

1 We would like to thank both reviewers for their constructive reviews and acknowledge their thorough
2 evaluation. We are pleased to learn that the reviewers appreciate our innovative modeling study to
3 identify assembly processes of species communities in a situation where knowledge and data regarding
4 ecological requirements and morphological/anatomical features of the model species are limited.

5 We first summarize the five major critical points raised by the reviewers and demonstrate how we will
6 account for them in our revised ms. In the second part, we then provide a point-by-point reply (in italics)
7 to all comments.

8 Major criticism (MC) and reply:

- 9 • MC1: missing figure with the geographic position of Lake Ohrid
10 *We will include a map showing the location of Lake Ohrid.*
- 11 • MC2: difficulties to see which and how certain variables were derived and used to infer the
12 importance of community assembly processes.
13 *The inferred importance of all three assembly processes is based on only two variables. The*
14 *hierarchical taxonomic classification of the gastropod species informed about the two selective*
15 *processes environmental filtering and species interaction. The observed species prevalence is the*
16 *only variable used for inferring the importance of dispersal limitation. No morphological*
17 *measures parameterized the process-importance (see MC3). However, from reading the*
18 *comments of referee #2 and talking to other colleagues we realized that our new analytical*
19 *approach needs to be explained in more detail. In the revised manuscript, we will therefore*
20 *include a flowchart sketching how this approach infers the processes of community assembly*
21 *based on the two variables. Moreover, we will provide a clearer explanation of the stepwise*
22 *community assembly (STEPCAM) approach in the Material and methods section.*
- 23 • MC3: questioning the validity of translating morphology into a metric of gastropods' niche and
24 therefore into the agent of species selection during the community assembly process.
25 *We used a taxonomic classification for inferring the importance of niche-based environmental*
26 *filtering and species interaction (see MC2). We will modify the respective section to make this*
27 *clearer to the reader. However, no matter whether morphological or taxonomical similarity is*
28 *used, this concern is a serious criticism. It questions fundamental assumptions about using*
29 *functional or phylogenetic metrics for estimating the relative importance of community assembly*
30 *processes. This methodological revolution shifted community ecology from a correlative*
31 *approach relating certain abiotic proxies with community composition to a process-based*
32 *perspective and facilitated the finding of general assembly rules (reviewed in Emerson and*
33 *Gillespie, 2008; McGill et al., 2006; Webb et al., 2002). The underlying assumption is that*
34 *ecological selection (i.e., natural selection without any sexual selection) results in similarity of*
35 *anatomical, morphological, and behavioral traits of species because environmental adaptations*
36 *and traits are valid metrics of niche. Phylogenetic analyses of community assembly assume that*
37 *closely related species do not differ much in traits because of their recent divergence and need to*
38 *inhabit similar environment due to environmental adaptation of their ancestors. Therefore,*
39 *phylogenetic measures, too, are a valid metric of niche (Pausas and Verdú, 2010). In this reply*

40 *letter (see below), we demonstrate that traits of closely related gastropod species of Lake Ohrid*
41 *resemble each other more than expected by neutral divergence. We also show that taxonomic*
42 *classification is a valid metric of niche.*

43 • MC4: circularity in defining first eco-zones within Lake Ohrid (i.e., areas of similar species
44 composition) and later use those areas to test whether they correlate with species distribution.
45 *First, we inferred the relative importance of community assembly processes. Then we delineated*
46 *eco-zones based on similarity in gastropod community composition and their geographic and*
47 *bathymetric location. Finally, we tested whether the importance of the assembly processes itself,*
48 *and not the distribution, differed among eco-zones. Of course, the assembly processes eventually*
49 *give rise to the species distribution but we do not consider both being equivalent and thus not*
50 *committing circular reasoning.*

51 • MC5: too far reaching implications of our actually inferred community assembly processes on
52 modes of speciation.
53 *We do think that there is a sound theoretical basis for relating assembly processes with*
54 *corresponding modes of speciation. However, in the revised ms, we will focus more on what we*
55 *actually tested and less on their evolutionary implications. We will also modify the title of our*
56 *manuscript accordingly as following: “Processes of gastropod community assembly in ancient*
57 *Lake Ohrid: a metacommunity perspective”*

58 **Reviewer #1 (Thomas Neubauer)**

59 **General comments**

60 The authors present a highly interesting study on the impact of community assembly processes on the
61 structure of gastropod communities in Lake Ohrid. While most other studies focus on single processes,
62 the authors apply an innovative and very comprehensive approach using up-to-date statistical analyses
63 and simulation techniques (and even inventing new ones), in order to integrate as much information as
64 possible. They convincingly demonstrate the importance of dispersal limitation, and to a lesser extent
65 environmental filtering and species interactions, and that the specific impact of each process varies
66 spatially. The results and conclusions on the non-exclusive roles of ecological and geographical speciation
67 are important advances in the study of speciation in ancient lakes and speciation in general.

