	7.40
Total animals[1]	—	995	—	382	776	616	964	1631

[1] *Cerithium punctatum* not counted. See Table S1.5.

Table 2. LCBD indices per year and p-values (after 9999 random permutations) for the three reef flat and edge transects. The LCBD indices for each transect are relative values summing to 1; p-values ≤ 0.05 and the corresponding LCBD indices are in bold. Column headings: years and months of the surveys.

	1967	1968	1969	1972	1974.	1977	1987	1997
	Oct.	Mar.	Mar.	Jan.	Oct.	Sept.	Jan.	May
Terme Sud transect								
LCBD per year	—	**0.28**	0.15	0.14	0.04	0.08	0.13	0.18
p-values	—	**0.0375**	0.3579	0.4382	0.9982	0.8892	0.4603	0.2249
Hélène transect								
LCBD per year	**0.40**	—	—	0.17	0.07	0.22	0.06	0.09
p-values	**0.0022**	—	—	0.4551	0.8427	0.2969	0.9014	0.7595
Manchot transect								
LCBD per year	—	**0.46**	—	0.11	0.16	0.07	0.09	0.11
p-values	—	**0.0009**	—	0.7593	0.4515	0.9804	0.8734	0.7392

587 Figure legends

588 Figure 1. Map of the Fangataufa atoll showing (a) the transects perpendicular to the shoreline

589 (black rectangles) and (b, c, d) their profiles at low tide. The horizontal lines above the profiles

590 identify the sampled transects, divided into zones: RE = reef edge, RF = reef flat, SZ =

591 supralittoral zone. Motu: reef islet with vegetation. ✱ Approximate position of the nuclear

592 firing platform for all atmospheric nuclear tests.

593 Figure 2. RDA biplots of the reef flat and reef edge data on (a) Terme Sud, (b) Hélène, and

594 (c) Manchot transects, showing the species (arrows) and sampling years (points). Name

595 abbreviations of species with small loadings on the canonical axes (short arrows) were

596 removed to improve legibility; see tables in Appendix S1 for full species names. The

597 explanatory variables (not shown) formed a 2nd-degree polynomial function of time. (Online

598 version in colour.)

599 Figure 3. Before-after statistics comparing the pre-test (1967 or 1968) to the post-test surveys.

600 (a,b) Terme Sud, (c,d) Hélène, and (e,f) Manchot transects. The indices, represented by points

601 joined by lines, are identified in the upper panel of each column; left: herbivores; right:

602 carnivores. The indices are described in *Statistical methods*. (Online version in colour.)

(a)

Manchot

N

∗

▨ : motu

Hélène

Terme Sud

2 km

(b) Terme Sud transect

RE | RF | SZ
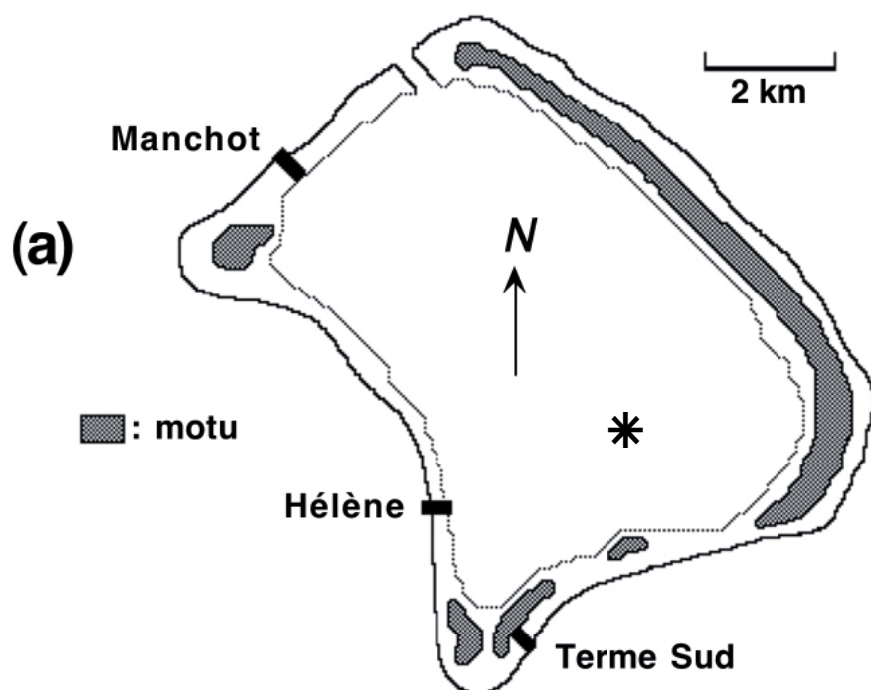
Scales for profiles

100 m

5 m

(c) Hélène transect

RE | RF | SZ
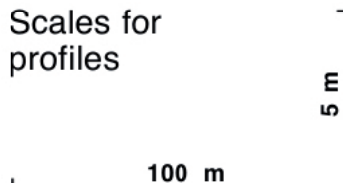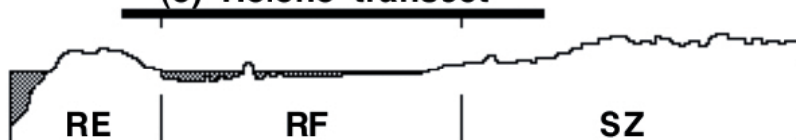
(d) Manchot transect

