

1 Functional diversity plays a role in driving β -diversity: Or does it?

2

3 David Murray-Stoker^{1,2,3}

4

5 ¹Odum School of Ecology, University of Georgia, Athens, GA 30602, U.S.A.

6 ²Present Address: Department of Ecology and Evolutionary Biology, University of Toronto,

7 Toronto, ON M5S 3B2, Canada

8 ³Present Address: Department of Biology, University of Toronto at Mississauga, Mississauga,

9 ON L5L 1C6, Canada

10

11 ORCID: <https://orcid.org/0000-0002-4774-6948>

12

13 E-mail: dstoker92@gmail.com

14 Keywords community diversity, functional diversity, metacommunity theory, open science,

15 structural equation modeling

16

17 **Abstract**

18 Patrick and Brown (2018) suggest that functional diversity of the species pool has an important
19 role in generating β -diversity. Using a combination of path analysis and model selection, they
20 ostensibly provide support for this hypothesis; however, they neglected to put theory and
21 modeling into proper ecological and statistical context. Here, I present a re-analysis of their data.
22 I conclude that the drivers of β -diversity are variable, with functional diversity typically having a
23 reduced, if any, role compared to consistently stronger roles played by γ -diversity or
24 environmental variation on structuring β -diversity.

25 **Introduction**

26 Environmental filtering is a common mechanism used to explain community assembly
27 (Poff 1997, Leibold et al. 2004). Under this framework, realized assemblages are derived from
28 the regional pool by a series of environmental variables selecting for taxa able to establish under
29 the local conditions. Derived from this framework is the hypothesized positive relationship
30 between environmental heterogeneity and β -diversity. Considering each community is comprised
31 of taxa able to occupy and persist in the local environmental conditions, greater variation in
32 environmental conditions in the region results in greater variation among communities due to
33 differential composition among habitats (Logue et al. 2011, Heino et al. 2013). This hypothesis
34 has been evaluated in terrestrial (Kraft et al. 2011, Cramer and Verboom 2017) and aquatic
35 (Grönroos et al. 2013, Heino et al. 2013, Astorga et al. 2014, Heino et al. 2017, Wojciechowski
36 et al. 2017) systems, but there is no conclusive support for the predominant drivers of β -
37 diversity.

38 Patrick and Brown (2018) suggested that functional diversity could play an important role
39 in generating β -diversity. Derived from the environmental filtering framework, they proposed

40 that greater functional differences among taxa in the region would allow for differential
41 composition among local communities, and this relationship would be greater at higher levels of
42 environmental heterogeneity or filtering. In other words, Patrick and Brown (2018) hypothesized
43 a positive relationship between functional diversity and β -diversity. This hypothesis is intuitive
44 in the broader context of the environmental filtering framework, and, through the use of
45 statistical modeling and causal inference, Patrick and Brown (2018) report functional diversity
46 having an important role in predicting β -diversity. Although the relative importance of functional
47 diversity as a predictor was generally less than environmental heterogeneity and greater than γ -
48 richness, they asserted that functional diversity was still important and useful as a predictor of β -
49 diversity. I contend that the study by Patrick and Brown (2018) does not adequately support this
50 conclusion.

51 I contest functional diversity as a driver of β -diversity and rather as a correlate of β -
52 diversity. This argument is based on the hierarchical and correlative nature of α -, β -, and γ -
53 diversity (Whittaker 1960) and the premise that functional diversity is dynamic, simultaneously
54 influencing and being influenced by (i.e. correlated to) α -, β -, and γ -diversity. I assert that
55 functional diversity is a constituent of community diversity and not an independent entity. I
56 hypothesized that models with correlations rather than causal pathways between or among
57 diversity metrics (i.e. functional, β -, and γ -diversity) would have better model support than
58 models proposed by Patrick and Brown (2018). Additionally, the relative importance of
59 functional diversity would be consistently less than the effects of environmental heterogeneity
60 and γ -diversity on β -diversity.