68 The hypothesis of the study is clear and the methods are sufficiently outlined and support the results.
69 Title and abstract reflect well the content of the paper. The paper is well written and structured and the
70 English is of a high quality. The authors give proper credit to published studies in the field.

71 I have only a few remarks, which rather are suggestions, and therefore recommend publication after
72 minor revision.

73 *Thank you!*

74

75 **Specific comments**

76 I would like to see an additional figure showing the geographic position of Lake Ohrid (similar to the one
77 you give in Föllner et al. 2015 Biogeosc. Disc.). This would help readers not familiar with the lake and
78 where it is located. The other figures are well made and essential to show sampling sites and eco-
79 zonation and to highlight the relative importance of the three processes depending on the eco-zones.

80 *We will include a map showing the location of Lake Ohrid (see MC1):*



81

82 *Figure 1. Location of Lake Ohrid and freshwater ecoregions.*

83 The authors mention three times in the text (Abstract, Introduction, Conclusion) that the findings
84 contribute to the goal of the SCOPSCO initiative. Maybe you could take it out in either the conclusion or
85 the abstract.

86 *True. We will therefore remove the explicit reference to the SCOPSCO initiative in the middle and at the*
87 *end of the introduction.*

88

89 **Reviewer #2**

90 **General comments**

91 The objective of this work is to use a largely endemic, diverse gastropod fauna to:

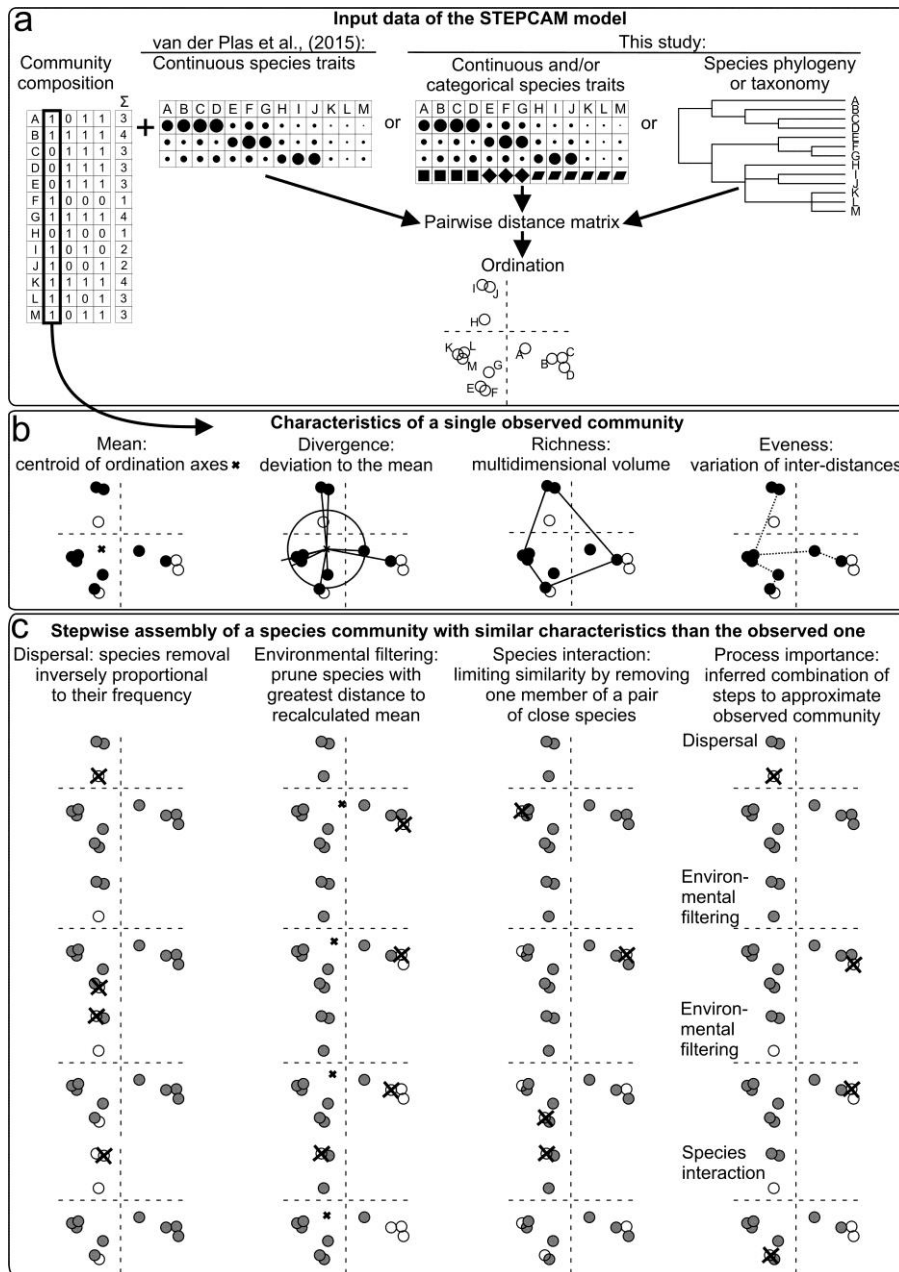
- 92 • Quantify and rank several ecological and evolutionary processes that are potential drivers of
93 community assembly using a simulation model
- 94 • Test whether lake depth or additionally refined 'eco-zones' are better correlated with these
95 quantified processes