RE | RF
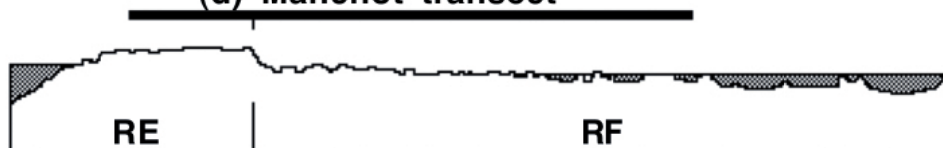
⇐Toward the ocean

Toward the lagoon⇒

(a) Terme Sud transect

(b) Hélène transect

(c) Manchot transect
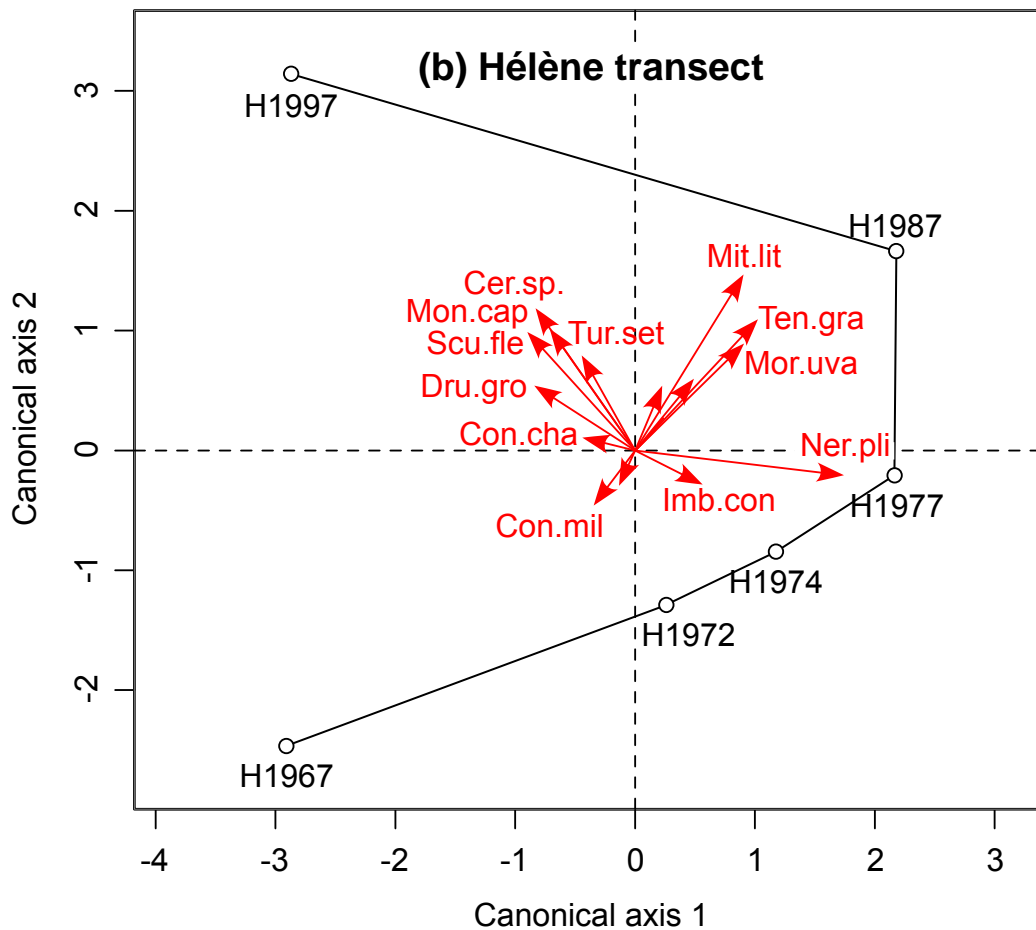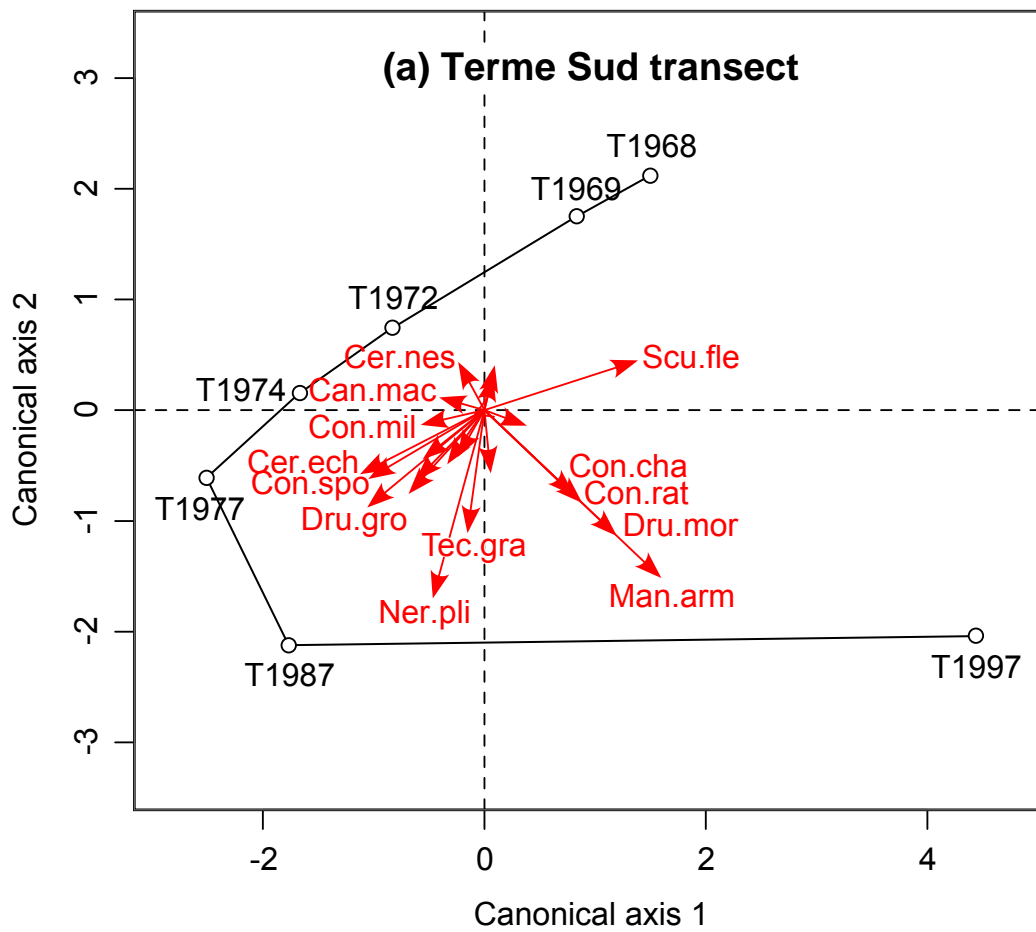