61 **Re-Analyses**

62 I first re-analyzed the data by testing the path models hypothesized by Patrick and Brown
63 (2018, see fig. 2) and the alternative path models presented here (fig. 1) by using structural
64 equation models and model selection techniques. I generally followed the methods outlined by
65 Patrick and Brown (2018), although I have provided more detailed methods in the appendix.
66 Models were fit for the whole community and each individual functional feeding group. I refer to
67 models by the number associated with the model structure. Models 1-5 were proposed by Patrick
68 and Brown (2018), while I proposed models 6-8.

69 I found that the top model or models varied among the full community and functional
70 feeding group subsets (table 1). Variation in top models notwithstanding, causal pathways
71 linking environmental heterogeneity or γ -diversity to β -diversity consistently had the strongest
72 effect. Environmental heterogeneity had significant effects on β -diversity for the whole
73 community and collector-gatherer and filter-feeder subsets; γ -diversity had significant effects on
74 β -diversity for the herbivore, shredder, and predator subsets; and functional diversity had
75 significant effects on β -diversity for the collector-gatherer and filter-feeder subsets. Even when
76 functional diversity effects on β -diversity were significant, these effects were considerably
77 reduced in relative importance (collector-gatherer model 4: functional diversity = 0.264,
78 environmental heterogeneity = 0.527) or negatively related to β -diversity (filter-feeder model 4:
79 functional diversity = -0.509, environmental heterogeneity = 0.419; filter-feeder model 5:
80 functional diversity = -0.502, environmental heterogeneity = 0.414). Net effects also showed that
81 functional diversity was generally of lower or negligible relative importance compared to the net
82 effects of environmental heterogeneity or γ -diversity (table 1).

83 Although the alternative models were only retained among the top models for the
84 predator community subset (table 1), results from the re-analysis drastically contradicted what

85 was presented by Patrick and Brown (2018, see table 2). Discrepancies were not just in relative
86 model support, but also goodness-of-fit tests and net effects of predictor variables; therefore, I
87 proceeded to also re-analyze the original model set (i.e. models 1-5). Again, there was variation
88 in the top model or models for the whole community and functional feeding group subsets (table
89 2). Causal pathways linking environmental heterogeneity or γ -diversity to β -diversity
90 consistently had the strongest effect. Importantly, a link between functional diversity and β -
91 diversity was only retained in the top model(s) for three of the six community sets (table 2); this
92 contrasts Patrick and Brown (2018), who report a link between functional diversity and β -
93 diversity in at least one top model for all six model sets. In the remaining community subsets,
94 models including a causal pathway between functional diversity and β -diversity were equivalent
95 to or outperformed by models without the causal pathway. Even when retained in the top models,
96 the causal pathway between functional diversity and β -diversity was only significant for two of
97 the three community subsets (collector-gatherer and filter-feeder subsets), and of reduced
98 importance for driving (i.e. collector-gatherer subset) or negatively-related to (filter-feeder
99 subset) β -diversity (table 2) when significant.

100 **Drivers of β -Diversity: Ecological Context**

101 Given the deviation between the results presented by Patrick and Brown (2018) and those
102 presented here, I argue this could have been prevented by incorporating and applying proper
103 ecological and statistical context. Regarding ecological context, Patrick and Brown (2018)
104 neglected to present or provide summary data on community composition. Given the nature of
105 the sampling design (i.e. first- to fourth-order streams), it is to be expected that collector-
106 gatherers, shredders, and predators would comprise the majority of community abundance and
107 biomass and play critical roles in food web structure and ecosystem functioning (Vannote et al.

108 1980, Rosi-Marshall and Wallace 2002). It would be more relevant to the ecology of the system
109 to focus on the dominant taxa and concomitant functional feeding group subsets, in terms of
110 relative abundance and biomass, rather than treating all functional feeding groups as equivalent.
111 Based on my re-analysis of the complete model set, functional diversity only had a significantly-
112 positive effect on driving β -diversity of collector-gatherers, and the magnitude of functional
113 diversity on β -diversity (standardized path coefficient = 0.264) was roughly half of the
114 magnitude of environmental heterogeneity (standardized path coefficient = 0.527); γ diversity
115 had a significant role in driving β -diversity of shredders (standardized path coefficient = 0.652)
116 and predators (standardized path coefficient range = 0.416-0.448).