96 This is the first application of this particular set of process-level ecological and evolutionary models to
97 gastropod community data in an ancient lake. Other metacommunity analyses have been done in other
98 systems, though the topic is in its infancy so the work is novel in its specific application. Its good to see a
99 freshwater mollusc radiation being used for this kind of interesting process-level question, and
100 gastropods are an appropriate focal group. Lake Ohrid is a fascinating, diverse model system.

101 The processes are stated to be neutral or selective. Dispersal limitation is considered a neutral process,
102 whereas selection by physical agents (what the authors call environmental filtering) or by biological
103 agents (here called species interaction) are active processes. The authors say they are looking for either a
104 gradual or stepped change in the relative importance of these processes in the lake, as this might then
105 help link biological and physical processes in the lake. They also mention that this informs on the role of
106 speciation+extinction in community assembly, but I find that connection un- or minimally- addressed by
107 the data in hand, as we don't yet have a phylogenetic context input into this analysis, nor do I see
108 extinction data being considered. It might simply be that the text needs to be clarified on this.

109 I have a key concern with this paper - it is difficult to see how the variables (the basic data, traits or
110 characters) going in to the analyses were derived and what they really reflect. Perhaps this just requires
111 clarification in both the text and supplement.

112 *We do understand that many readers may have difficulties to precisely understand our modeling*
113 *approach. This might be due to the facts that the concepts applied are still in their infancy and that the*
114 *actual approach used has been existing for few months only (also see MC2 and MC3). In the revised*
115 *version of our ms, we will therefore include a more detailed description of our approach as well as a new*
116 *flowchart for our community assembly model (Fig. 2). We will also add a description (Readme.txt) to the*
117 *supplements with all steps for reproducing our analyses. All necessary files plus a script for running the*
118 *analyses on one click were already included in the original version of the ms. Please note that we never*
119 *spoke about extinctions in our ms. However, according to the reviewer's suggestion, our discussion will*
120 *stays closer to our analyses of community assembly, and implications on speciation will be down-toned*
121 *(MC5).*



