Reef Geoscience Group

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Dear Editor

We thank you and the anonymous reviewer for the comments on the manuscript. Again all the points raised were valuable and gave us the opportunity to improve the manuscript. The main concern of the reviewer was about the temporal analysis of pooled abundance data within the two-way PERMANOVA design. We understand the reviewer's concern and have edited the manuscript to provide a detailed justification about our statistical approach within the text and to the reviewer.

The main changes to the manuscript include adding a new figure to supplementary material under the recommendation of the reviewer, making minor corrections in tables and in the redaction of the manuscript, and changes in the order of coral species in figure 4 to facilitate cross-panel comparisons in all directions. The changes made to the previously submitted manuscript are described in detail below.

We hope that this updated version of the manuscript is now suitable for publication in PeerJ.

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On behalf of all authors

General comments

Overall, I feel this version is much improved and that it has addressed the main issue about method-biases I had raised in my previous comments. There is also greater clarity in how the data were handled and analyzed. Because of the latter, there is one potentially additional significant issue that has caught my attention, which is the use of number of colony counts in the 2019 dataset and the number of chain links in the 1979/1985 to derive estimates of relative abundance to compare between periods. My sense is that numbers of chain links inform mainly about spatial living coverage of the different coral species, irrespective of their colony numbers, so it is not quite clear that these two metrics are directly comparable. In my view, a more meaningful comparison would have involved deriving estimates of relative abundance based on actual colony counts for both periods (since these data seem available) OR based on surface area covered by each coral in 2019 (since the data on both colony counts and colony size also seem available) and number of chain links in 1979/1985 period. Having said that, the authors have supplemented their key analyses with presence/absence data, which should be fairly robust to these data handling decisions, and the general patterns seem to hold (Table 2). As such, I would endorse the manuscript for publication after minor revisions provided that the authors give appropriate consideration to my specific comments below.

Reply: *We thank the reviewer for the detailed and thorough review of our paper. Regarding temporal analysis of the abundance data, which we believe is the main source of the concern, we have expanded our considerations in the response to the comment 2.0 below and in the discussion (line 326-332).*

Specific comments

Comment 1.1: Line 50-53 – It is not clear what does the "however" make reference to – I get the sense that the point here is that you can have coral grounds that are not geologically accretionary because they have been subject to high levels of physical erosion by hurricanes and they are thus basically made of coral fragment remains. If that is what is meant, introducing the term non-accretionary in that sentence would help as a contrast to the previous sentence.

Reply 1.1: *We agree and have added the term.*

Comment 1.2: Line 80-83 – This sentence is not clear – are the surveys the ones in the paper or those from a different study? Moreover, the objective is not very clear – I presume that it is to assess the extent to which homogenization has occurred in these two geomorphologically different zones? It would be good to mention that historical data from the 70's will be compared to recent data for that purpose to inform about the specific temporal period of interest.

Reply 1.2: *We agree and have modified the text (lines 80-83)*

Comment 1.3:Line 133 –comma should come after citation brackets

Reply 1.3: *Done*

Comment 1.4: Line 134 – after b), sentence should star in lower case

Reply 1.4: *Done*

Comment 1.5: Line 142 – Please clarify that the IVI for the pre-1990's data is only based on the 1985 dataset.

Reply 1.5: *We agree and have modified the text (lines 142-143)*

Comment 1.6:Line 153-154 – I think the key idea here is that if the method-biases are small relative to the real signal of change, then the latter would still be reliably and meaningfully detected. The Nadon and Jokiel references could then be used to argue that previous studies comparing the two methods indicate that such method biases appear indeed to be small - the later conceptual framework (i.e. method biases being small relative to the true signal) is probably better because using the term "virtually indistinguishable" might require clarification about whether or not their tests had sufficient power, which is often not the case.

Reply 1.6: *We agree and have modified the text accordingly (lines 156- 161)*

Comment 1.7:Line 163-167 - Good. I also agree that diversity metrics are likely to be less affected by method-biases than % coverage ones.