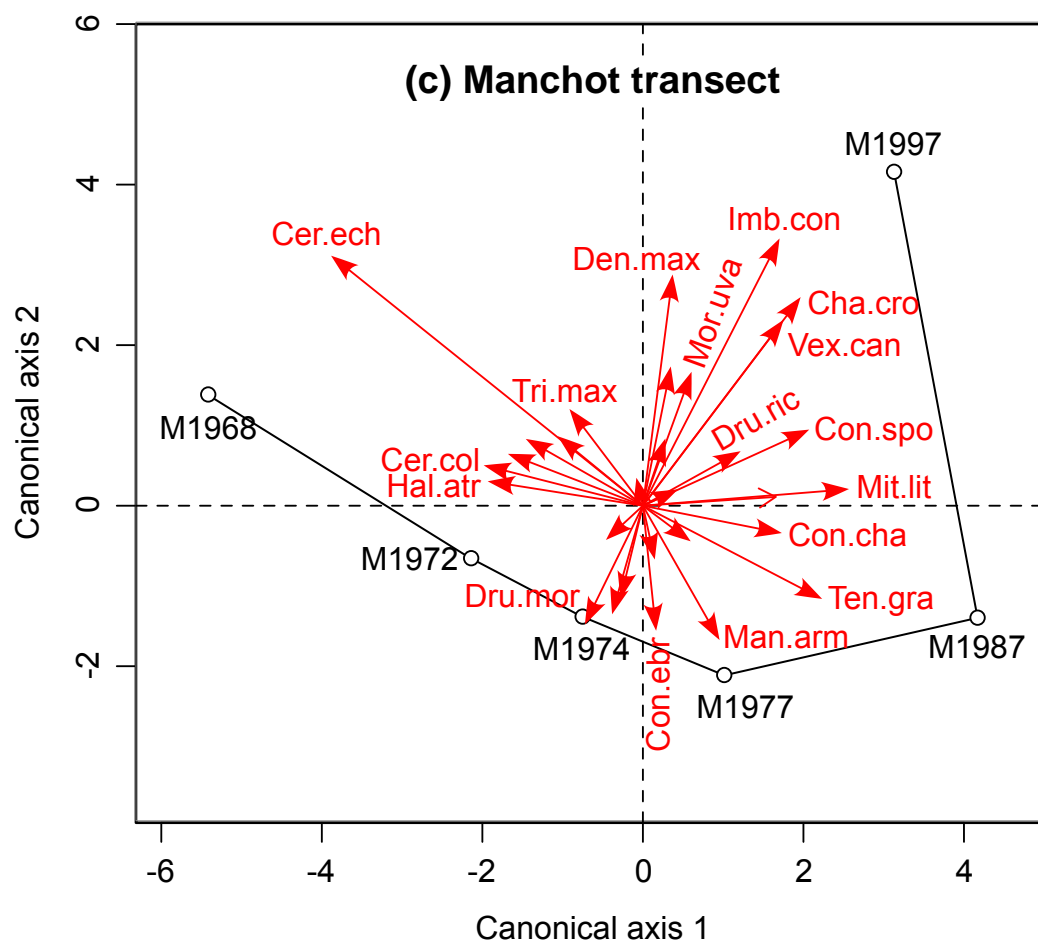
(a) Terme Sud, Herbivores
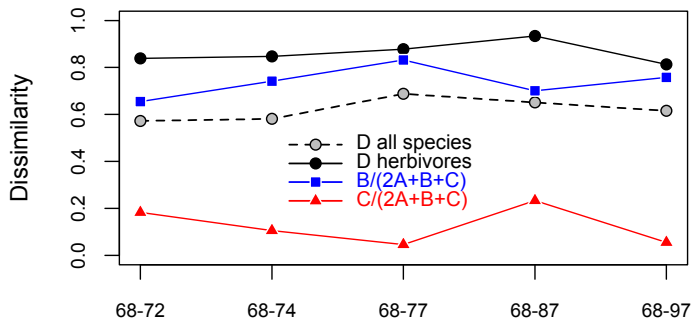
(b) Terme Sud, Carnivores
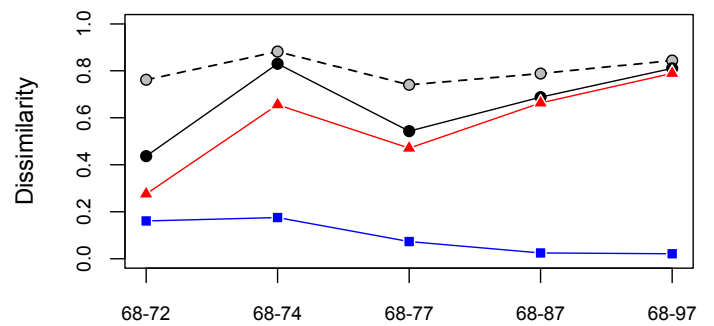
(c) Hélène, Herbivores