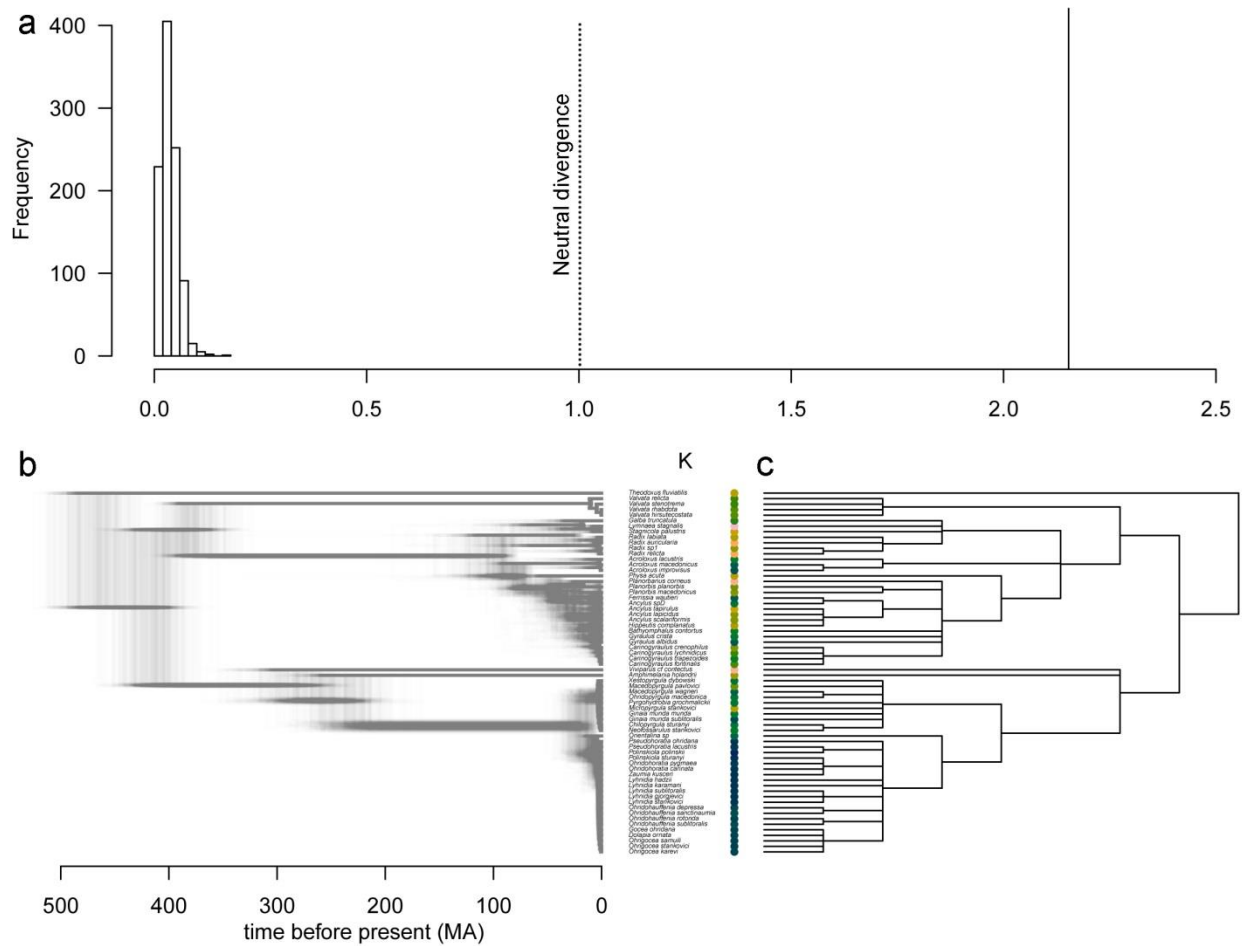
122

123 *Figure 2. Illustration of the distance-based stepwise community assembly model (STEPCAM). (a) The*
 124 *model is parameterized by species' frequencies and either species traits or a species phylogeny or a*
 125 *hierarchical taxonomic classification, respectively. (b) For the focal species community, four, depending*
 126 *on the input, either functional or phylogenetic/taxonomic indices are calculated (for details see Villéger et*
 127 *al., 2008). (c) These index-values are the targets for the modeled community. A simulation starts with all*
 128 *species, stepwise removes species according to the three processes dispersal limitation, environmental*
 129 *filtering, and species interaction, and stops when the same number of species as in the focal community*
 130 *is reached. The process-combination that generates a species community with minimum differences*
 131 *between observed and generated index-values is inferred through Approximate Bayesian Computation*
 132 *within a Sequential Monte Carlo framework.*

133 The ecological variables reflecting ‘niche’ are derived in an unspecified way from morphology. The
134 authors say “these ecological requirements are assumed to be reflected by morphological features
135 because the latter are often under selection”. I could not find an explanation of how morphology was
136 translated to be a metric of niche. How was phylogenetic constraint (or signal, or history) removed from
137 morphology so that it reflects ecological niche in a reliable, repeatable way? This seems essentially
138 impossible at a broad scale – gastropods look quite different based on their evolutionary lineages. The
139 argument that because selection can influence (at least some aspects of) morphology (in some
140 gastropods), does not justify then using morphology as an overall metric of selection, and thus of an
141 even more derived variable of ecological niche. Examples of selection changing gastropod morphology
142 are of course numerous, but the transfer function is usually complex and lineage-specific, often working
143 on quite fine scales. In addition, there are many examples of apparently non-adaptive differences in
144 morphology, such as colour patterns on cone shells. Going from selection >> morphology is a black box
145 that is a challenging puzzle within a single lineage; doing it as a blanket process doesn’t seem
146 supportable. As the potential agents of selection on Ohrid snail shell morphology aren’t specified, it is
147 not clear what part of the ecological system morphological differences might reflect. As an example, do
148 these snails all have shell-crushing predators, and do these respond more to changes in shell thickness,
149 sculpture or size? In addition, measuring molluscan morphology is an analytical challenge. Accretionary,
150 spiral growth means one has to disentangle homologous and non-homologous changes in more explicit
151 ways than for organisms with unitary growth. I could not find explanation of how this key variable for the
152 analyses was derived, and I can’t readily imagine how it can be used for its stated purpose in the analysis.
153 Perhaps this just needs clearer explanation.