117 **Drivers of β -Diversity: Statistical Context**

118 Patrick and Brown (2018) also ignored important statistical context, partly derived from
119 neglecting ecological context but also by conducting suspect analyses and subsequent
120 presentation of results. First, I argue that applying the models to the whole community and each
121 functional feeding group subset is a quasi-form of p-hacking. Rather than focusing on dominant
122 taxa or groups relevant to the ecology of their study systems, Patrick and Brown (2018) had six
123 model sets (i.e. the whole community and five functional feeding group subsets) in which to find
124 a role for functional diversity driving β -diversity, enabling the identification of statistical
125 significance without integrating ecological relevance. Moreover, only one out of five models
126 would contradict their hypothesis, increasing the potential to find a statistically-significant but
127 ecologically-contentious result. Second, I contend that the presence of a causal pathway between
128 functional diversity and β -diversity is irrelevant because that does not indicate if the pathway is
129 statistically significant, although this is purportedly how Patrick and Brown (2018) evaluated
130 model results (see table 3). By not acknowledging if the pathway was significant, Patrick and

131 Brown (2018) did not put the results into the appropriate context. Causal pathways could
132 improve overall model fit, but it is fallacious to conflate improving model fit with having a
133 significant effect on β -diversity, which is ostensibly the argument made by Patrick and Brown
134 (2018). Finally, I claim the presentation of results is highly misleading. Patrick and Brown
135 (2018) report the net effects of correlational pathways or pathways excluded from the respective
136 model as 0.000 (see table 2). It is specious to report a net effect of 0 for a pathway that was not
137 modeled, and the nature of correlational pathways in structural equation models precludes
138 reporting direct or indirect effects mediated by correlational pathways (Grace 2006). Reporting
139 net effects as null or not applicable, as done in this comment, would have been a better way to
140 present the results as it accurately reflects model structures.

141 **Concluding Remarks**

142 I contend that critical errors in the evaluation and subsequent interpretation of hypotheses
143 led to spurious claims by overlooking fundamental ecological and statistical context. Although
144 my alternative models were not consistently among the top models (table 1), I demonstrate that,
145 as predicted, environmental heterogeneity and γ -diversity had consistently stronger and
146 significant effects on β -diversity compared to effects mediated by functional diversity.
147 Importantly, I show that results presented by Patrick and Brown (2018) are not reproducible, and
148 this lack of reproducibility is concerning because it is avoidable. Patrick and Brown (2018)
149 provided data and used open-access software for analyses, but analytical scripts were not
150 archived alongside the data. Additionally, the supplementary data were partial; no raw
151 environmental or community data were provided, limiting critical evaluation by reviewers and
152 readers. Given the growing call for a culture shift with regards to open access, data archiving,
153 and reproducibility in ecology and evolution (Hampton et al. 2015, Roche et al. 2015),

154 publishing full data and analytical scripts should be done whenever possible to preclude the
155 presentation of irreproducible results. In summary, I discourage the use of results presented by
156 Patrick and Brown (2018) because further analyses demonstrate the results are incorrect.
157 Although functional diversity is important for linking community and ecosystem ecology
158 (McGill et al. 2006, Petchey and Gaston 2006), evidence from Patrick and Brown (2018)
159 suggests functional diversity does not generate β -diversity. Instead, environmental variation and
160 diversity within the regional species pool are the primary drivers underlying β -diversity.

161 **Appendix**

162 Structural equation models (SEMs) were constructed to evaluate the causal pathways
163 through which environmental variation, functional diversity, and γ -diversity structure β -
164 diversity. Structural equation models are tests of fit to the data, and model fit was assessed by
165 comparing expected and observed covariance between predictor and response variables using
166 chi-square tests (Grace 2006). Structural equation models were considered consistent with the
167 data when expected and observed covariance was not significantly different (i.e. $p > 0.05$).
168 Hypothesized SEMs were then compared using Akaike's information criterion (AIC, Burnham
169 and Anderson 2002), Δ AIC (change in AIC value, Burnham and Anderson 2002), and AIC
170 weight (relative support for the model, Burnham and Anderson 2002). Model selection occurred
171 in two distinct phases. First, SEMs had to have good fit to the data ($p > 0.05$) and be considered
172 statistically equivalent (Δ AIC < 2.00). Second, SEMs with comparable AIC weights were
173 selected as the top models within the model set and then included in model interpretation and
174 discussion. All SEMs were estimated by maximum likelihood. Path coefficients, which show the
175 direction and magnitude of the causal relationship between variables, were standardized to allow
176 for the comparison of relationship strengths within each SEM (Grace 2006). All variables were