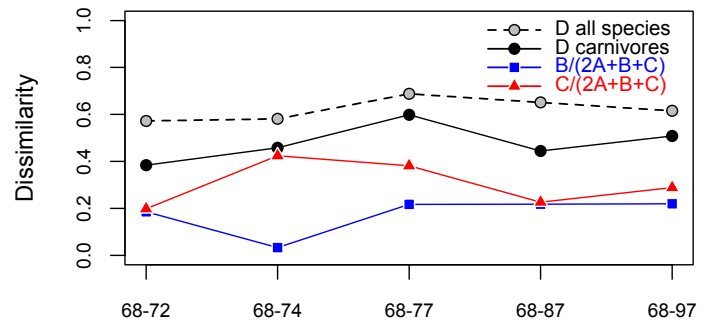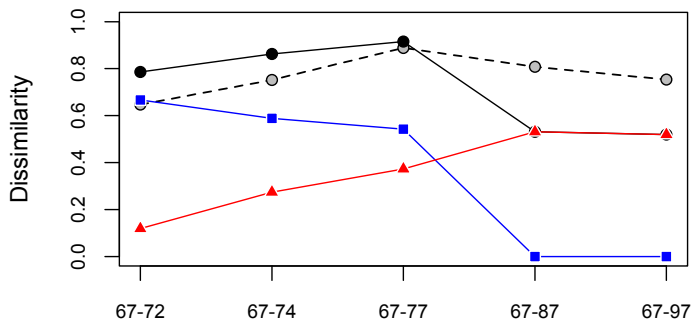
(d) Hélène, Carnivores
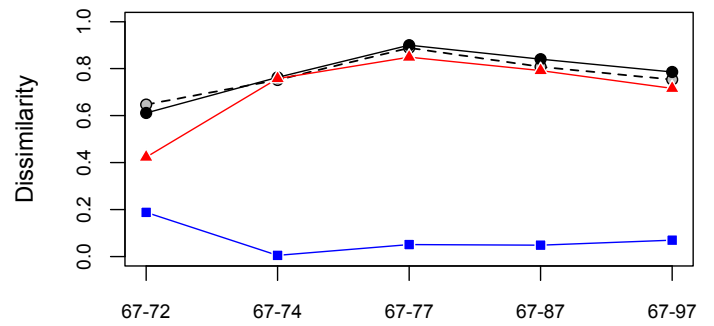
(e) Manchot, Herbivores
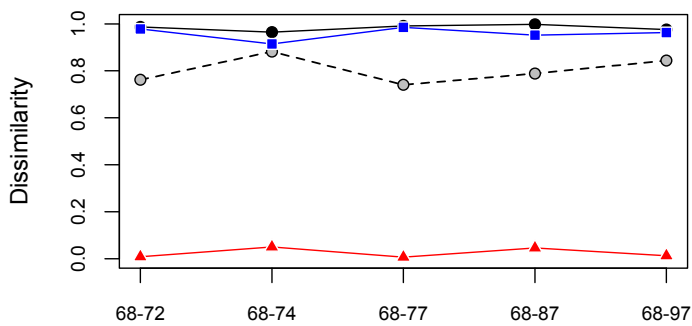
(f) Manchot, Carnivores