Comment 1.8:Line 172 – replace "…which has difficulties dealing with this using …" with "…which makes it difficult to deal with using …"

Reply 1.8: *Done*

Comment 1.9: Line 175 – 185 - I feel that the method-bias issue has been sufficiently addressed in the "Method biases and uncertainties section" and I do not think that any further action is needed. In the previous section the authors provide sufficient arguments to conclude that, although method-biases are likely, the main choice of metrics by the authors (i.e. diversity metrics), along with findings from other studies cited comparing the two specific methods at hand, suggest that these method-biases are likely to be small relative to the effects that the authors are investigating in this particular study. It is not perfect, but it is probably enough to help justify their statistical approach and it is much better than not saying anything about potential method-biases (as it was in the previous MS version).The problem I see now in this section (lines 175-185) is that it provides a sense that method-biases can be somehow dealt with once the data have been collected. This is not true unless it is via the use of calibration/conversion curves linking both methods, which the authors do not have. I would thus recommend removing lines 175-179 and any subsequent reference to method-biases in this section. The various standardizations of the data can probably remain as they are.

Reply 1.9: *We agree and have modified the text accordingly and removed the reference to method-biases in this section (lines 179-180).*

Comment 2.0: Line 180-182 – Why are colony counts used to estimate relative abundance in the 2019 dataset considering that chain links are used to do the same in the 1979/1985 dataset? Using colony counts does not seem to consider that different coral species differ markedly in size. You can have a small-sized coral species (A. agaricites, P. astreoides) scoring very high in relative abundance even though overall it covers much less living space than a few but bigger coral species (Orbicella spp). This clarification is important because using the chain links to estimate relative abundance in the 1979/1985 datasets will better reflect the spatial living coverage of the different species than the actual number of colonies (unless I am missing something) [see Loya 1972 Mar Biol 13:100-122 as an example of a study using line transects to calculate both relative abundance (based on no of colony counts under a chain) and living coverage (based on no of chain links under the chain) of a coral community]. It would have made more sense to transform the 2019 dataset in relative spatial living coverage data (rather than relative abundance data), since the colonies were counted and sized, prior to calculating their relative abundance to compare with the 1979/1985 dataset. Alternatively, the colony counts of the 1979/1985 data could be used (instead of the chain links) to calculate the relative abundance of each species to compare with the 2019 dataset (as in Loya 1972). As it stands now, it might seem like comparing apples (2019: colony count estimates) with oranges (1979/1985: living coverage index), which if true could contribute to artificially create differences between time periods. I suspect I might not be the only one wondering about this and so this data handling decision will require further clarification. Perhaps one draconian (but more robust) way to deal with this potential problem would be to focus on presence/absence data only throughout the manuscript - this approach is already done in the “Diversity” column of Table 2; presence/absence data could also be used for Figures 4 and 5.

Reply 2.0: *We accepted the reviewer's suggestion and have performed the temporal analysis of abundance data after transforming absolute abundance from 2019 data into relative coverage to reduce the disparate nature of raw abundance data in time (line 182-185). These approaches did not alter the results of temporal comparative analysis based on contrasts for factor year. The reviewer also suggests a focus on presence/absence data throughout the MS, however, the concern about analysis of pooled abundance data only affects the temporal comparison, whereas abundance-based pairwise analyses of factor zones are uncompromised.*

Moreover, from the perspective in which the MS was conceived, the zonal analyses are essential. As a consequence, we consider that both abundance and presence-absence results are complementary, not mutually exclusive. We reiterate that the main goal of the MS is the comparative analysis between geomorphic zones (see lines 76-78, 166-169 and 204-206) and we therefore compare the historical and contemporary data separately. In those pairwise analyses, we neither combine nor mix benthic methods. For the historical data (pre 1990s: 1979 and 1985) we only used the chain method, while for the 2019 year we only used the data collected from belt transects. In table 2 (PERMANOVA pairwise tests) we present the results in this manner and also highlight the benthic method involved in each case). We tackled the remaining issue of method bias and disparate nature of raw data extensively in the ‘Method

Biases and Uncertainties' section, and expanded our justification for dual abundance/diversity approach in the discussion (324-332)

Comment 2.1 Line 220 – consider removing the commas

Reply 2.1: *Done*

Comment 2.2 Line 243- consider removing the commas

Reply 2.2: *Done*

Comment 2.3 Line 255 – Replace "Montastrea annularis complex" with "Orbicella…"

Reply 2.3: *Done*

Comment 2.4 Fig 2 – clarify in figure header that data from 1979 and 1985 were pooled together in panels C and D.