177 scaled (i.e. centered on the mean and then divided by the standard deviation) prior to analysis.
178 Scaling was done on the full dataset and then on each functional feeding group subset
179 individually. Statistical analyses were conducted using R (version 3.4.3, R Core Team 2017)
180 using the lavaan (Rosseel 2012) and AICcmodavg (Mazerolle 2017) packages; R code for the re-
181 analyses is deposited at figshare ([10.6084/m9.figshare.6163841](https://doi.org/10.6084/m9.figshare.6163841)).

182 **Literature Cited**

183 Astorga, A., R. Death, F. Death, R. Paavola, M. Chakraborty, and T. Muotka. 2014. Habitat
184 heterogeneity drives the geographical distribution of beta diversity: the case of New
185 Zealand stream invertebrates. *Ecology and Evolution* 4:2693-2702.

186 Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a
187 practical information-theoretic approach. Second edition. Springer, New York, New
188 York, USA.

189 Cramer, M. D., and G. A. Verboom. 2017. Measures of biologically relevant environmental
190 heterogeneity improve prediction of regional plant species richness. *Journal of*
191 *Biogeography* 44:579-591.

192 Grace, J. B. 2006. Structural equation modeling and natural systems. Cambridge University
193 Press, Cambridge, United Kingdom.

194 Grönroos, M., J. Heino, T. Siqueira, V. L. Landeiro, J. Kotanen, and L. M. Bini. 2013.
195 Metacommunity structuring in stream networks: roles of dispersal mode, distance type,
196 and regional environmental context. *Ecology and Evolution* 3:4473-4487.

197 Hampton, S. E., S. S. Anderson, S. C. Bagby, C. Gries, X. Han, E. M. Hart, M. B. Jones, W. C.
198 Lenhardt, A. MacDonald, W. K. Michener, J. Mudge, A. Pourmokhtarian, M. P.

- 199 Schildhauer, K. H. Woo, and N. Zimmerman. 2015. The Tao of open science for ecology.
200 Ecosphere 6:120.
- 201 Heino, J., M. Grönroos, J. Ilmonen, T. Karhu, M. Niva, and L. Paasivirta. 2013. Environmental
202 heterogeneity and β diversity of stream macroinvertebrate communities at intermediate
203 spatial scales. *Freshwater Science* 32:142-154.
- 204 Heino, J., J. Soininen, J. Alahuhta, J. Lappalainen, and R. Virtanen. 2017. Metacommunity
205 ecology meets biogeography: effects of geographical region, spatial dynamics and
206 environmental filtering on community structure in aquatic organisms. *Oecologia*
207 183:121-137.
- 208 Kraft, N. J., L. S. Comita, J. M. Chase, N. J. Sanders, N. G. Swenson, T. O. Crist, J. C. Stegen,
209 M. Vellend, B. Boyle, M. J. Anderson, H. V. Cornell, K. F. Davies, A. L. Freestone, B.
210 D. Inouye, S. P. Harrison, and J. A. Myers. 2011. Disentangling the drivers of β diversity
211 along latitudinal and elevational gradients. *Science* 333:1755-1758.
- 212 Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D.
213 Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez. 2004. The
214 metacommunity concept: a framework for multi-scale community ecology. *Ecology*
215 Letters 7:601-613.
- 216 Logue, J. B., N. Mouquet, H. Peter, H. Hillebrand, and G. Metacommunity Working. 2011.
217 Empirical approaches to metacommunities: a review and comparison with theory. *Trends*
218 in Ecology and Evolution 26:482-491.
- 219 Mazerolle, M. J. 2017. AICcmodavg: Model selection and multimodel inference based on
220 (Q)AIC(c). R package version 2.1-1. <<https://cran.r-project.org/package=AICcmodavg>>