Appendices S1–S3 to:

Legendre P, Salvat B. 2015 Thirty-year recovery of mollusc communities after nuclear experimentations on Fangataufa atoll (Tuamotu, French Polynesia). *Proc. R. Soc. B* **282**, xxxx.

Appendix S1

COMMUNITY COMPOSITION DATA TABLES

Table S1.1. Gastropod counts for the various sampling years, on the reef flat and reef edge of the Terme Sud transect. 7 quadrats on the reef edge, 15 on the reef flat; 24 species. Column headings: years and months of the surveys.

Species	1968.3	1969.3	1972.1	1974.10	1977.9	1987.1	1997.5	Feeding category
Scutellastra flexuosa	127	0	0	6	0	3	14	H
Turbo argyrostomus	0	2	0	0	0	0	0	H
Turbo setosus	60	7	37	26	24	13	23	H
Nerita plicata	0	4	6	5	3	38	6	H
Cerithium echinatum	0	5	0	14	3	12	0	H
Cerithium nesioticum	0	0	15	0	0	0	0	H
Cerithium sp.	0	0	17	0	0	0	3	H
Tectarius grandinatus	0	0	0	0	1	4	1	H
Canarium maculatus	0	5	0	2	1	2	0	H
Monetaria moneta	0	0	4	1	1	1	1	H
Tenguella granulata	37	7	26	32	29	31	41	C
Morula uva	45	27	83	108	109	81	46	C
Drupa grossularia	0	0	2	8	1	9	0	C
Drupa morum	0	0	0	0	0	0	13	C
Drupa ricinus	104	12	71	96	21	42	40	C
Mancinella armigera	0	0	0	0	0	0	33	C
Imbricaria conovula	0	0	5	1	7	2	1	C
Mitra litterata	43	79	60	149	105	38	85	C
Conus chaldaeus	0	0	0	0	0	0	5	C
Conus ebraeus	3	0	5	9	4	7	2	C
Conus miliaris	19	11	6	24	31	25	7	C
Conus nanus	5	3	4	7	11	9	5	C
Conus rattus	0	0	0	0	0	0	6	C
Conus sponsalis	3	1	1	1	10	18	0	C

Table S1.2. Gastropod counts for the various sampling years, on the supralittoral zone of the Terme Sud transect. 13 quadrats, 5 species. Column headings: years and months of the surveys.

Species	1968.3	1969.3	1972.1	1974.10	1977.9	1987.1	1997.5	Feeding category
Nerita plicata	13		7	28	17	54	32	H
Littoraria coccinea	0		0	0	0	0	9	H
Tectarius grandinatus	253		47	57	69	45	150	H
Tenguella granulata	0		0	0	1	0	1	C
Thalessa aculeata	0		0	0	0	0	1	C

Table S1.3. Gastropod counts for the various sampling years, on the reef flat and reef edge of the Hélène transect. 4 quadrats on the reef edge, 31 on the reef flat; 17 species. Column headings: years and months of the surveys.

Species	1967.10	1969.3	1972.1	1974.10	1977.9	1987.1	1997.5	Feeding category
Scutellastra flexuosa	29		2	1	5	32	40	H
Turbo setosus	8		7	6	0	37	17	H
Nerita plicata	0		5	14	22	9	0	H
Tectarius grandinatus	0		0	0	0	1	0	H
Cerithium sp.	0		0	0	0	0	12	H
Dendropoma maxima	22		79	33	59	76	76	D
Monetaria caputserpentis	0		0	0	0	0	8	H
Tenguella granulata	1		27	33	30	47	29	C
Morula uva	64		95	436	945	551	335	C
Drupa grossularia	6		1	4	0	4	12	C
Drupa ricinus	19		57	103	117	74	97	C
Imbricaria conovula	0		3	3	1	1	0	C
Mitra litterata	2		41	82	29	120	84	C
Conus chaldaeus	6		6	5	3	3	10	C
Conus miliaris	14		2	13	1	5	3	C
Conus nanus	68		28	80	27	38	33	C
Conus sponsalis	7		3	8	20	10	9	C

Table S1.4. Gastropod counts for the various sampling years, on the supralittoral zone of the Hélène transect. Number of quadrats: see footnotes. 3 species. Column headings: years and months of the surveys.

Species	1967.10	1969.3	1972.1	1974.10	1977.9	1987.1	1997.5	Feeding category
Nerita plicata[1]	12	34	5	21	10	21	3	H
Tectarius grandinatus[1]	450	24	14	112	161	136	146	H
Littoraria coccinea[2]	105	0	0	0	3	96	113	H

[1] Abundances of these species were counted on 10 quadrats with surface area summing to 60 m^2.

[2] That species extended much farther up the supralittoral zone than the other two species. Its abundance was counted on 67 quadrats summing to 402 m^2.

Table S1.5. Mollusc (and one echinoderm) counts for the various sampling years, on the reef flat and reef edge of the Manchot transect. 12 quadrats on the reef edge, 30 on the reef flat; 31 species. Column headings: years and months of the surveys.

Species	1968.3	1972.1	1974.10	1977.9	1987.1	1997.5	Feeding category
Gastropoda							
Scutellastra flexuosa	0	0	0	2	0	0	H
Turbo setosus	0	2	0	0	0	4	H
Nerita plicata	0	2	5	1	0	0	H
Cerithium columna	13	0	3	0	0	0	H
Cerithium echinatum	432	6	11	3	0	10	H
Cerithium punctatum[1]	0	0	0	0	112000	0	H
Cerithium zebrum	0	0	17	0	0	0	H
Canarium maculatus	1	0	1	1	0	0	H
Dendropoma maxima	36	22	2	9	28	76	D
Monetaria caputserpentis	1	0	3	0	23	3	H
Monetaria moneta	9	0	1	0	0	0	H
Tenguella granulata	4	16	92	78	76	61	C
Morula uva	142	112	30	116	170	316	C
Drupa grossularia	13	35	2	11	2	10	C
Drupa morum	5	3	1	5	3	0	C
Drupa ricinus	8	9	15	18	26	40	C
Thalessa aculeata	0	0	0	0	0	1	C
Mancinella armigera	0	1	1	1	7	0	C
Engina siderea	7	0	0	0	0	0	C
Imbricaria conovula	3	6	16	8	6	202	C
Mitra litterata	17	85	455	119	387	585	C
Vexillum cancellarioides	0	0	0	1	2	13	C
Conus chaldaeus	1	7	15	9	18	17	C
Conus ebraeus	20	17	13	32	44	7	C
Conus flavidus	0	0	0	0	2	0	C
Conus miliaris	18	16	11	12	16	16	C
Conus nanus	54	35	58	94	62	85	C

Conus sponsalis	5	2	2	16	39	29	C

Bivalvia

Chama croceata	31	0	8	48	46	147	F
Tridacna maxima	4	0	1	0	0	1	F

Echinodermata

Halodeima atra	171	6	13	32	7	8	D

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[1] *Cerithium punctatum*: That small species (adult size 10-12 mm) was only found in 1987 where it was present in large abundance, probably the result of a temporary pullulation. The number quoted was obtained by estimation from a series of very small quadrats. That species was not included in the calculations of H and $N_1 = \exp(H)$ mollusc diversity indices in Table 1, but it was included in the calculation of species richness. It was not included in any of the other analyses reported in this paper.