154 *Please note we translated our taxonomic classification into a metric of niche and did not use morphology.*
155 *We fully agree with the reviewer about the power of morphological transfer functions. This is exactly the*
156 *reason why we did not use morphology for the calculation of our similarity matrices but taxonomy. The*
157 *latter appears to be much less prone to problems of homoplasy in gastropods from Lake Ohrid as the*
158 *taxon has been studied exceptionally well in the past years (e.g., Albrecht et al., 2006; Föller et al., 2015;*
159 *Hauswald et al., 2008; Schreiber et al., 2011; Wilke et al., 2007). Ricotta et al., (2012) showed that the*
160 *conclusions of community assembly studies drawn by using phylogenetic or taxonomic distances are*
161 *equivalent. However, in phylogenetic and functional community analyses both, phylogenies and*
162 *morphological traits are shown to be valid metrics of ecological niche (see MC2; Pausas and Verdú, 2010;*
163 *Webb et al., 2002). In fact, phylogenetic and functional community analyses often assess the equivalency*
164 *of both metrics by testing for a phylogenetic signal in traits (i.e., closely related species resemble each*
165 *other more than expected by neutral divergence) and do not aim to remove it. For this reply letter, we*
166 *quantified the volume of our gastropod species through the Archimedes principle and found a strong*
167 *phylogenetic signal in our taxonomic classification (Fig. 3). We could only use volume as a measure of*
168 *body size because most other morphometric measures are not comparable among distantly related*
169 *species (see the specific comment on non-homologous characters below). Body size is directly related to*
170 *the ecological niche of the species because it restricts potential position in microhabitats. We will keep*
171 *the valid point of species divergence along differential utilization of food resources in mind (see two other*
172 *points of criticisms below, but also Sitnikova et al., (2012, 2014) for resource partitioning in ancient lakes*
173 *gastropods and some analytical challenges related to it). Because we did not use shell morphology (see*

174 MC2) we also did not specify any agent of selection on this phenotype. There are no major shell-crushing
 175 predators, only a small area in the western side of Lake Ohrid with few crabs.



176
 177 *Figure 3. Closely related species show higher similarity in their body size than expected by neutral (i.e.,*
 178 *non-adaptive) divergence. We found a (a) significant and stronger phylogenetic signal K (Blomberg et al.,*
 179 *2003) of body size (colored dots) in our (c) taxonomic classification than in (b) 1000 hypothetical*
 180 *phylogenetic histories. Because no comprehensively dated phylogeny of freshwater gastropods including*
 181 *young and old splits exists, we inferred hypothetical phylogenetic histories based on published*
 182 *phylogenetic trees (Albrecht et al., 2007, 2008; Dinapoli and Klussmann-Kolb, 2010; Föller et al., 2015;*
 183 *Hauswald et al., 2008; Jörger et al., 2010; Wilke et al., 2007; Zapata et al., 2014). These known tree*
 184 *topologies, dated speciation events and genera memberships ('prior knowledge') were subjected to a*
 185 *Bayesian inference in BEAST 1.8.2 (Drummond and Rambaut, 2007) that simulates hypothetical*
 186 *phylogenetic histories and their uncertainties by sampling from these priors only. Uncertainty is shown by*
 187 *the overlay of the hypothetical phylogenies.*
 188 *Because of the stronger phylogenetic signal of an important niche metric in our taxonomic classification,*
 189 *we are confident that for our analysis of community assembly processes this classification is an even*
 190 *more robust variable than a dated phylogeny.*

191 Similarly, the variables that were to reflect dispersal were apparently derived from current species
192 distributions. This again seems many steps removed from what is intended to be the causal variable of
193 limited ability to reach new habitats. I would expect that one couldn't comment on dispersal without
194 some indication of gene flow, i.e., data from population genetics, and discussion of potential dispersal
195 stages (e.g. if eggs, juveniles, or brooding mothers are likely to travel passively or actively. Reference in
196 this section to adult movement rates for gastropods in mark-recap studies does not seem particularly
197 enlightening as dispersal may well happen through passive means at other life stages.) While I have
198 sympathy that population genetic data is not yet available for these taxa, I'm not convinced that current
199 distributions are a contradiction-free proxy for dispersal. Again perhaps this just needs clearer
200 explanation.

201 *A principal assumption of the STEPCAM model is that current distribution patterns are caused by past*
202 *dispersal processes (Janzen et al., 2016; van der Plas et al., 2015). In fact, in the absence of environmental*
203 *heterogeneity, dispersal limitation is the only process that can cause differences in species' frequencies*
204 *because environmental filtering and species interaction (e.g., competition for resources) cannot act. The*
205 *species' frequencies are therefore used to parameterize the model (Fig. 2) without intermediate steps.*

206 *Dispersal itself can be limited by several abiotic and biotic factors. We have no indication that water*
207 *currents are involved in creation of distribution patterns (and thus could act as dispersal mean). As for*
208 *other life stages than adults as potential dispersal stages, we need to stress here that with the exception*
209 *of one widespread species (Viviparus cf. contectus) no brooding occurs among Lake Ohrid gastropods (see*
210 *Michel, (1994) for consequences of reproductive strategies on species distribution). Eggs are either laid*
211 *on solid surfaces or might be carried by the adults. We therefore think that mark-recapture studies give*
212 *an informative estimate of the mainly active dispersal capacity.*

213 *Of course it would be nice to have a population-genetics based background for each of the species living*
214 *in Lake Ohrid for estimating gene-flow und thus (indirectly though) dispersal rates. As the reviewer*
215 *admits, this is wishful thinking rather than reality for the time being.*

216 Another variable used was a matrix of classification similarity – using taxonomy plus a level of common
217 clade membership to derive a similarity metric. This looks straightforward enough, but needs to have the
218 classification itself presented. The classification used to generate the data is referenced as a composite
219 of three past works, but this composite needs to be provided somewhere in order to be repeatable. It
220 should also be noted that of course classification similarity will have some redundancy on the
221 morphological metric. Limpets are in their own family with a high 'dissimilarity score' from hydrobiids in
222 this measure, but they will also have a great difference in the shape metric.