- 221 McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology
222 from functional traits. *Trends in Ecology and Evolution* 21:178-185.
- 223 Patrick, C. J., and B. L. Brown. 2018. Species Pool Functional Diversity Plays a Hidden Role in
224 Generating β -Diversity. *The American Naturalist* 191:E159-E170.
- 225 Petchey, O. L., and K. J. Gaston. 2006. Functional diversity: back to basics and looking forward.
226 *Ecology Letters* 9:741-758.
- 227 Poff, N. L. 1997. Landscape filters and species traits: towards mechanistic understanding and
228 prediction in stream ecology. *Journal of the North American Benthological Society*
229 16:391-409.
- 230 R Development Core Team. 2017 R: a language and environment for statistical computing. R
231 Foundation for Statistical Computing, Vienna, Austria. <<https://cran.r-project.org/>>
- 232 Roche, D. G., L. E. Kruuk, R. Lanfear, and S. A. Binning. 2015. Public data archiving in ecology
233 and evolution: how well are we doing? *PLoS Biology* 13:e1002295.
- 234 Rosi-Marshall, E. J., and J. B. Wallace. 2002. Invertebrate food webs along a stream resource
235 gradient. *Freshwater Biology* 47:129-141.
- 236 Rosseel, Y. 2012. lavaan: an R package for structural equation modeling. *Journal of Statistical*
237 *Software* 48:1–36.
- 238 Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The
239 river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37:130-
240 137.
- 241 Whittaker, R. H. 1960. Vegetation of the Siskiyou mountains, Oregon and California. *Ecological*
242 *Monographs* 30:279-338.

243 Wojciechowski, J., J. Heino, L. M. Bini, and A. A. Padial. 2017. Temporal variation in
244 phytoplankton beta diversity patterns and metacommunity structures across subtropical
245 reservoirs. *Freshwater Biology* 62:751-766.