Table S1.6. Scientific names of molluscs and echinoderms found on Fangataufa Atoll during the 1967 to 1997 surveys following current nomenclature. Third column: synonym names used in Lanctôt *et al*. (1997). Feeding categories: H = herbivore, C = carnivore, D = detritivore, F = filter feeder.

Family	Species	Synonyms used in Lanctôt *et al*. (1997)	Feeding category
Gastropoda			
Patellidae	*Scutellastra flexuosa* (Quoy & Gaimard, 1834)	*Patella flexuosa*	H
Turbinidae	*Turbo argyrostomus* Linnaeus, 1758		H
	Turbo setosus Gmelin, 1791		H
Neritidae	*Nerita plicata* Linnaeus, 1758		H
Cerithidae	*Cerithium columna* Sowerby, 1834	*Cerithium torulosum*	H
	Cerithium echinatum Lamarck, 1822	*Cerithium mutatum*	H
	Cerithium nesioticum Pilsbry & Vanatta, 1906		H
	Cerithium punctatum Bruguière, 1792		H
	Cerithium zebrum Kiener, 1841		H
	Cerithium sp.		H
Littorinidae	*Littoraria coccinea* (Gmelin, 1791)	*Littorina coccinea*	H
	Tectarius grandinatus (Gmelin, 1791)		H
Strombidae	*Canarium maculatus* (Sowerby, 1842)	*Strombus maculatus*	H
Vermetidae	*Dendropoma maxima* (Sowerby, 1825)		D
Cypraeidae	*Monetaria caputserpentis* (Linnaeus, 1758)	*Cypraea caputserpentis*	H
	Monetaria moneta (Linnaeus, 1758)	*Cypraea moneta*	H
Muricidae	*Tenguella granulata* (Duclos, 1832)	*Morula granulata*	C
	Morula uva (Röding, 1798)		C
	Drupa grossularia Röding, 1798		C
	Drupa morum Röding, 1798		C
	Drupa ricinus (Linnaeus, 1758)		C
	Thalessa aculeata (Deshayes @Milne Edwards, 1844)		C
	Mancinella armigera (Link, 1807)		C
Buccinidae	*Engina siderea* (Reeve, 1846)	*Engina alveolata*	C
Mitridae	*Imbricaria conovula* (Quoy & Gaimard, 1833)		C
	Mitra litterata Lamarck, 1811		C

Costellariidae	*Vexillum cancellarioides* (Anton, 1839)		C
Conidae	*Conus chaldaeus* (Röding, 1798)		C
	Conus ebraeus Linnaeus, 1758		C
	Conus flavidus Lamarck, 1810		C
	Conus miliaris Hwass in Bruguiere, 1792		C
	Conus nanus Sowerby, 1833		C
	Conus rattus Hwass in Bruguiere, 1792		C
	Conus sponsalis Hwass in Bruguiere, 1792		C

Bivalvia

| *Chamidae* | *Chama croceata* Lamarck, 1819 | *Chama imbricata* | F |
| *Cardiidae* | *Tridacna maxima* (Röding, 1798) [1] | | F |

Echinodermata

| *Holothuriidae* | *Halodeima atra* Jaeger, 1833 | | D |

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[1]The small giant clam *Tridacna maxima*, a filter feeder, obtains most of the nutrients it requires from zooxanthellae living in its tissues.

Appendix S2

COMPARISON OF THE EVOLUTION OF THE TWO OUTER REEFS THROUGH TIME

The Terme Sud (T) and Hélène (H) transect community composition data were compared through a canonical analysis (RDA) of the supralittoral zone data on the one hand and of the reef flat and reef edge data on the other.

The mollusc data collected at matching dates after the *Canopus* nuclear test were used as response data for that comparison, that is, the sampling years {1972, 1974, 1977, 1987, 1997}; the data were subjected to a $\log(y + 1)$ transformation. The explanatory variables were a binary variable distinguishing the two sites (Terme Sud and Hélène) and a 2nd-degree orthogonal polynomial function of time, which allowed each time series to be represented by a folded curve in the ordination plots.

For the **supralittoral zones**, only three species were used in the analysis: *Nerita plicata*, *Littoraria coccinea* and *Tectarius grandinatus*. The other two species found on Terme Sud were anecdotal (Table S1.2). Figure S2.1 shows that the difference between the Terme Sud and Hélène time series, which is significant (partial RDA p-value = 0.043), is associated with greater abundances of *Nerita plicata* on Terme Sud during all 5 years, and greater abundances of *Tectarius grandinatus* (from 1974 to 1987) and *Littoraria coccinea* (from 1977 to 1997) on Hélène (Tables S1.2 and S1.4).