Reply 2.4: *Done*

Comment 2.5 Line 270 – insert "the" before "two zones"

Reply 2.5: *Done*

Comment 2.6 Line 273 -274 – Please clarify - is it correct to use the value of the Pseudo-F ratio as a measure of effect strength when comparing among PERMANOVA factors?, which is likely to differ across factors?

Reply 2.6: *We have now corrected the manuscript and used the correct estimator for the effect strength under our statistical design (random/fixed multi factors: Estimates of components of variations; Underwood & Petraitis 1993 and Anderson 2017).*

Comment 2.7 Figure 4 – Is it possible to show the same species rows across all four panels to facilitate cross-panel comparisons in all directions? Please see my previous comments (on lines 180-182) about what these abundance estimates actually likely reflect for each method/time period. Also, it should be "…fourth root…" in header text.

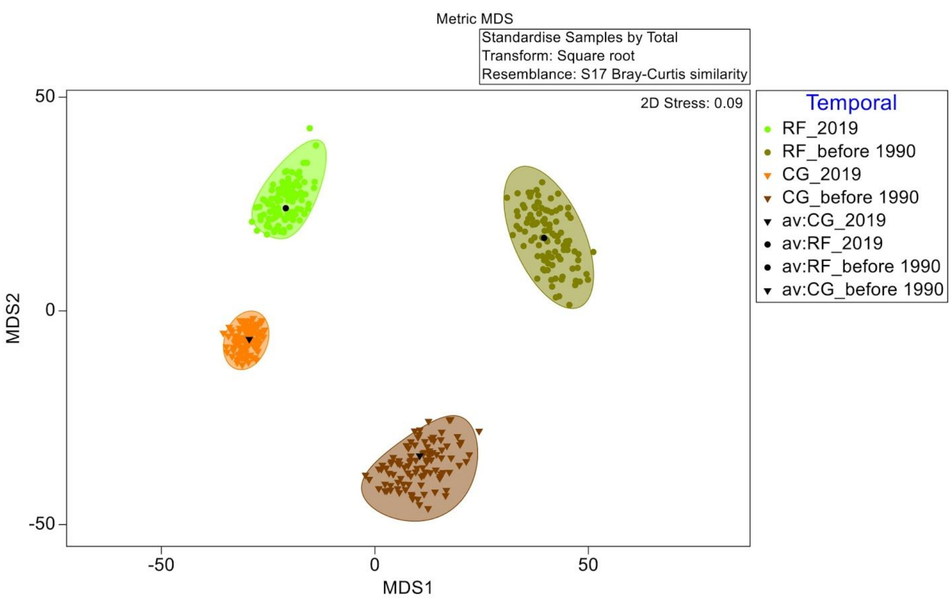
Reply 2.7: *Done*

Comment 2.8 Table 2 – Please clarify that normal (not in bold) font in under the two-way PERMANOVA header corresponds to the contrasts – I presume that the lines under the Factor Year x Zone also correspond to contrasts, but these (unlike the ones above under Factor Year) were never mentioned in the Methods (but I might have missed it) and it is not quite clear what they represent – moreover, one line has "RF,CG 1979" and the line below "RF/CG (79/85)" –not clear how the use of "," versus "/" is to be interpreted. Also, something seems wrong with the last two lines under the PERMANOVA (pair-wise tests) header (repetition of terms). Finally, the 2nd and 3rd sentence of the Table 2 header would benefit from some re-phrasing.

Reply 2.8: *We agree and have modified table 2 and its header in the manuscript to include the recommendations.*

Comment 2.9 In relation to the PermDisp tests, is it necessary to do all pair-wise comparisons? Why not simply focus on the within-zone temporal comparisons (the 3rd and 4th lines under the header)? It would facilitate digesting these results. Also, how does the fact that the variance in CG differs between pre-1990's and 2019 affect interpretation of the PERMANOVA results for CG, which presumably still assume similar dispersion between time periods when comparing centroids?