246 **Tables**

247 Table 1. Summary of all the path models in the re-analyses.

Group	Fit (P)	AIC	ΔAIC	AIC Weight	γ-Richness on FD	FD on β	Environmental Dispersion on β	γ-Richness on β
Whole Community								
2	0.468	510.65	0.00	0.19	NULL	NA	0.411	-0.096
4	0.452	510.75	0.10	0.18	NULL	0.085	0.391	NULL
5	0.700	510.82	0.17	0.17	0.210	0.085	0.390	0.018
3	0.382	512.03	1.38	0.09	NULL	0.108	0.410	-0.119
8	0.382	512.03	1.38	0.09	NULL	NULL	0.410	NULL
7	0.964	512.11	1.46	0.09	0.210	NULL	0.414	-0.097
6	0.964	512.11	1.46	0.09	0.210	NA	0.414	-0.097
1	0.964	512.11	1.46	0.09	0.210	0.109	0.414	-0.097
Collector-Gatherer								
4	0.799	500.70	0.00	0.31	NULL	0.264	0.527	NULL
8	0.764	502.23	1.53	0.15	NULL	NULL	0.520	NULL
3	0.764	502.23	1.53	0.15	NULL	0.250	0.520	0.085
5	0.740	502.29	1.59	0.14	0.173	0.263	0.525	0.045
7	0.717	503.82	3.12	0.07	0.173	NULL	0.517	0.127
6	0.717	503.82	3.12	0.07	0.173	NA	0.517	0.127
1	0.717	503.82	3.12	0.07	0.173	0.248	0.517	0.127
2	0.211	504.21	3.51	0.05	NULL	NA	0.511	0.130
Herbivore								
2	0.973	494.92	0.00	0.46	NULL	NA	-0.192	0.500
8	0.895	496.92	2.00	0.17	NULL	NULL	-0.193	NULL
3	0.895	496.92	2.00	0.17	NULL	0.009	-0.193	0.499
7	0.770	498.78	3.86	0.07	0.047	NULL	-0.194	0.502
6	0.770	498.78	3.86	0.07	0.047	NA	-0.194	0.502
1	0.770	498.78	3.86	0.07	0.047	0.009	-0.194	0.502
4	0.004	508.06	13.13	0.00	NULL	0.031	-0.167	NULL
5	0.001	509.92	15.00	0.00	0.047	0.031	-0.167	0.001
Filter-Feeder								
5	0.467	496.24	0.00	0.24	0.254	-0.509	0.419	-0.129
4	0.272	496.61	0.38	0.20	NULL	-0.502	0.414	NULL
1	0.355	497.57	1.33	0.12	0.254	-0.530	0.400	-0.037
7	0.355	497.57	1.33	0.12	0.254	NULL	0.400	-0.037
6	0.355	497.57	1.33	0.12	0.254	NA	0.400	-0.037
3	0.198	497.95	1.71	0.10	NULL	-0.528	0.399	0.098
8	0.198	497.95	1.71	0.10	NULL	NULL	0.399	NULL
2	< 0.000	512.46	16.22	0.00	NULL	NA	0.337	-0.021
Shredder								
2	0.726	462.37	0.00	0.37	NULL	NA	0.021	0.652
3	0.759	463.61	1.24	0.20	NULL	0.104	0.033	0.635
8	0.759	463.61	1.24	0.20	NULL	NULL	0.033	NULL
7	0.459	465.60	3.23	0.07	0.160	NULL	0.033	0.651
6	0.459	465.60	3.23	0.07	0.160	NA	0.033	0.651
1	0.459	465.60	3.23	0.07	0.160	0.104	0.033	0.652
4	< 0.000	483.78	21.41	0.00	NULL	0.207	0.051	NULL
5	< 0.000	485.78	23.41	0.00	0.160	0.207	0.051	0.033
Predator								
1	0.664	504.15	0.00	0.19	0.129	0.136	0.239	0.434
7	0.664	504.15	0.00	0.19	0.129	NULL	0.239	0.434
6	0.664	504.15	0.00	0.19	0.129	NA	0.239	0.434
2	0.228	504.29	0.14	0.18	NULL	NA	0.237	0.448
8	0.206	505.12	0.97	0.12	NULL	NULL	0.246	NULL
3	0.206	505.12	0.97	0.12	NULL	0.139	0.246	0.428
5	0.008	511.55	7.40	0.00	0.129	0.192	0.345	0.025
4	0.006	512.52	8.37	0.00	NULL	0.193	0.346	NULL

248 Note: All models were compared for the full community and each functional feeding group using

249 Akaike's information criteria (AIC). The difference in AIC scores (ΔAIC) is relative to the

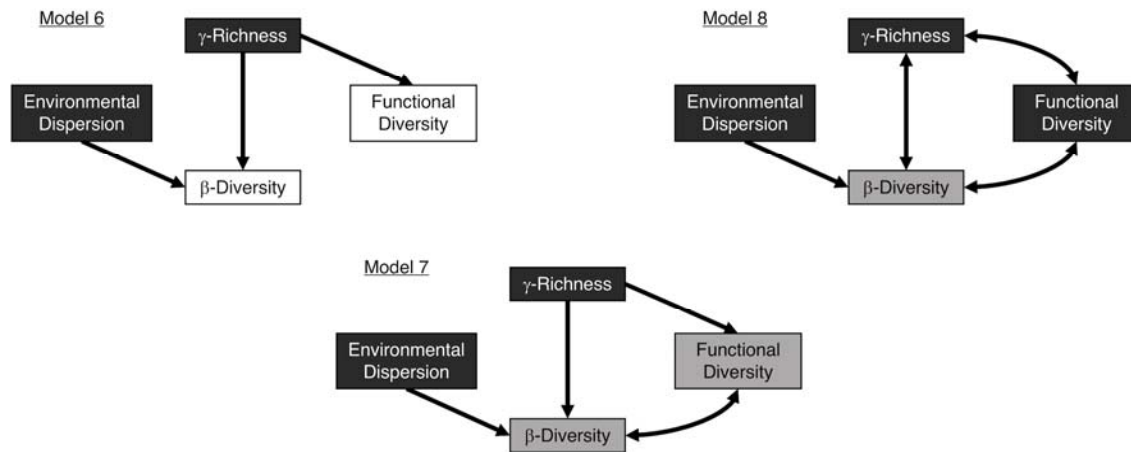
250 model with the lowest AIC score, and model weight is the relative support of the individual
251 model within the model set. Models in boldface had good fit to the data ($\chi^2 > 0.05$) and $\Delta AIC <$
252 2.00, and italicized models had the greatest relative support. Net effects are the sum of the direct
253 and indirect effects mediated by unidirectional causal pathways; correlational pathways between
254 variables cannot be included when calculating net effects. If correlations were the singular or
255 mediating pathway modeled between the variables, the effects are reported as NULL. FD =
256 functional diversity; NA = not applicable (i.e. no causal pathway in the model).