For the **reef flat and reef edge zones**, all 25 species (Tables S1.1 and S1.3) were used in the analysis. Figure S2.2 shows that the difference between the Terme Sud and Hélène time series, which is highly significant (partial RDA p-value = 0.008), is associated with greater abundances on Terme Sud of the species pointing to the left of the plot, and greater abundances on Hélène of the species pointing to the right.

Indicator species analysis (Dufrêne & Legendre 1997, De Cáceres & Legendre 2009; R package *indicspecies*, De Cáceres & Jansen 2011) of the reef flat and edge data showed that seven species were significant indicators, at the 0.05 significance level, of one or the other transect:

• *Conus miliaris* was found in greater abundance on Terme Sud during all five surveys, whereas *Conus ebraeus* and *Monetaria moneta* were found exclusively on Terme Sud;

• *Morula uva*, which was the most abundant species on both transects, was found in much greater abundance on transect Hélène. *Conus chaldaeus* and *Conus nanus* were also more abundant on Hélène, whereas *Dendropoma maxima* was only found on Hélène.

The main message of the triplot (figure S2.2) is that the two transects had greatly different species compositions and that different species (red arrows pointing left and right) were driving the evolution of the assemblages on the Terme Sud (left) and Hélène (right) reef flats and edges.
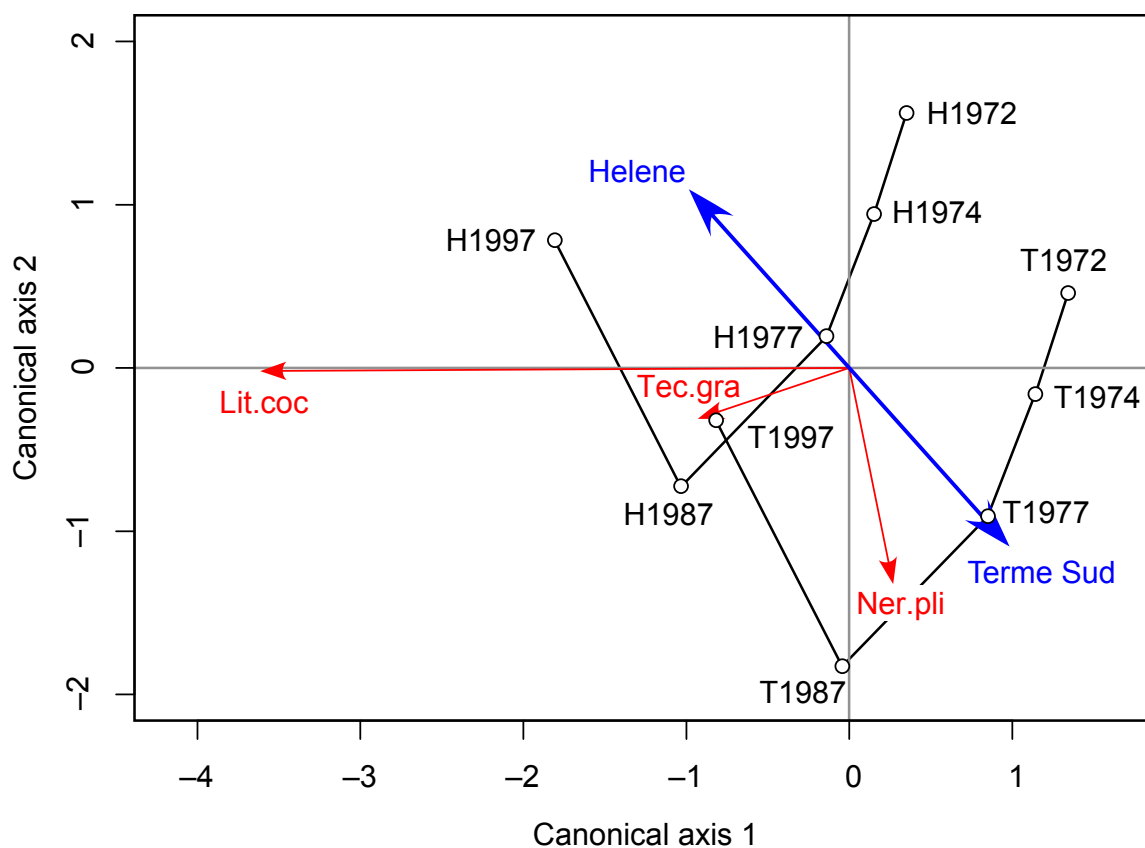
Figure S2.1. RDA triplot comparing the evolution through time of the communities in the supralittoral zones of the two transects (Terme Sud and Hélène, represented by blue arrows with large arrowheads). Black lines materialize the survey time sequence. Species are represented by thin red arrows. Species abbreviations: see Appendix S1. The year points labelled T correspond to Terme Sud are those labelled H to Hélène. The explanatory variables year and year² are not shown.
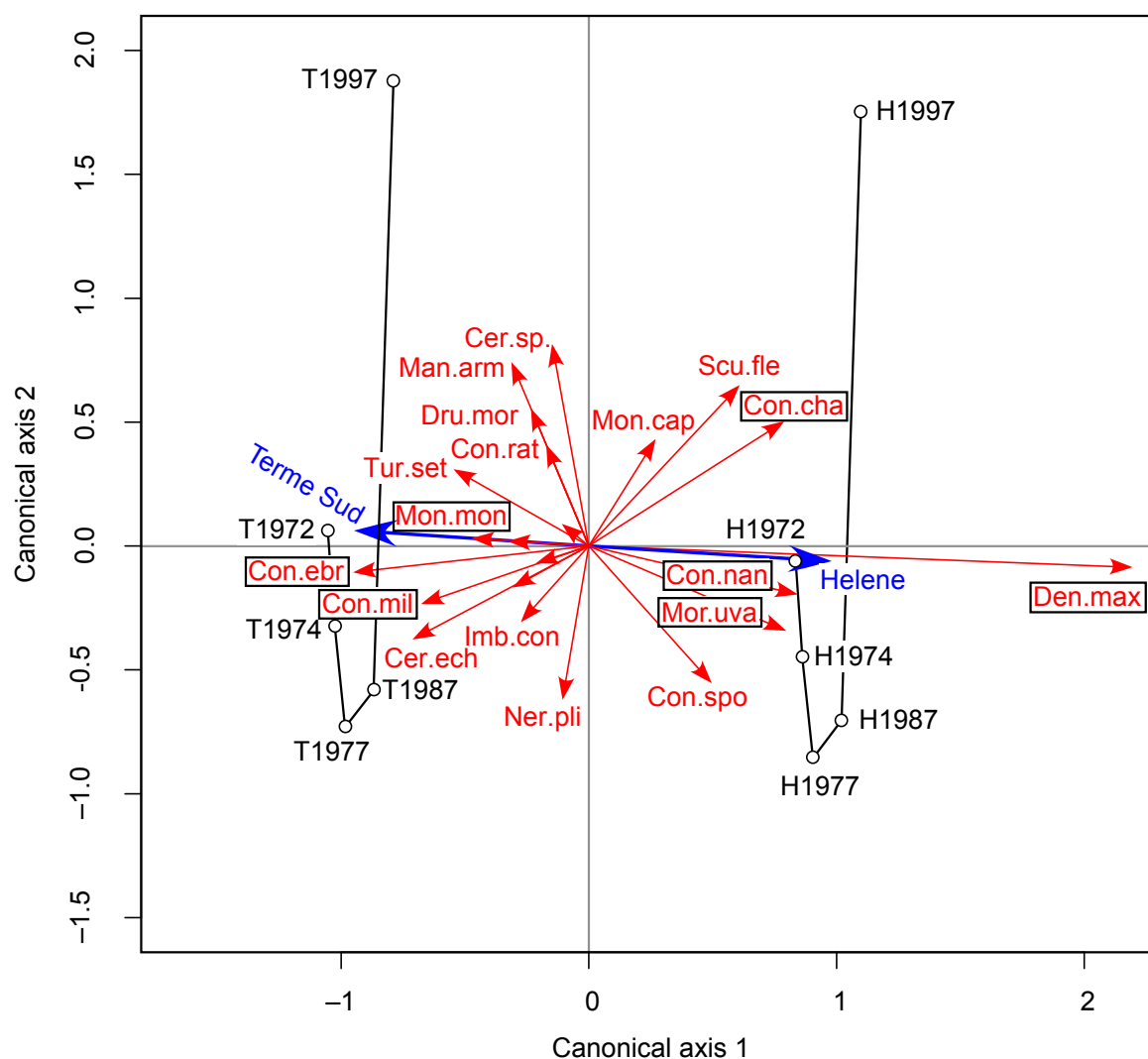
Figure S2.2. RDA triplot comparing the evolution through time of the communities on the reef flats and edges of the two transects (Terme Sud and Hélène, represented by blue arrows with large arrowheads). Black lines materialize the survey time sequence. Species are represented by thin red arrows. Significant indicator species at the $\alpha = 0.05$ level have boxed names. Species abbreviations: see Appendix S1. Names of species with the shortest arrows were not printed to make the plot easier to read. The explanatory variables year and year^2 are not shown.