223 *We respectfully disagree with the reviewer as our analysis, indeed, is reproducible: the pairwise*
224 *classification similarity, together with all scripts were already included in the supplements of our original*
225 *ms. Now, we also provide a supplementary figure (see Fig. 3c) and a separate "Readme.txt" for*
226 *reproducing our whole community assembly analysis (See also criticism #15 in the editorial questions*
227 *below).*

228 *Moreover, apart from gastropod community composition, the 'classification similarity' was the only*
229 *variable used in our study (see MC2). In fact, we did not use morphology in the original manuscript. We*
230 *only employed one morphological trait here in the reply letter to support an equivalency between*
231 *'classification similarity' and morphology, both assumed to reflect the niche of a species (e.g., Emerson*
232 *and Gillespie, 2008; McGill et al., 2006; Webb et al., 2002).*

233 Is this classification similarity also the same as the ‘relatedness’ variable that is mentioned in the ABC-
234 SMC model run?

235 *Yes, it is. We modified the respective sentence and now refer to ‘phylogenetic or taxonomic distances’,*
236 *just as we did in line 6 of the same page (16087).*

237 It seems that the variable of ‘ecozones’ are partly determined by depth, and then given added
238 granularity by using species distributions to define them further, subdividing them in to an added lateral
239 component. They then correlate better with data on distributions. Isn’t this circular? Aren’t the real
240 environmental causal variables some combination of depth (linked with food availability, wave energy,
241 oxygenation, other species presence, etc.), substrate, sedimentation, water chemistry, etc.?

242 *See our reply to MC4. It is not circular reasoning, because we first inferred the relative importance of*
243 *assembly processes and later tested whether those differ among eco-zones, which are characterized by*
244 *similar gastropod community composition and space. The assembly processes are supposed to have*
245 *caused the gastropod community composition but they are not the same. We do not search for ‘causal*
246 *variables’ that are later typically interpreted as proxy for processes, but instead infer the process directly.*
247 *In our previous study of causal variables (Hauffe et al., 2011) we showed that depth and nutrient related*
248 *proxies correlate with gastropod community composition. Moreover, we identified a strong spatial*
249 *autocorrelation in gastropod community composition. We interpreted these correlations as the processes*
250 *of environmental filtering and dispersal limitation. However, in the current study we quantified these*
251 *processes directly, as it is recommended for modern community analyses (McGill et al., 2006).*

252 For each of these variables it seems that they are a highly derived, combined measure that is some
253 distance away from what they are purporting to measure. I would feel much more comfortable with
254 more clearly defined metrics in each case – things like the actual ecological variables, measures of gene
255 flow, habitat descriptors. As it is, I’m not really sure what is being correlated with what, and if there is
256 any explanatory power left after the underlying variables have been confounded in so many ways.

257 *As explained above (MC2 and MC3), the variables are neither derived nor combined but the taxonomic*
258 *classification informs about two different processes (but see also Figure 2). It is strongly believed that this*
259 *approach has its merits because it makes the importance of processes directly comparable (Janzen et al.,*
260 *2016; van der Plas et al., 2015). If we would quantify gene flow among populations of individual species,*
261 *we still a) would not know how dispersal influences community composition, and b) could not compare it*
262 *with how strong environmental variables correlate with community composition. The STEPCAM model*
263 *does not provide a direct measure of explanatory power like in such correlative studies (e.g., the*
264 *coefficient of determination; r^2). We discussed with the developers (see our acknowledgments) such a*
265 *possibility but there were good statistical reasons against it. However, van der Plas et al., (2015) showed*
266 *indirectly the explanatory power of the STEPCAM model by comparing generated community composition*
267 *with the observed one ($r^2 = 0.3$). Moreover, these authors provided a sensitivity analysis showing that the*
268 *analysis infers correctly the processes, which were used to generate artificial test-data of community*
269 *composition.*

270

271 It is also not clear to me how the reflexive nature of the model's analytical sampling is correlated to, or
272 informs on, real-life processes. On this point the paper should be examined by a modeler (or statistician)
273 who has extensive experience with these kinds of models in general.

274 *We do think dispersal, environmental filtering, and species interaction are real-life processes assembling*
275 *species communities. However, we do acknowledge that real-life processes are more complex. For*
276 *instance, the developer of the model already suggested that the processes act on individuals and not*
277 *species (van der Plas et al., 2015). We discussed methodological issues with the programmers of the*
278 *model (see our acknowledgments).*

279 I also felt that the paper would benefit from discussion of additional comparisons with research at the
280 boundary of ecological and evolutionary processes in other lakes. For example, I would have expected
281 discussion of the decades of results from Frans Witte and Ole Seehausen's labs on Lake Victoria cichlids.
282 Sexual, trophic, habitat selection (etc.) all play in to diversification, extinction and community dynamics
283 and have been ranked by their strength and timing of effects on the Victoria cichlid species flocks.