257 Table 2. Summary of the candidate path models proposed by Patrick and Brown (2018), with
 258 models reported in order of AIC and Δ AIC.

Group	Fit (P)	AIC	Δ AIC	AIC Weight	γ -Richness on FD	FD on β	Environmental Dispersion on β	γ -Richness on β
Whole Community								
2	0.468	510.65	0.00	0.26	NULL	NA	0.411	-0.096
4	0.452	510.75	0.10	0.25	NULL	0.085	0.391	NULL
5	0.700	510.82	0.17	0.24	0.210	0.085	0.390	0.018
3	0.382	512.03	1.38	0.13	NULL	0.108	0.411	-0.119
1	0.964	512.11	1.46	0.12	0.210	0.109	0.414	-0.097
Collector-Gatherer								
4	0.799	500.70	0.00	0.44	NULL	0.264	0.527	NULL
3	0.764	502.23	1.53	0.20	NULL	0.250	0.520	0.085
5	0.740	502.29	1.59	0.20	0.173	0.263	0.525	0.045
1	0.717	503.82	3.12	0.09	0.173	0.248	0.517	0.127
2	0.211	504.21	3.51	0.08	NULL	NA	0.511	0.130
Herbivore								
2	0.973	494.92	0.00	0.66	NULL	NA	-0.192	0.500
3	0.895	496.92	2.00	0.24	NULL	0.009	-0.193	0.499
1	0.770	498.78	3.86	0.10	0.047	0.009	-0.194	0.502
4	0.004	508.06	13.14	0.00	NULL	0.031	-0.167	NULL
5	0.001	509.92	15.00	0.00	0.047	0.031	-0.167	0.001
Filter-Feeder								
5	0.467	496.24	0.00	0.36	0.254	-0.509	0.419	-0.129
4	0.272	496.61	0.37	0.30	NULL	-0.502	0.414	NULL
1	0.355	497.57	1.33	0.19	0.254	-0.530	0.400	-0.037
3	0.198	497.95	1.71	0.15	NULL	-0.528	0.399	0.098
2	< 0.000	512.46	16.22	0.00	NULL	NA	0.337	-0.021
Shredder								
2	0.726	462.37	0.00	0.58	NULL	NA	0.021	0.652
3	0.759	463.61	1.24	0.31	NULL	0.104	0.033	0.635
1	0.459	465.60	3.23	0.11	0.160	0.104	0.033	0.652
4	< 0.000	483.78	21.41	0.00	NULL	0.207	0.051	NULL
5	< 0.000	485.78	23.41	0.00	0.160	0.207	0.051	0.033
Predator								
1	0.664	504.15	0.00	0.39	0.129	0.136	0.239	0.434
2	0.228	504.29	0.14	0.36	NULL	NA	0.237	0.448
3	0.206	505.12	0.97	0.24	NULL	0.139	0.246	0.428
5	0.008	511.55	7.40	0.01	0.129	0.192	0.345	0.025
4	0.006	512.52	8.37	0.01	NULL	0.193	0.346	NULL

259 Note: All models in the re-analysis were compared for the full community and each functional
 260 feeding group. Models are ordered and formatted following Table 1.

261 **Figures**



262

263 Figure 1. Alternative path models to those proposed by Patrick and Brown (2018). Models

264 display the hypothesized relationships between environmental dispersion, γ -richness,

265 functional diversity, and β -diversity. Exogenous (independent) variables are represented in

266 black boxes, endogenous (dependent) variables in grey boxes, and response-only variables in

267 white boxes. Single-headed arrows represent causal pathways, and double-headed arrows

268 represent correlational pathways.