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Appendix S3

A CHANNEL DUG IN THE NORTHERN PORTION OF THE ATOLL CROWN

The inner-reef communities were subjected to another major man-made impact. Fangataufa atoll was originally a completely closed atoll without passes and no important exchange of water between the ocean and the lagoon. Water entered the lagoon through small and shallow channels between islets, called "hoas" [1,2] (http://www.atolls-polynesie.ird.fr/glossaire/coupatol.htm), found mostly on the eastern side of the atoll where the Hélène site is located, and across reef flats found for example in the northern portion of the rim near the Manchot site. Through these hoas and flats, oceanic waves pushed water into the lagoon where the level was always a little higher, by some decimetres, than the mean ocean level. This is not the case in an open atoll, which has one or several passes. In these atolls, the tidal exchange of water between the ocean and the lagoon is immediate and the water level is nearly identical in the lagoon and the ocean.

In June 1965, a channel was dug in the northern portion of the atoll crown to give transport ships access to the lagoon in order to build the nuclear testing facilities. The channel is about 100 m wide, 350 m long and 8 m deep and plays the same role as a natural pass in an open lagoon.

This opening caused a lowering of the water level by about 30 cm in the lagoon, with immediate impact on the reef flat communities on the lagoon side of the atoll crown, including the Manchot transect, sampled from 1968 to 1997, which is included in the present study. Due to the lowering of the water level inside the lagoon, a portion of the Manchot reef flat emerged at low tide.

Unfortunately, no comparative survey data are available from the period before the opening of the channel. The anthropogenic lowering of the water level in the lagoon affected only the inner reefs, including the Manchot transect, and not Terme Sud and Hélène which are facing the ocean and are separated from the lagoon by a motu (islet made of sand, coarse coral rubble and sediment, with some vegetation in most cases).

References

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