284 *According to this suggestion, we will focus in the discussion of our revised ms on community assembly*
285 *and down-tone the implications on speciation processes (see MC5). We refrain of discussing more*
286 *evolutionary studies, especially of cichlids that diversify under strong sexual selection. However, we refer*
287 *to a new study on cichlid community composition in Lake Tanganyika using the same model and showing*
288 *the same tendencies in importance of assembly processes (Janzen et al., 2016).*

289 **Specific comments**

290 In the Introduction the authors make a bold statement in a few starting sentences that changes in
291 climate, geology, etc, only affected species abundances and community compositions, not speciation and
292 extinction. However in the next set of sentences they say that abundance and composition "indirectly
293 fostered species divergence Speciation, and extinction processes, in turn, also affect the spatial
294 structure of extant communities". This reads like a 'yes-but-no-but-yes' bit of waffle, setting up the
295 paper to be unclear throughout. My feeling was that the paper should be more modest in overall aims,
296 but try to be clearer about what actually is being tested, what was shown, what it might mean, and how
297 much confidence we can have in the results. It seems to a paper testing community assembly with fairly
298 straightforward (but minimal) data on presence absence, but it gains its strength through having many
299 sample sites and using simulation to generate statistical context.

300 *We will rework the respective parts.*

301

302 The Methods section lists:

303 Gastropod sampling and taxonomic classification –

304 This covers information on:

- 305 • Geography of sites – good and necessary – and supported by a map.
- 306 • A general statement on the classification similarity metric – but this needs to be supported by
307 the actual classification. A further explanation on the classification/taxonomy/relatedness metric
308 follows a full page later, but this should be moved up in the section on variables (traits).
309 *We do not understand this comment because we explain the taxonomic classification directly*
310 *after the geography of sites.*

311 And lacks:

- 312 • Details on how abundance data was taken (or was it? From the supplementary files all I can see
313 is a P/A (presence/absence species/site occurrence list, but species richness is included in the
314 output, which often includes an abundance measure, and is also mentioned in the ABC-SMC
315 model text). E.g, were consistent surface areas sampled, time counts done, volumes from grabs
316 picked, etc?
- 317 • Specifics on what kind of species richness metric was used
- 318 • Explanation of morphological/environment metric – this will require quite a lot of clarification, as
319 it's a complicated thing and I'm not sure it works
- 320 • Explanation of dispersal metric (called a dispersal limitation metric, which is essentially an
321 inverse). Isn't it simply an occurrence metric?

322 *Correct. We used presence/absence data and the simple count of species as richness metric. Now we will*
323 *mention these facts explicitly in the manuscript. Strong habitat heterogeneity requires different sampling*
324 *strategies and species abundancies would not be comparable. In littoral stretches of approximately 50 m*
325 *length, we always collected with 3-5 persons for an hour. We sampled depths > 5 m until a dredge was*
326 *half-full or, in case of extremely rocky substrate, 10 min passed. Unpublished species accumulation curves*
327 *for different habitats show that we reached an asymptotic relationship between species richness and*
328 *specimens. This means, with an increasing number of sampled specimens we did not find more species*
329 *and our simple metric of species richness is robust. More sophisticated richness metrics either include*
330 *(e.g., Shannon diversity) or correct (rarefaction indices, e.g. Chao) for variation in species abundancies,*
331 *but as mentioned above, number of sampled specimens depend on sampling strategy. In any case, our*
332 *analysis of community assembly requires simple species counts.*

333 *For the issue of missing explanation of morphological and dispersal metric see above.*

334 (note in this section the authors say “Species flocks likely evolved intralacustrine [sic] and are common in
335 Lake Ohrid.” - but by definition a species flock evolved within the system. Better to just call them
336 endemic clades that include several genera’.)

337 *Done. Thank you for the suggestion.*

338 Dispersal limitation – The paper says “STPCAM simulates dispersal limitation by randomly removing
339 species with a probability inversely related to their relative frequency in the regional species pool.” – is
340 this a jackknife or a bootstrap resampling method (with or without replacement)? It is not clear to me
341 how this informs us about dispersal limitation. I would have thought data on dispersal would need
342 population genetic information on gene flow. Doesn’t this simply show that narrow-range taxa have a
343 greater influence on differentiating communities? The narrow range could be due to other factors than
344 lack of dispersal, for example, lack of appropriate substrate.