Reply 2.9: *We have modified table 2 to address this comment. Regarding reviewer's concern about how PERMDISP results affect interpretation of PERMANOVA we would like to highlight that PERMDISP do not invalidate PERMANOVA, rather PERMDISP is a complementary test that aid the interpretation of the PERMANOVA results. It means that in addition to the differences in centroids there are also differences in dispersion (verify in the mMDS below that the difference is clear)(verify in the mMDS below that the difference is clear) (verify in the mMDS below that the difference is clear) . Both analyzes indicate that there was a change in the composition (PERMANOVA result) and heterogeneity in distribution (PERMDISP result) of the coral species in those geomorphic zones from 1979 (85) to 2019 (lines 298-300).*



Bootstrap Averages Plot of Bray-Curtis Similarity matrix of square root transformed abundance data previously standardized by Total

Number of bootstraps per group: 100. Minimum rho: 0.99. Bootstrap regions: 95%. Optimum m: 8 rho: 0.993 / Parameters: Kruskal stress formula: 1

Minimum stress: 0.01 / Stress values: 3D: 0.05, 2D: 0.09

Comment 3.0 Fig 5 – Note that the permdisp value in the figure does not correspond with the one in the table. Replace "Montastrea annularis complex" with "Orbicella annularis…"

Reply 3.0: *Agreed. This is now amended in the MS*

Comment 3.1 Line 294-306 – I think it is important to acknowledge that (1) both zones have changed markedly over time, and (2) that they done so in a manner that has led to some homogenization. I think this is the best interpretation of Fig 5 (i.e. it not only about homogenization, which could imply only one zone changing).

Reply 3.1: *Agreed. That is the sense of those lines and we further specify in which way the zones have changed.*

Comment 3.2 Line 300 – I do not recall any reference to these values (21.9% and 52.5%) in the Results section or supplementary material, but I might have missed it.

Reply 3.2: *Agreed. This has been amended now in the MS (line 303) and referring those values in the supplementary material (Data S4. B)*

Comment 3.3 Line 313 – it might be important to distinguish between functional, taxonomic and ecological homogenization even from the Introduction and clarify which of these the MS is dealing with.

Reply 3.3: *Agreed. Throughout the manuscript we repeatedly allude to the constraints of detected partial homogenization (only in colony size and some ecological indexes) but not in taxonomic groups which we consider have implications for the geomorphological and geological approach of ecological studies. We consider this is solved in the discussion.*

Comment 3.4 Line 318-319 – This idea is good and further developed in Line 326-335 – it might be better to integrate these two into a single paragraph at once – the Lines 320-250 dealing with the robustness of the results, which is an important consideration, could then come at the end or in a different paragraph.

Reply 3.4: *We accepted reviewer suggestion and modified the text in the manuscript to include this recommendation (lines 327-338)*

Comment 3.5 Line 320 – I agree that any analysis based on the presence-absence data will be more reliable. As a suggestion, consider doing a similar figure to Fig 5, but based on presence/absence data to include as supplementary material.

Reply 3.5: *We accepted the recommendation, and have added the Figure as supplementary material Data S5 PCO Presence absence. This figure is now referred to in the MS in line 283 and 292- 294.*

Comment 3.6 Line 344 – consider adding the word “partial” in front of convergence.

Reply 3.6: *Done*

Comment 3.7 Line 349 – this line would benefit from further development or details on the “regional species succession reported by Aronson and Precht (2001)”; enough so that the reader does not need to go to the cited paper to get a clearer sense of what it is implied.

Reply 3.7: *We modified the text in the manuscript to include this recommendation (lines 352-355)*

Comment 3.8 Line 371-372 - Please clarify - Not clear if the contrast with Valles et al refers to identifying ecological patterns within reef types (rather than among reef types) or by using geomorphic zones or metrics other than coral coverage or a combination of any of these.

Reply 3.8: *We modified the text in the manuscript to clarify the contrast: (lines 383-387)*

Comment 3.9 Line 376 – missing bracket.

Reply 3.9: *Done*

Comment 4.0 Line 397-399- I was not sure about the basis for this statement about recruitment failure –it would benefit from further development or clarification in the Discussion or in the Conclusion itself.

Reply 4.0: *We modified the text in the manuscript to clarify our conclusions.*