345 *This concerns MC2 and MC3. STEPCAM is neither a jackknife nor a bootstrapping method because the aim
346 is not to evaluate the robustness of a result. See Fig. 2 and the additional explanations given in lines
347 200-204 for the purpose of species removal. Of course, narrow-range taxa do have a greater influence on
348 differentiating communities because widespread species are present in most sites and cause high
349 similarity among communities. If a narrow range would be determined by the availability of appropriate
350 substrate, this should be reflected in a species community by the co-occurrence of closely related species
351 of presumed niche similarity. Therefore, the relative importance of the environmental filtering over the
352 dispersal limitation process shows the influence of abiotic variables.*

353 Environmental filtering – this seems to be an analytical pruning of species that are outliers, based on the
354 metrics (traits) assessed and production of a comparison community by simulation. This assumes
355 selection is for greater homogeneity, not for greater diversity. It is the classic debate about the relative
356 roles of stabilizing, vs disruptive (or diversifying) vs directional selection. Intuitively, I would expect some
357 diversifying selection if a habitat had diverse structure and roles, as is indicated by having elevated
358 biodiversity. Just a bit more explanation of this would help the reader be less dubious, I’d think.

359 *This relates to MC2 and MC3. Yes, the modeling step can be compared with pruning of extremes.
360 According to the assumptions of phylogenetic community ecology for environmental filtering,
361 co-occurring species should indeed be selected by homogeneity in their ecological requirements (Webb et
362 al., (2002); see Fig. 2). Hubert et al., (2015) showed the importance of spatial and temporal scales in the
363 corresponding metacommunity speciation model. A high within habitat diversity could exceed the habitat
364 diversity of the whole ecosystem, which equals a homogenous landscape. This scenario predicts
365 community assembly through dispersal and species diversification via geographical barriers and a neutral
366 divergence of traits. In contrast, smaller variation within than among habitats leads to a community
367 assembled by environmental filtering and ecological speciation with directional trait divergence (Hubert
368 et al., 2015).*

369 The Methods section on analysis has parts of the definition of the variables mixed in. This makes it
370 harder to see exactly what the whole data set comprises and how it was derived. For example, the
371 authors explain that: “The similarity between simulated and observed communities is the sum of
372 absolute differences between four indices (i.e., richness, evenness, divergence, and mean distance to the

373 community centroid) based on traits or relatedness.” But there hasn’t been a definition of these indices
374 earlier, and the basic data does not seem to be available in the supplement.

375 *This, again, refers to MC2 and MC3. We will clarify the meaning of the indices using a new flowchart (Fig.*
376 *2) and a revised method section. These are only a measure for evaluating how similar a simulated and*
377 *the observed gastropod community composition are and were discussed in the original description of the*
378 *STPCAM model (van der Plas et al., 2015).*

379 Often the term ‘gastropod composition’ is used. Shouldn’t this be ‘gastropod community data’ or
380 ‘community species composition’? Gastropod composition would mean what the snails are made of, e.g.,
381 carbon, nitrogen, water, mucous, etc... Community composition is the smaller units that communities are
382 made of, i.e., species. Data is a clearer, simpler word however, so might be preferable.

383 *Correct. The term ‘gastropod composition’ is, indeed, misleading. We will therefore use ‘gastropod*
384 *community composition’ in all cases where we refer to the gastropod species composition of the sampling*
385 *sites.*

386 While I also have done analyses on gastropod communities as an analytical topic, I will add that I think a
387 more realistic portrayal of biotic communities should include other taxa. Snails might very well have
388 much stronger interactions with their food, predator and parasite neighbours than with other
389 gastropods. But I also agree that we have to start somewhere in figuring out how ecological communities
390 are assembled, so limiting by taxon is a reasonable first pass. It might be a good idea to mention this
391 early on, however. (Only in the end do the authors mention a comparison with diatoms).

392 *We fully agree with the reviewer and in the revised ms, we therefore will stress that we performed a case*
393 *study. Robert E. Ricklefs would certainly agree with the perspective of host-parasite interactions driving*
394 *biodiversity, although acknowledging that this “community-level relationship...are only beginning to be*
395 *analysed” (Ricklefs, 2015). Unfortunately, we are only at the beginning of creating an inventory of*
396 *ancient lake parasites (Kmentová et al., 2016; Vanhove et al., 2015) or characterizing major features of*
397 *trophic networks in ancient lakes, such as bacteria (De Wever et al., 2008), fungi (Čomić et al., 2010), or*
398 *the complexity of trophic chains (Doi et al., 2012). According to a recent critical review of multiple*
399 *definitions and actual use of the term ‘community’ (Stroud et al., 2015), our gastropod community*
400 *composition falls in-between ‘community’ and ‘assemblage’. However, the term ‘community’ is better*
401 *known by a broader audience and adding the higher-level taxon (i.e., using ‘gastropod community*
402 *composition’ as the reviewer suggested) elucidate the considered taxonomic scale of co-occurring species*
403 *(Stroud et al., 2015).*

404 The results show that things are all different in the SE of the lake - clearly the springs have a major effect,
405 turning the processes around.

406 *Exactly.*

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